A REVIEW OF THE ARCHAEOCETI

BY

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_Basilosaurus cetoides_ (Owen)


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_Basilosaurus cetoides_ (Owen)

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_Basilosaurus cetoides_ (Owen)

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_Basilosaurus cetoides_ (Owen)


PLATE 5

_Basilosaurus cetoides_ (Owen)

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_Basilosaurus cetoides_ (Owen)

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_Basilosaurus cetoides_ (Owen)

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_Zygohorhiza kochii_ (Reichenbach)

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_Zygohorhiza kochii_ (Reichenbach)

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_Zygohorhiza kochii_ (Reichenbach)

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*Protocetus* sp.

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United States National Museum, Washington, D. C.

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*Zygophiza kochii* (Reichenbach)


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*Dorudon osiris* (Dames)

Skull, No. M. 10228. Fig. 1, dorsal view; Fig. 2, ventral view. About 1/4 nat. size. British Museum (Natural History), London, England. Upper Eocene, Qasr-el-Sagha stage, Fayum, Egypt.

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*Dorudon osiris* (Dames)

Skull, No. M. 10228. Fig. 1, lateral view, about 1/4 nat. size; Fig. 2, posterior view, about 1/4 nat. size. British Museum (Natural History), London, England. Upper Eocene, Qasr-el-Sagha stage, Fayum, Egypt.

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Skull, No. 11626. Fig. 1, dorsal view; Fig. 2, ventral view. About 1/4 nat. size. Württembergische Naturkundemuseum, Stuttgart, Germany. Upper Eocene, Qasr-el-Sagha stage, Fayum, Egypt.

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*Dorudon stromeri* (Kellogg)

Skull (type specimen), No. 1904. XII. 134e. Fig. 1, lateral view, about \( \frac{1}{2} \) nat. size; Fig. 2, posterior view, about \( \frac{1}{2} \) nat. size.

Paläontologische Sammlung, Alte Akademie, Munich, Germany. Upper Eocene, Qasr-el-Sagha stage, Fayum, Egypt.

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Paläontologische Sammlung, Alte Akademie, Munich, Germany. Upper Eocene, Qasr-el-Sagha stage, Fayum, Egypt.

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Paläontologische Sammlung, Alte Akademie, Munich, Germany. Upper Eocene, Qasr-el-Sagha stage, Fayum, Egypt.

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Paläontologische Sammlung, Alte Akademie, Munich, Germany. Lower upper Eocene, Birket-el-Qurun stage, Fayum, Egypt.

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*Dorudon intermedius* (Dart)

Skull (type specimen), No. M. 10173. Fig. 1, dorsal view; Fig. 2, ventral view. About \( \frac{1}{2} \) nat. size.

British Museum (Natural History), London, England. Lower upper Eocene, Birket-el-Qurun stage, Fayum, Egypt.
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Dorudon intermedius (Dart)

Skull (type specimen), No. M. 10173. Fig. 1, lateral view, about \( \frac{1}{2} \) nat. size; Fig. 2, posterior view, about \( \frac{1}{2} \) nat. size. British Museum (Natural History), London, England. Lower upper Eocene, Birket-El-Qurun stage, Fayum, Egypt.

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Protocetus atavus Frasa

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A REVIEW OF THE ARCHAEOCETI

INTRODUCTION

The Archaeoceti, or toothed whales with non-telescopede skulls, have been discussed in considerable detail by a number of investigators. Among these investigators there have prevailed great personal differences of opinion as to the significance of particular structures and, consequently, as to the classification of the animals that possessed them. Widely divergent opinions, inferences, interpretations and other speculations in regard to the archaeocetes have therefore been advanced. Because of the recent great increase of our knowledge of the Cetacea in general, it has been recognized that a restudy of the original archaeocete material in the light of subsequent acquisitions and, in particular, a first-hand comparison of Old and New World species would necessitate some modifications of our rather generally accepted concepts. An attempt is here made to correlate the results of such first-hand observations with the speculations of various investigators and to integrate the data derived from palaeontology with that derived from taxonomy, comparative anatomy, and embryology.

If it be admitted that the structural organization of these marine forms has been correctly interpreted as pointing toward an earlier racial history on land where biotic associations and physical circumstances of the environment were decidedly unlike those subsequently encountered in the sea, then the Archaeoceti present one of the most striking known examples of specialization for a particular kind of habitat. These animals nevertheless present a number of perplexing problems, not only as to their origin, relationships, and the factors limiting their dispersal, but also as to the antecedent stages which have led to their adaptation to pelagic conditions of life.

For the elucidation of some of the fundamental problems of cetacean classification and phylogeny, the archaeocetes furnish some important documentary evidence. Unfortunately the known forms, when compared with each other, exhibit only minor degrees of differentiation and many of their structural peculiarities yield equivocal or incomplete clues to interrelationships. Structurally, the Archaeoceti are likely to remain one of the most unique among the groups of mammals that reached their maximum evolutionary advance during Eocene time.

This investigation is based chiefly on a review of the archaeocete material in European and American museums. This material includes types that represent a number of important stages in the archaeocete evolutionary series, beginning with the somewhat generalized and rather diminutive Protocetus alatus and culminating in the gigantic and aberrantly specialized Basilosaurus cetoides.

The present review is offered as a progress report and is by no means final, for a more comprehensive treatment of the subject would require complete skeletons of some of the critical types, intensive exploration of marine strata, and a knowledge of antecedent forms during the lower Eocene and older geological time. The filling of the gaps between the archaeocetes of the middle Eocene and their pre-tertiary predecessors offers a fruitful field for future investigation.
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Through the active interest of Dr. C. Wythe Cooke, U. S. Geological Survey, arrangements were made for the examination of important archaeocete material from the Ocala limestone of Georgia and Florida. Included in this material were portions of a skeleton of Basilosaurus cetoides which was collected in Houston County, Georgia, and deposited in the U. S. National Museum by Dr. Leon P. Smith, Dean of Wesleyan College at Macon, Georgia. Lieut. D. A. Harris, U. S. N., deposited on loan the mandibles of Zygorhiza kochii which he had found in Crisp County, Georgia.

Photographs of specimens in European museums mentioned in this report were furnished through the courtesy of Professor Stromer, Doctor Berckhemer, and Mr. Hopwood. W. R. B. Oliver, director of the Dominion Museum, Wellington, New Zealand, kindly furnished photographs and measurements of the Kekedenodon teeth described by Hector. The remaining photographs, unless otherwise indicated, are the work of Gurney I. Hightower of the National Museum photographic laboratory. Through the able cooperation of Sydney Prentice, especial care has been taken in the preparation of the line drawings and reconstructions illustrating the North American archaeocetes. These figures have been drawn to scale by orthographic projection. Norman H. Boss has likewise rendered valuable assistance in the collection and preparation of the skeletal material belonging to the North American archaeocetes.

The continued support of the Carnegie Institution of Washington made possible the assembling of additional archaeocete material in Alabama, the examining of archaeocete material in European and American museums, and the adequate illustrating of the material studied. The United States National Museum under the Smithsonian Institution has liberally supported this project by providing the necessary facilities for the study and preparation of material, by arranging for the loan of specimens, and by granting permission for visits to other institutions in the United States and Europe.
CHRONOLOGICAL RÉSUMÉ OF DISCOVERIES OF ARCHAEOCETE REMAINS

One hundred years have elapsed since the attention of the readers of the Transactions of the American Philosophical Society was directed to the finding, within the present boundaries of the State of Louisiana, of the remains of an extinct whale which had been washed out of a marl bank belonging to the upper Eocene Jackson formation. Some 28 vertebrae had been exposed, after long continued rains, by the slump of a hill near the Ouachita River in southern Caldwell Parish. One of these vertebrae was sent in 1832 by Judge H. Bry to P. S. Du Ponceau, president of the American Philosophical Society, who instructed Dr. Richard Harlan to publish an account of the discovery. Because of its supposed reptilian affinities, Harlan proposed to call the animal represented by this bone "the king of lizards," Basilosaurus. The question of the affinities of Basilosaurus immediately aroused world-wide controversy. It was not until January 1839, when Dr. Harlan arrived in London, England, with additional fossil remains which had been found in 1834 and 1835 on the plantation of Judge John G. Creagh in Clark County, Alabama, that the precise relationships of Basilosaurus were recognized. Included among the fossil bones which Harlan brought with him were teeth which Professor Richard Owen was permitted to section and study. On the basis of a microscopic examination of these teeth, Owen was enabled to demonstrate conclusively the mammalian nature of this animal. Consequently, Owen proposed to substitute for Basilosaurus the name Zeuglodon cetoides, in allusion to the yoke-like appearance of the cheek teeth and the whale-like structure of the vertebrae.

Several years after the publication of Owen's views, another important discovery was made on the plantation of Judge Creagh in Clark County, Alabama, by S. B. Buckley, who in 1842 excavated a skeleton of Basilosaurus that consisted of portions of the head and of the forelimb, and a vertebral column extending to a length of 65 feet. These remains were shipped to the office of the Geological Survey of New York at Albany, where they were studied and described by Ebenezer Emmons. Subsequently (not later than July 5, 1847), they passed into the possession of Dr. John Collins Warren at Boston (Warren, 1860, vol. 1, p. 373; vol. 2, pp. 9, 225) in whose museum they remained for many years. The collection also contained the celebrated "Warren Mastodon" and a portrait of a sea-serpent sketched by a member of a yachting party on July 30, 1875, in Nahant Bay off Lynn, Massachusetts. This sketch led the Rev. J. G. Wood (The Atlantic Monthly, vol. 53, June 1884, pp. 807–814) to suggest that the animal observed and sketched was "a cetacean animal, which, if not an actual zeuglodon, has many affinities with that creature." The animal, however, was more probably a giant
squid. For years after the death of Dr. Warren, this private collection was maintained by Dr. J. C. Warren Jr., but finally, it was placed in storage. In 1906, three of its most valuable specimens, the zeuglodon, the mastodon, and the portrait of the sea-serpent, were purchased by the American Museum of Natural History in New York City.

The interest aroused by these discoveries induced Dr. Albert Koch, a German collector, to visit Alabama. Koch arrived at Claiborne, Alabama, in January 1845. After three weeks of reconnaissance in that vicinity he moved his headquarters to Clarksville. Professor Charles Lyell (1846, p. 313) is the authority for the statement that Koch obtained archaeocete remains near this second locality. Among these were part of a head; also vertebrae representing about 30 feet of the spinal column. While at Clarksville, however, Koch received the news that remains of this animal were rather plentiful near the old Court House in Washington County, Alabama. Having made the necessary arrangements for the transportation of his collections, Koch set out for the old Court House, and on arrival there on March 15, 1845, he immediately commenced excavating a skeleton. Several wagon loads of bones were assembled at Washington Old Court House. From these bones, representing, as we now know, five or more individuals, Koch reconstructed an animal measuring 114 feet in length. This composite skeleton, which Koch (1845) supposed to represent a new species “Hydrargos sillimanii,” was exhibited as a sea-serpent for some weeks in the Apollo Rooms on Broadway in New York City. Later, it was shipped to Germany and exhibited in the principal cities of Europe.

Soon after Koch returned to Europe a joint memoir (1847) was published by C. G. Carus, H. B. Geinitz, A. F. Günther, and H. G. L. Reichenbach in which an attempt was made to correlate and interpret all available geological, anatomical, and zoological evidence relating to the composite archaeocete. These investigators, however, failed to recognize some of the most obvious mistakes made by Koch, who seemingly ignored the published conclusions of Owen in regard to the mammalian nature of this animal and attempted to construct a typical reptile skull out of his heterogenous fragments of archaeocete skulls belonging, as was shown later, to two distinct species of quite different proportions. Some inaccuracies in the skull as reconstructed by Koch were corrected by Carus, but some of the fragments were not sufficiently freed from the enveloping matrix to reveal their peculiarities. Hence the imperfect cranium of the small Jackson archaeocete, which was placed by Koch in the palatal region of his restoration, was misidentified. Curiously enough the cochlear portions of the opposite periotic bones were identified as palatine teeth. It is fair to state, however, that those who discussed this cranial fragment were impressed by its small size, and that because of this size they inferred that it must have belonged to a smaller form. It was accordingly named Basilosaurus kochii by Reichenbach.

After this material came into the possession of the Royal Anatomical Museum of Berlin, most of it was adequately prepared for study. In 1847, Johannes
Müller began his investigations of the material that had been collected by Koch in 1845. Müller's careful studies (1849) corroborated the statements made by Wyman (1845), Lister (1846), and Lyell (1846) that Koch's skeleton was a composite one, although this was denied by the collector. According to Koch's own assertion, as is pointed out by Müller, his collections were made at three places, one near Clarksville and two near the old Court House in Washington County, Alabama. Müller (1849, p. 3) states that he was able to recognize portions of skulls belonging to four different individuals in the Koch collection. Various inaccuracies in the restoration by Koch are pointed out by Müller, who also for the first time adequately described and figured the small archaeocete skull, erroneously identified as a palatal fragment by Carus and Reichenbach.

The archaeocete collection made by Koch in 1845 was purchased on April 15, 1847, by the King of Prussia for the Royal Anatomical Museum in Berlin. With the proceeds of this sale Koch was enabled in 1846 to visit Alabama again and resume his search for archaeocete remains. He now found a nearly complete head and both mandibles of the smaller archaeocete (*Zygorhiza kochii*) in Choctaw County, Alabama, and a second skeleton of *Basilosaurus* with a fairly good skull in the vicinity of Washington Old Court House. This second collection was shipped to Dresden, Germany, where the work of preparation for exhibition was begun. After eight months' work this skeleton was ready for display on May 6, 1849. The skeleton was afterward exhibited for some weeks at Breslau, Vienna, and Prague, and later, although the exact details are unknown, it was brought to New Orleans (Koch, 1853). In 1855 or 1856, it was placed on exhibition in St. Louis. Eventually, it was sold to the museum (Curiosity Shop) owned by Edward Wyman in that city. In 1863, this skeleton was acquired by Wood's Museum in Chicago where it remained until destroyed during the great fire of October 9, 1871.

Some time prior to June 3, 1845, Dr. Robert W. Gibbes of Columbia, South Carolina, acquired various fragments of a skull and associated mandibles of one of the small archaeocetes. This specimen was found in a marl pit on the plantation of R. W. Mazzyck in Berkeley County, South Carolina, about three miles distant from the junction of the Santee Canal with the head waters of the Cooper River. The greenish drab sands in which this specimen occurred belong to the Santee limestone marl. Following a visit to Albany, New York, where he examined the *Basilosaurus* skeleton collected by Buckley, Dr. Gibbes became convinced that the South Carolina archaeocete represented a new form, which he named *Dorudon serratus*.

All of the material thus far obtained had come from Eocene horizons.

The first proof that the archaeocete stock had continued to exist throughout Oligocene time was afforded by the discovery of a molar tooth in the lower Miocene Burdigalian calcareous sandstone at Saint-Médard-en-Jalle near Bordeaux, France. This tooth was described and figured by Eugene Delfortrie (1873), who named the animal to which it belonged *Zeuglodon vasconum*.
A few thoracic vertebrae belonging to the Anatomical Museum of the University of Kiev, which had been found in deposits of lower Oligocene age near Chigirin in Ukraine, U. S. S. R., were described by J. F. Brandt (1873a). To this animal was given the name *Zeuglodon paulsonii*, in honor of Professor Paulson, who was the first to recognize the affinities of the vertebrae. The geological age of this archaeocete remained unknown until 1912. In that year Fedorovsky published a description of 7 lumbar, 1 sacral, and 2 caudal vertebrae, a chevron bone, and a few rib fragments. These bones were found in a green glauconitic sand near a small village (Korobow Chutor) in the Zmyev District of Ukraine, U. S. S. R. All of the known occurrences of *Zeuglodon paulsonii* in Ukraine, according to Fedorovsky, are referable to the Kharkov stage of the lower Oligocene.

In 1872, Dr. Arthur Wanklyn, who for some years had been studying the upper Eocene Barton clay, discovered a skull of an archaeocete in the Barton Cliff in Hampshire, England. The specimen was excavated without any serious mishap, but local assistants had the misfortune to drop the skull while carrying it to the top of the cliff. An effort was made to gather the fragments, which were taken to the home of Dr. Wanklyn. H. G. Seeley was requested to prepare an announcement of the discovery and fortunately made a few hasty notes before leaving for London. Inasmuch as it was expected that Dr. Wanklyn would bring the specimen to London later, the matter was allowed to rest for the time. After the death of Dr. Wanklyn, the specimen could not be found. Professor Seeley then published his notes (1875) and named the animal *Zeuglodon wanklynii*.

During the progress of the Geological Survey of New Zealand in 1880, teeth and bones of an archaeocete were found by Alexander McKay in the Waitaki Valley, Otago, in a calcareous greensand belonging to the Oamaru system. For these remains, Hector (1880) proposed the name *Kekenodon onamata*. Many years later, remains of this archaeocete were found at other localities in New Zealand (Park, 1905). Some difference of opinion still exists as to the age of the Kekenodon beds, Professor J. M. McDonald and Allan Thomson refer them to the upper Wairekan stage of the Oligocene, while Professor James Park believes that they belong to the lower Hutchinsonian or upper Ototaran stage of the middle Miocene.

Under the name *Balaenoptera juddi*, Seeley (1881b) has described a caudal vertebra which came from the Brockenhurst beds at Roydon in Hampshire, England. Some years later (1902, p. 174), Seeley was inclined to question the fancied resemblance of this vertebra to those of finback whales; he suggested that it may have belonged instead to *Zeuglodon wanklynii*. The last-mentioned allocation seems to have been acceptable to Andrews (1907).

Professor W. Dames (1883) was the first to report the occurrence of archaeocetes in the Eocene deposits of the Fayum, Egypt. Included in a collection made for the Royal Mineralogical Museum of the University of Berlin in 1879 by Dr. G. Schweinfurth were bones belonging to at least two distinct species of archaeocetes, the larger of which was represented by two vertebrae and numerous rib
fragments, the smaller by an axis, an anterior thoracic vertebra, and the hinder portions of two crania. During the winter of 1885–86, Dr. Schweinfurth visited the escarpments north of the lake (Birket-el-Qurun). Near Qasr-el-Sagha he collected additional archaeocete remains, including the mandible later described by Dames (1894) under the name of *Zeuglodon osiris*.

Current stories in regard to the singular abundance of remains of archaeocetes in the Gulf States led the United States National Museum in 1894 to consider field work in that region. Accordingly Charles Schuchert was detailed to investigate some of these reported occurrences and to collect if possible a specimen for the exhibition series. On arriving at Cocoa, Choctaw County, Alabama, on November 2, 1894, Schuchert began his search and within a short time successfully excavated the head of one individual and twenty-four consecutive vertebrae of another, beginning with the atlas and ending with the third lumbar vertebra, in addition to the ribs and the major elements of the forelimb. This material formed the basis for the restoration of the *Basilosaurus cetoides* skeleton exhibited at the Atlanta Exposition in 1895. Inasmuch as the assembled skeleton was incomplete, Schuchert again returned to Alabama. In November 1896 he found, near Fall in Choctaw County, the hinder portion of another individual. This consisted of thirty-five consecutive vertebrae counting from the penultimate one forward, as well as the pelvis and one vestigial thigh bone (femur). Schuchert's material was prepared for exhibition in the United States National Museum, where this mounted skeleton has been exhibited in the hall of fossil mammals during the past 20 years. The pelvic girdle and femur found by Schuchert were described and figured by F. A. Lucas (1900a). This paper by Lucas attracted the attention of Professor O. Abel, who at that time was actively engaged in the study of extinct cetaceans. Concluding that these elements had been misidentified, he (1906) attempted to demonstrate that the innominate bones of *Basilosaurus* possessed all the essential characteristics of the ankylosed coracoid and precoracoid of certain living and extinct penguins. Abel felt that the avian affinities of these bones were so obvious that it was necessary to recognize as *Alabamornis gigantea* the supposed extinct bird to which he believed them to have pertained. With regard to the femur, Abel decided that it must have belonged to the forelimb of the same bird and that it was in all probability the humerus. It may be stated, however, that Professor Abel no longer considers this allocation as tenable. The head, neck and forelimb and other portions of the skeleton collected by Schuchert have been described and figured by James W. Gidley (1913).

On October 30, 1903, two imperfect cetacean vertebrae were collected by O. Nordenskjöld and Joh. Gunnar Anderson near the coast on the northeastern part of Seymour Island in West Antarctica. These vertebrae were associated with numerous bones belonging to extinct penguins, and all were derived from a sandstone formation which has been correlated by Dr. Otto Wilekens (Wiman, 1905, p. 37) with the Patagonian marine sandstone formation. To Professor Carl Wiman (1905) was delegated the task of preparing a report on the vertebrate re-
mains secured by the Swedish South Polar Expedition and he identified the above-mentioned vertebrae as belonging to a *Zeuglodon sp.* Professor Ernst Stromer (1908b, p. 147) states that although these vertebrae are very similar to the caudal vertebrae of *Zeuglodon*, so are also the vertebrae from the Linz white sands in Austria which are referred to the odontocete *Squalodon [=Patriocetus] ehrlichii* by Brandt (1874b, pp. 39–40). Stromer, furthermore, insists that the caudal vertebrae of archaeocetes are distinguished from those of the typical whales by the reduction of the neural spines, and by the divergence and large size of the metapophyses (processus obliquomammillares).

Although H. J. L. Beadnell commenced the geological survey of the Fayum depression in 1898, no archaeocete remains of any particular value were collected there until 1900. In that year a large number of lumbar and caudal vertebrae, subsequently identified (Andrews, 1906) as belonging to *Zeuglodon isis*, were collected by Beadnell and Dr. C. W. Andrews near Dimé in the Fayum. Beadnell afterward found an incomplete left mandible of the same animal near the western end of Birket-el-Qurun in beds of upper Eocene age. In April 1901 Andrews accompanied Beadnell to the region north of the lake, and, at the close of a successful field season, he made arrangements to revisit the district in the following spring. During the winters of 1902–03 and 1903–04, Beadnell conducted expeditions in the Fayum depression and large collections were made for the Geological Museum at Cairo. While engaged on this survey Beadnell collected a nearly complete skull and an associated imperfect right mandible in a valley 12 kilometers west southwest of Gar-el-Gehannem in beds of the Birket-el-Qurun series. This skull became the type of *Prozeuglodon atrox* (Andrews, 1906). The archaeocete material in the Geological Department of the British Museum (Natural History) at London was in part collected by Andrews in the spring seasons of 1902 and 1903, and in part donated by the Egyptian Government. Among the specimens acquired by the British Museum are a remarkably well-preserved skull of *Dorudon osiris*, an incomplete skull of *Dorudon intermedius*, and a natural endocranial cast of *Dorudon sensitivus*. These specimens have been described by Dart and Andrews (1923). Besides these, there is a partly disarticulated skull of *Prozeuglodon atrox* which was described by Andrews (1906). Andrews states that only a portion of the collections made by the Geological Survey of Egypt is catalogued in his memoir (1906). The somewhat distorted skull of *Dorudon osiris* in the Cairo Geological Museum should be mentioned in this connection, since the cast of the cranial cavity described by Elliot Smith (1903) was obtained from this specimen. To the same species also are referred a left mandible and a number of lumbar and caudal vertebrae.

In the interval between January 14 and March 9, 1902, Dr. Ernst Stromer (1903a) and Dr. Max Blanckenhorn visited the neighborhood of Qasr-el-Sagha in the Fayum, where a collection was made that included a good skull and mandible of *Dorudon osiris* as well as other remains that were described under the name *Zeuglodon zittelii*. In 1904, Stromer was commissioned by the Senckenbergischen naturforschenden Gesellschaft, Frankfurt a. M., to return to the Fayum and search
for additional archaeocete material. Under a cooperative project financed by interested patrons, Richard Markgraf was employed to make collections for the Württembergische Naturaliensammlung, Stuttgart, and for the Paläontologische Sammlung, Alte Akademie, Munich, in the Mokattam limestone near Cairo and in the northern part of the Fayum. One unexpected discovery followed another and almost at the outset of field work in 1903, Markgraf found the unique skull and other skeletal remains of *Protocetus atavus* (Fraas, 1904a) in the lower Mokattam white limestone near Cairo. At a higher level of the same formation, Markgraf in 1904 found the badly crushed and damaged skull of *Eocetus schweinfurthi* (Fraas, 1904a). The wide-spread interest aroused by these discoveries resulted in continued support for palaeontological exploration in the Fayum, where, during 1904 and 1905, Markgraf collected skeletal remains of archaeocetes that have since been identified by Stromer (1908b) as belonging to *Dorudon osiris*, *Dorudon zitteli*, and *Prozeuglodon isis*. In 1906, Professor Eberhard Fraas joined Markgraf in the Fayum and brought back with him to Stuttgart a well-preserved skull and a considerable portion of the skeleton of the large species, *Prozeuglodon isis*. Continued field work by Markgraf in 1907 brought to light the remarkably well-preserved natural endocranial cast of *Dorudon osiris*, which was subsequently described and figured by Stromer (1908b). The exploration of the fluvio-marine beds was the main objective of the expedition sent into the Fayum region by the American Museum of Natural History in 1907 and, although no extended search was made for archaeocete material in the upper Eocene marine beds, a somewhat crushed skull of *Dorudon osiris* was collected by Dr. Walter Granger.

Portions of two left mandibles belonging to *Pappocetus lugardi* (Andrews, 1920), which were discovered in a hard pyritic clay in the Omobialla District, southern Nigeria, were presented by Sir Frederick Lugard and Sir J. Eaglesome to the British Museum (Natural History). The formation in which this small aracheocete occurs is referred to the upper Lutetian stage by Newton (1922).

Returning again to North America, one notes that the hinder portion of a skull of *Basilosaurus cetoides* was found on November 14, 1913, by G. C. Fraser in the Ocala limestone quarry operated by the Oakhurst Lime Company in Marion County, Florida (Cooke, 1915, p. 113). Two isolated caudal vertebrae belonging to an archaeocete were found near an articulated series of 15 sirenian trunk vertebrae in the lower upper Eocene Yegua formation in Burleson County, Texas, during 1921, by John Navratil. Three anterior lumbar vertebrae with short centra, belonging to a rather large archaeocete, were obtained by Dr. C. Wythe Cooke on October 11, 1925, from the Ocala limestone exposed on the east bank of Flint River, Crisp County, Georgia. During October 1929 Norman H. Boss and Remington Kellogg made a search for archaeocete remains in Washington and Choctaw Counties, Alabama, and in Clarke County, Mississippi. Three incomplete skeletons of *Zygorrhiza kochii*, including one with a well-preserved skull and both mandibles, were collected. Portions of the rostrum and both mandibles, vertebrae, and ribs of *Basilosaurus cetoides*, which were blasted out of the Ocala limestone by
employees of the Georgia Lime Rock Company at Perry, Georgia, were obtained for Wesleyan College at Macon, Georgia, by Professor Leon P. Smith during August 1932. An incomplete skull, both mandibles, and a number of vertebrae belonging to an immature individual of *Zygophysotherium kochii* were found in April 1933, near Jackson, Mississippi, by Edwin Underwood and Gladden Caldwell. An isolated vertebra belonging to a small archaeocete related to *Protocetus* was found in the middle Eocene Cook Mountain [=Crockett] formation in Leon County, Texas, during 1934 by Dr. H. B. Stenzel. And Lastly, during July 1935, Professor M. F. Bancroft obtained a lumbar vertebra in a hitherto unrecognized early Tertiary marine horizon on the west coast of Vancouver Island, British Columbia.

**CLASSIFICATION OF THE ARCHAEOCETI**

Although some of the archaeocetes are rather completely known as to the skeleton, an adequate understanding of the lineage of this group must await the acquisition of information concerning the structural characters of antecedent types occurring in geologic horizons older than the middle Eocene. The basic cranial structure of the middle Eocene archaeocetes is not appreciably different from that of the more specialized upper Eocene forms. It thus becomes necessary to use the advanced and specialized characters of the dentition and of the skeleton in drawing our conclusions as to the division of the Archaeoceti into families and lesser groups. These modified structures tend to mask the more significant heritage characters, through the understanding of which the genetic relationships of these specialized forms to the stem stock must ultimately be determined.

Turning now to the features that have served as a basis for the recognition of the assumed natural divisions of the Archaeoceti, it will be observed that the resemblances are primitive heritage characters and the differences are specialized deviations from the more generalized characters of the group. Specialization has proceeded along several different lines. As might have been expected, divergences of opinion as to the derivation of the Archaeoceti have led to the formulation of several systems of classification. Some of the more important classification schemes are those of Fraas (1904a), Stromer (1908b), Abel (1913), and Miller (1923). A definite and final solution for this vexing problem of archaeocete classification is at present difficult to reach, because the evidence for the derivation of this group must remain peculiarly susceptible to misinterpretation so long as generalizations have to be based on isolated observations.

Within the group Archaeoceti, there are now recognized three families, the (1) Protocetidae, (2) Dorudontidae, and (3) Basilosauridae. It is agreed, however, that there are some valid objections to the naturalness of this classification. Those genera that have retained either some indication of the original tritubercular pattern of cusps on the cheek teeth or normal articular relations of the zygapophyses on the hinder dorsal vertebrae and on the lumbar vertebrae are allocated to the Protocetidae. The genera that have a specialized serrate type of cheek tooth,
and hinder dorsal and lumbar vertebrae with centra of more or less normal proportions as well as a modified condition of the articular relations of the zygapophyses are referred to the Dorudontidae. To the Basilosauridae are referred the larger forms that have a specialized serrate type of cheek tooth, and abnormally lengthened centra on the hinder dorsal, lumbar, and anterior caudal vertebrae.

Each family of the Archaeoceti seems to be divisible into several branches, each of which is supposed to represent a phylogenetic unit.

Protocetidae
  Group I—Protocetus, Pappocetus.
  Group II—Eocetus.
Dorudontidae
  Group III—Dorudon, Zygorhiza.
  Group IV—Kekenodon, Phococetus.
Basilosauridae
  Group V—Prozeuglodon, Basilosaurus.
  Group VI—Platyosphys.

The genera placed in Group I are, so far as known, restricted to the middle Eocene and are thought to be nearest to the stem stock of the Archaeoceti. Traces of the original tritubercular pattern of the cusps are discernible on the hinder upper cheek teeth. The normal articular relations of the zygapophyses of the hinder dorsal and of the lumbar vertebrae are retained. From members of this group some of the later archaeocetes undoubtedly developed along several lines of radiation.

In the sum of its structural characters, Protocetus is unquestionably more closely related to the land-dwelling predecessors of the Archaeoceti than are any of the other known forms. Moreover, Protocetus has been regarded by several investigators as a fairly primitive archaeocete, of a kind which might have been structurally ancestral to some of the later forms. Of Pappocetus, only the mandible with its milk dentition is now known. In view of the characters of the dentition of Protocetus and Pappocetus, and the structural peculiarities of the hinder dorsal vertebrae and of the lumbar vertebra of Protocetus, it seems hardly fitting to place them in the same family as the other more specialized archaeocetes. So distinctive are the differences that if they be disregarded in this instance, then all the archaeocetes should be recognized as belonging to a single family.

The genus Eocetus of the middle Eocene must have split off at a somewhat earlier time from a Group I type of ancestor. This genus is too far advanced in dental characters and in the alteration of the centrum length of the lumbar vertebrae to constitute a generalized stock ancestral to some of the later archaeocetes.

If the presence of a specialized serrate type of cheek tooth is a valid distinction, then all the remaining archaeocetes stand apart from the Protocetidae. Fraas, Stromer, and Abel did not divide the Zeuglodontidae, which according to their schemes of classification included all archaeocetes with a specialized serrate type of cheek tooth, into lesser groups. Miller, however, recognized the characteristic difference between the vertebrae of the smaller and the larger forms, and pointed
out the desirability of establishing two families, the Basilosauridae and the Dorudontidae.

The smaller forms referred to the family Dorudontidae, so far as they are known, are distinguishable by having centra of nearly normal proportions on the hinder dorsal vertebrae and on the lumbar vertebrae. The larger forms referred to the family Basilosauridae all have the centra of the hinder dorsal vertebrae, of the lumbar vertebrae, and of the anterior caudal vertebrae abnormally lengthened. In the past the smaller forms seem to have been linked to the larger forms on the basis of the specialization of the cheek teeth. The resemblances between the Dorudontidae and the Basilosauridae can hardly be explained by convergence, since the differences that separate them do not have the same basic significance as the points of resemblance in the construction of the skull and skeleton. These resemblances in the cheek teeth are more plausibly interpreted as heritage characters carried over in both families from a common ancestral stock.

In Group III, the genus *Dorudon* persisted in the upper Eocene without undergoing any appreciable evolutionary changes in the dentition and skeleton. The most obvious alterations are seen in the several types of occipital shields. The genus *Zygorhiza* represents a slightly modified type, in that the upper cheek teeth have acquired a well-developed cingulum. These genera do not appear to be directly ancestral to any of the later types.

The lower Miocene genus *Kekenodon* in Group IV is characterized by having cheek teeth with three roots, although the crowns of these teeth are serrated. In the retention of three roots, the genus appears to be rather primitive, but the serrated crown denotes specialization. The skeletal characters of *Kekenodon* are unknown.

Features of special interest in the middle and upper Eocene genera comprising Group V are the extraordinary lengthening of the centra of the hinder dorsal, of the lumbar, and of the anterior caudal vertebrae. The cheek teeth in the permanent dentition are essentially like those of Group III.

The lower Oligocene genus *Platysophys* comprising Group VI is a type whose relationships are uncertain. It is characterized in part by having the antero-posterior diameter at the base of the transverse process nearly equivalent to the length of the elongated centrum of the anterior lumbar vertebrae.

**ARCHAEOCETI**


Bones of rostrum and cranium retaining their normal mammalian relationships; no telescoping; facial region elongated; braincase narrow, elongate, and not shortened antero-posteriorly; intertemporal region tubular; temporal fossae large; parietals normal in relation to other bones and meet on midline, forming a strong sagittal crest; supra-occipital shield high, bounded by prominent backward projecting lambdoidal crests; exoccipitals extended laterally; parietals, frontals, maxillaries and the elongated premaxillaries
are the largest of the skull bones; forehead flattened; supraorbital process of frontal broadened, extended laterally beyond jugal portion of zyggomatic arch, and arched at extremity; nasal bones elongated, situated almost wholly in front of level of anterior margins of supraorbital processes; posterior portion of narial cavity relatively undisturbed, and turbinal bones are present; hinder margin of dorsal narial fossa at level of Pm1 or at most moved backward to level of interval between Pm1 and Pm2, about half-way to orbit; ascending process of premaxillary not reaching to frontal, but terminating behind level of antorbital foramen (above Pm2 or Pm3) and conspicuously extended anteriorly beyond extremity of maxillary; proximal end of maxillary absents against the supraorbital process of frontal superiority, and inferiorly projects backward below the latter; jugal slender and laterally flattened; lachrymal lodged in part in anterior rim of orbit, between preorbital portion of supraorbital process and the jugal; zygomatic process of squamosal slender, with prominent postglenoid process, and with glenoid articular surface tending toward a vertical position; palatines not extending forward beyond level of Pm4; bony palate prolonged backward by plate-like outgrowths from lower borders of both the palatines and the pterygoids, forming an inclosed passage for the internal choanae; jaws seemingly used mainly as a pair of forceps, with long, narrow, beak-shaped rostrum, in which the anterior teeth are widely spaced; incisive foramina eliminated by linear contact of premaxillaries along the midline; mandible very long and slender, with large coronoid process, and relatively loose symphysis.

Permanent dental formula: I \(\frac{1.3.4}{2.3.4} \), C \(\frac{1}{1} \), Pm \(\frac{1.2.3.4}{1.2.3.4} \), M \(\frac{1.2.3}{1.2.3} \) or \(\frac{1.2.3}{1.2.3} \); anterior teeth (I to Pm\(\frac{1}{2}\)) widely spaced; hinder cheek teeth (Pm\(\frac{1}{2}\) to M\(\frac{1}{2}\)) closely approximated, usually forming a closed series; mandibular cheek teeth have two roots; Pm3, Pm4 and M1 three-rooted in *Protocetus* and *Kekenedon*; Dpm3 and Dpm4 three-rooted in *Prozeuglodon isis*, *Dorudon ostris*, and *Zygorkhiza kochii*.

Seven free cervicals, with relatively short centra; dorsal vertebrae possibly varying from 12 to 15; anterior dorsals have neural spines sloping obliquely backward; remaining dorsals have nearly vertical neural spines; about 13 lumbar vertebrae; one or two sacral vertebrae; caudal vertebrae numerous; anterior caudals have low neural spines, and large strongly divergent metapophyses; anterior ribs two-headed; posterior ribs single-headed and slender; sternum consists of several segments.

Forelimbs short; scapula high, with long flat acromion and small slender coracoid; humerus flattened laterally, with very long deltoid crest and a well-developed trochlea on distal end; flexible elbow joint; ulna flattened laterally, with distinct olecranon; radius flattened laterally and bowed forward; carpus imperfectly known; metacarpals and phalanges slender.

**BASILOSAURIDAE**


Gigantic carnivorous archaeocetes, attaining a length of from 40 to 65 feet; maximum length of skull about 5 feet; parietal region of skull quite narrow; squamosal forms a large part of external wall of braincase; temporal fossae very large; premaxillaries and maxillaries elongated; large pterygoid fossae for accessory air sinuses of middle ear; permanent dental formula: I \(\frac{1.2.3}{1.2.3} \), C \(\frac{1}{1} \), Pm \(\frac{1.2.3.4}{1.2.3.4} \), M \(\frac{1.2.3}{1.2.3} \); incisors caniniform; upper Pm1 has a relatively small sub-conical crown; remainder of upper cheek teeth (Pm2 to M2) have conspicuous accessory denticles on anterior and posterior cutting edges of their laterally compressed crowns; lower premolars (Pm2 to Pm4) have accessory denticles on
anterior and posterior cutting edges of crowns; lower molars (M₁ to M₃) have accessory denticles restricted to posterior cutting edges of crowns; neck conspicuously short; trunk and tail elongated; centra of posterior dorsal, of lumbar and sacral, and of anterior caudal vertebrae conspicuously elongated and have a low medially placed neural arch.

**BASILOSAURUS**


1849. *Hydrarchus* Müller, Über die fossilen Reste der Zeuglodonten von Nordamerika, Berlin, p. 3. (Emendation of *Hydrarchos* Koch, 1845.)


Permanent dental formula: I₁,₂,₃,₄ / C₁ / Pm₁ 1,₂,₃,₄ / M₁,₂ ; deciduous dental formula not known.

The hinder upper cheek teeth, Pm₂ to M₂, have two roots and also form a closed series; Pm₃ is the largest of the upper cheek teeth, corresponding to the carnassial of flesh-eating mammals; crown of Pm₁ is more molariform than caniniform in appearance; Pm₄ is the largest of the lower cheek teeth; rostrum equivalent to 54 per cent of condylobasal length of skull; greatest width of supraoccipital shield equivalent to more than 90 per cent of distance from dorsal margin of foramen magnum to apex of shield; hyoid apparatus consisting of a small hexagonal basihyal and a pair of laterally flattened thyrohyals which are about two-thirds as long as the slender curved stylohyals (epihyal + stylohyal); forelimb slender; scapula unusually broad in proportion to height, the greatest vertical diameter being about three-fourths of greatest antero-posterior diameter, with anterior angle abruptly truncated and posterior angle produced, and with slender coracoidal and elongated flat acromial processes, both directed downward and forward; head of humerus unusually large, and greater and lesser tuberosities not sharply differentiated; elbow hinged and non-rotary; shaft of radius with prominent anterior angle-like prominence; shaft of ulna much narrower than olecranon process; metacarpals and phalanges slender and elongated; innominate bone atrophied, with vestigial iliac process, with small acetabulum which retains traces of cotyloid notch and the pit for attachment of ligamentum teres, and with relatively small thyroid foramen; femur relatively small, slender and functionless.

Vertebral column consisting of 7 cervical, 15 dorsal, 13 lumbar, 2 sacral, and at least 21 caudal vertebrae; cervical vertebrae with compressed centra, no ankylosis of consecutive centra, but with flexibility limited by interlocking of the processes; atlas with vertebral foramen at base of transverse process much larger than transverse foramen in neural arch for first spinal nerve, and with long hypapophysial process; axis with short narrow transverse processes and elongated neural spine; transverse processes of third to fifth cervicals, inclusive, have a narrow process which arises near base of ventral edge and projects forward and downward; lower transverse processes of sixth cervical greatly elongated; transverse processes of seventh cervical decidedly more robust than diapophyses of first dorsal, perforated at base by large vertebral foramen, and continuous dorsally with lateral oblique buttress supporting prezygapophysis; trunk and tail elongated; no remnant of an anapophysis, projecting backward from base of hinder face of diapophysis,
exists on any of the eight anterior dorsals; the five posterior dorsals, all of the lumbars, and the sacrals have excessively elongated centra, relatively short, thin and rather wide neural spines, as well as short narrow transverse processes disproportionate to length of centrum, and have the postzygapophyseal portion of neural arch separated from succeeding vertebra by increasing intervals proportional to length of centrum; sacral vertebrae differ from preceding lumbar and succeeding caudals in having the somewhat trihedral extremities of their transverse processes thickened and roughened; the manubrium, the largest of the sternal segments, is somewhat elongated; and the xiphosternum is a short quadrangular segment, deeply bifurcated posteriorly.

**Basilosaurus Cetoïdes (Owen)**


1843. *Hydracrosus stillimani* Koch, Hydrosos, or great sea-serpent, of Alabama, New York, pp. 16, fig. (published subsequent to Sept. 2, 1845).


**Type locality**—A hill about 200 yards from the Ouachita River (Harlan, 1834, pp. 398, 400), approximately 50 miles south of Monroe, in the southeastern part of Caldwell Parish, Louisiana. Jackson formation, upper Eocene.

**Type specimen**—An imperfectionly preserved centrum measuring 14 inches in length and 7 inches in breadth, and belonging either to a posterior dorsal or an anterior lumbar vertebra. 1 No. 12944A, Academy of Natural Sciences of Philadelphia; collected by Judge H. Bry in 1832.

1 Originally deposited in the Cabinet of the American Philosophical Society. On November 2, 1849, the curators were authorized by the society to deposit with the Academy of Natural Sciences of Philadelphia as an indefinite loan the fossil organic remains belonging to the society. This arrangement was accepted by John Cassin on behalf of the academy. For further details see, Trans. Amer. Philos. Soc. (n.s.), vol. 4, p. 492, 1834, and *op. cit*., vol. 5, No. 44, pp. 110–112, March 1850.
*Referred specimens*—(1) According to S. B. Buckley (1846, p. 129), the maxillary fragment with three cheek teeth in place and with two empty alveoli, which Harlan took with him to London and from which Owen determined the mammalian nature of this archaeocete, was found three-quarters of a mile distant from the house of Judge John G. Creagh. From the U. S. Land Office records it has been ascertained that in 1830 and in 1836 Judge John G. Creagh bought a total of ten subdivisions of government land in the vicinity of a landmark known as "The Rocks," St. Stephens meridian, Section 35, Township 9 North, Range 1 East, Clark County, Alabama. The house of Judge Creagh was located in the Northeast ¼ of Northeast ¼ of Section 35, Township 9 North, Range 1 East. The *Basilosaurus* bones, which were sent in 1834 and 1835 by Judge Creagh to Timothy Abbott Conrad and were subsequently studied by Dr. Richard Harlan, comprised a maxillary fragment with alveoli, a section of a mandible 18 inches in length, an isolated molar tooth, a left humerus, several dorsal and lumbar vertebrae, a few caudal vertebrae, and fragments of ribs. These bones were found at a locality 3 miles distant from the same house, presumably southeast according to Buckley. Thus the spot where these remains were collected was located apparently either in Section 12 or 13, Township 8 North, Range 1 East, Clark County, Alabama. Ocala limestone, upper Eocene.

Strictly speaking, the name *Zeuglodon cetoides* was based on the material which Dr. Harlan submitted to Professor Owen for examination. Owen specifically mentions the following specimens from Clark County: (a) Two portions of bone belonging to the upper jaw, the larger one containing three teeth and the smaller one the alveoli of two others; (b) a fragment of a tooth, comprising the base of the crown and the upper portion of the root; (c) a cast of a mandible with four teeth; (d) a left humerus; (e) fragments of ribs; and (f) the twelfth dorsal vertebra figured by Harlan in 1835. This material seems to have passed into the possession of Dr. Samuel George Morton and subsequently was transferred to the Academy of Natural Sciences of Philadelphia. Some of these specimens have not been located. Anterior section of right mandible (Harlan, 1835, p. 353, pl. 23, fig. 1) now broken near the middle, Nos. 12945 and 12946; and a twelfth dorsal vertebra (Harlan, 1835, p. 355, pl. 24, fig. 1), No. 12948, Academy of Natural Sciences of Philadelphia. Plaster casts of right maxillary (Harlan, 1835, p. 351, pl. 22, fig. 1), No. 839; and a left humerus (Harlan, 1835, p. 356, pl. 22, fig. 6), No. 840, Division of Vertebrate Palæontology, U. S. National Museum.

(2) In the year 1842, S. B. Buckley (1846) excavated a vertebral column of *Basilosaurus cetoides*, which extended to a length of 65 feet, on the plantation of Judge John G. Creagh and at a site about half a mile distant from the latter's house. This house was situated in the Northeast ¼ of the Northeast ¼ of Section 35, Township 9 North, Range 1 East. The place of discovery was thus located in either Section 34 or 35, Township 9 North, Range 1 East, Clark County, Alabama. Among the skeletal elements associated with these vertebrae were the anterior extremity of the rostrum with incisor teeth, the posterior ends of both mandibles, three or more cheek teeth, a portion of a scapula, one entire humerus and the head of another, radius and ulna, and fragments of several ribs. This specimen was shipped to Ebenezer Emmons and was stored for a time in the office of the Geological Survey of New York at Albany. Following the publication of Emmons' reports (1845, 1846) on these skeletal remains, the material passed into the possession of Dr. John C. Warren of Boston about 1847. These skeletal remains were purchased in 1906 by the American Museum of Natural History. No. 10400, Department of Vertebrate Palæontology, American Museum of Natural History. Ocala limestone, Upper Eocene.

(3) The posterior end of the mandible with four damaged cheek teeth in situ, which was figured by Emmons (1846, p. 228, pl. 1, fig. 1), was found by Buckley (1846, p. 128)
"near the summit of the hard grey limestone bluff, about a mile from Suggsville," Clark County, Alabama. Ocala limestone, Upper Eocene.

(4) A portion of a head and vertebrae, "extending to a length of 30 feet, were procured by Mr. Koch in 1845, at a place which I [Sir Charles Lyell, 1846a, p. 313] visited, 4½ miles southwest from Clarksville, Alabama, in company with Mr. Picket, who assisted in the exhumation made by Mr. Koch." Though Dr. Albert Koch repeatedly denied that his assembled skeleton, which was exhibited at New York and Boston, was reconstructed from portions of several individuals, he inadvertently discloses in his published accounts of this animal that this criticism was correct. Reference is made to this Clark County locality in one of Koch's publications. Koch (1846, p. 10) in describing his activities at Clarksville states that he intended to search again for zeuglodont remains at a place near Fattilliby Creek [= Tattilaba Creek] and later on (1846, p. 12) he remarks that arrangements had been made to have a man [presumably Mr. William Picket] search for such remains on the plantation of the deceased Judge Kie [= Creagh]. Israel Slade (Wheeler, 1935, p. 69) declared that he had found these zeuglodont remains in the spring of 1845 on Judge Creagh's plantation, but that Koch had bribed his men to let him have the bones.

A dorsal cranial fragment (Carus, 1847, pl. 1, pl. 2, fig. 1; Müller, 1849, pl. 8, figs. 1–2), No. 15484 (M-32), Geologisch-Paläontologisches Institut und Museum der Universität, Berlin. Ocala limestone, Upper Eocene.

(5) The composite skeleton of Hydrargos sillimanii (Koch, 1845a), subsequently renamed Hydrarachos harlani (Koch, 1845b), which was exhibited in New York by Dr. Albert C. Koch, consisted in part of remains listed under (4) and in part of additional skeletal remains from the following localities: (a) On the prairie near the Old Court House in Washington County, according to Dr. Lister (1846, p. 95), "Koch found a considerable portion of the bones constituting the Hydrarachos," including some bones belonging to the forelimbs, ribs, and vertebrae; (b) the bones assumed by Koch to represent the skull and the mandible were found "in a heap of stones, where they had been thrown by the negroes when the land was cleared for cultivation" (Lister, 1846, pp. 95–96); and (c) "some wagonloads" of bones were procured at another place seven miles distant from the spot where Koch obtained his most interesting specimens (Lister, 1846, p. 96). The Old Court House in Washington County, Alabama, was located as follows: Southwest ¼ of Section 9, Township 8 North, Range 3 West.

In 1896, Schuchert was informed by Daniel M. Williamson, a farmer living near Fail, Alabama, that he was the boy who directed Koch to places where zeuglodont bones were found. The remains listed under (b) according to Williamson were found on the old Tolman plantation which was located 1.7 miles south of Cullomburg, Washington County, Alabama, in Section 1, Township 8 North, Range 3 West. We are told by Dr. Koch (1851, p. 55) that the zeuglodont remains collected in the spring of 1845 were found at a locality one German mile distant from the farm of Colonel Prince. Taking all these statements into consideration, it would appear that the archaeocete remains mentioned under (c) were collected in Washington County, Alabama, in Section 1, Township 8 North, Range 4 West. Upper Jackson formation, Upper Eocene.

Contemporary accounts indicate that Koch's so-called sea-serpent bore the name Hydrargos sillimanii, when it was first placed on exhibition, but later at the direct request of Professor Silliman the name was changed to Hydrarachos harlani. This same assemblage of Basilosaurus remains, representing at least five different individuals, was afterward studied by Johannes Müller and he, ignoring all previously published names, proposed the name Zeuglodon macrospondylus for the form with elongated centra. Thus all three of the above-mentioned names were based on the same assemblage of bones, which were obtained at the localities enumerated above. For further details regarding the vertebrae used by
Koch in the construction of the composite skeleton exhibited at New York and at Dresden, see *Pontogeneus brachyspondylus*. On April 15, 1847, in consequence of an order signed by King Friedrich Wilhelm IV which granted Koch during his lifetime a yearly pension of 1000 Reichstaler, this reconstructed skeleton came into the possession of the “anatomisch-zootomische Museum” of Berlin, of which Johannes Müller was the director (Dietrich, 1934, p. 101).

Four fragments of the dorsal portion of the cranium and the supraorbital process of the right frontal (Müller, 1849, pl. 6, figs. 1–2; pl. 9, figs. 1–2; pl. 10, figs. 4–6); No. 15485 (M-35), Geologisch-Paläontologisches Institut und Museum der Universität, Berlin.

Fragment of left maxillary (Müller, 1849, pl. 5, fig. 3), a smaller fragment of right maxillary (Müller, 1849, pl. 5, fig. 2), a portion of hinder end of left mandible (Müller, 1849, pl. 11, fig. 7), an upper molar, probably M1 (Carus, 1847, pl. 4, fig. 3; Müller, 1849, pl. 4, fig. 3), Pm3 (Carus, 1847, pl. 4, fig. 1; Müller, 1849, pl. 12, fig. 2), Pm4 (Müller, 1849, pl. 12, fig. 6), Pm5 (Müller, 1849, pl. 14, fig. 4), two series of imperfectly preserved vertebræ, and a restored right humerus. Geologisch-Paläontologisches Institut und Museum der Universität, Berlin.

(6) Dr. Albert C. Koch (1851, p. 55) states that a skull and skeleton of *Basilosaurus cetoides* was discovered on February 7, 1848, in a prairie field which was bounded on three sides by small streams and surrounded on all sides by woods. Furthermore this washed-out uncultivated field belonging to Colonel Prince is described by Koch as being located almost on the boundary line between Choctaw and Washington Counties. This farm is now known locally as the old Ben Turner place, although it has been owned more recently by John Mackeller, and the exact location of the field mentioned by Koch is as follows: Northeast 1/4 of Southwest 1/4 of Section 36, Township 9 North, Range 4 West, Choctaw County, Alabama.

This skeleton was transported to Dresden, Germany, where preparation was completed on May 6, 1849. Afterward, it was exhibited at Breslau, Vienna, and Prague. Dr. Koch then returned to the United States with this skeleton and put it on exhibition in New Orleans (Dana, 1875). In either 1855 or 1856, it was exhibited by Koch in St. Louis and later sold to the “Curiosity Shop” in the same city. Finally, the skeleton was acquired by Wood's Museum in Chicago (Bates, 1863, p. 5), where it was destroyed by the great fire of October 9, 1871.

(7) Skull with missing portions restored, but having I3, Pm1, Pm2, Pm3 in place on the left side; an essentially complete left mandible with Pm4 in place; and all of the hyoids with the exception of the right thyrohyal are present. These skeletal elements were used in reconstructing the skeleton on exhibition in the United States National Museum. The following additional elements likewise belong to this individual: Right jugal, left palatine and ankylosed hamular portion of pterygoid; artificial endocranial cast; I1 from left premaxillary; both canines; Pm1, M1, and M2 from right maxillary; I1, Pm2 and M3 from left mandible; three incomplete and poorly preserved cervical vertebrae, including the atlas, axis, and third cervical; the incomplete first dorsal; the right scapula, complete with exception of anterior angle and coracoid process; the crushed left humerus; an unusually large manubrium and a median sternal element; and several rib fragments. From the upper Jackson formation, about 1 ½ miles southeast of Melvin, Choctaw County, Alabama; near center of Section 24, Township 11 North, Range 5 West, in wash at bottom of slope on old Sanford Mitchell field (now owned by Robert Land). No. 4674, Division of Vertebrate Paleontology, U. S. National Museum; collector, Charles Schuchert; November 8–16, 1894.

(8) Twenty-four consecutive vertebrae (Lucas, 1900a, p. 327), extending from the atlas to the second lumbar, inclusive. The 7 cervicals, the 15 dorsals, and the anterior-
most lumbar were used in reconstructing the skeleton on exhibition in the United States National Museum. The following additional elements likewise belonging to this individual were utilized in the reconstructed skeleton: 13 ribs, more or less complete; 4 sternal elements; the right and the left scapula; the left humerus with proximal one-third missing; the left ulna and the left radius; the distal half of the right ulna is missing; and the essentially complete right radius. The following parts of this individual are in the reference collection: The hinder portion of the left mandible; a short section of the eroded right mandible; 12 from left premaxillary; Pm1 from right maxillary; 13 from right mandible; M2 from left mandible; the right tympanic bulla; two large osseous nodules; and several rib fragments. From the upper Jackson formation, about 2 miles southeast of Melvin, Choctaw County, Alabama; Northeast 1/4 of Southeast 1/4 of Section 24, Township 11 North, Range 5 West. No. 4675, Division of Vertebrate Palaeontology, U. S. National Museum; collector, Charles Schuchert; November 17–24, 1894.

(9) An incomplete left tympanic bulla. From the upper Jackson formation, about two miles southeast of Melvin, Choctaw County, Alabama; Southeast 1/4 of Section 24, Township 11 North, Range 5 West. No. 4677, Division of Vertebrate Palaeontology, U. S. National Museum; collector, Charles Schuchert; November 27, 1894.

(10) The left periotic in situ between exoccipital and squamosal; a fragment of the left premaxillary; two single rooted teeth (?incisors) with damaged crowns; the centre of four anterior dorsal vertebrae; the distal half of the right humerus; and fragments of four ribs. From the Ocala limestone, in a cove below Cedar Reach Rock, about 43 miles below the mouth of Patsaliga Creek, on Conecuh River, Escambia County, Alabama. No. 6087, Division of Vertebrate Palaeontology, U. S. National Museum; collector, G. Harcus; April 1909.


(12) The hinder portion of an imperfect cranium with incomplete right squamosal, and with the right exoccipital, right condyle, left exoccipital, and left squamosal missing. From the light cream-colored Ocala limestone in quarry of Oakhurst Lime Company (Plant No. 2, Florida Lime Co.), about 2 miles southeast of Ocala, Marion County, Florida (Cooke, 1915, p. 113). No. 11121, Division of Vertebrate Palaeontology, U. S. National Museum; collector, G. C. Fraser; November 14, 1913.

(13) The right scapula, complete with exception of the eroded vertebral edge. From the upper Jackson formation, about 2 miles southeast of Melvin, Choctaw County, Alabama; Northeast 1/4 of Southeast 1/4 of Section 24, Township 11 North, Range 5 West. No. 11783, Division of Vertebrate Palaeontology, U. S. National Museum; collector, Charles Schuchert; October 19, 1896.

(14) Manubrium of sternum. From the upper Jackson formation, 3 miles west of Isney, Choctaw County, Alabama, and west of the Bucatunna River, on the washed-out slope of a hillside on the northeast side of the road in Wayne County, Mississippi; Section 33, Township 10 North, Range 5 East. No. 12064, Division of Vertebrate Palaeontology, U. S. National Museum; collectors, Norman H. Boss and Remington Kellogg; October 10, 1929.

(15) Thirty-five consecutive vertebrae (Lucas, 1900a, p. 327), extending from the penultimate caudal to the second lumbar, inclusive. The 21 caudals, the 2 sacrals, and the 12 lumbars were used in reconstructing the skeleton on exhibition in the United States National Museum. The following additional elements likewise belonging to this individ-
ual were utilized in the reconstructed skeleton: The right and the left innominate bones; and the complete right femur. The following parts of this individual are in the reference collection: 4 chevron bones; the head of the left humerus; the proximal portion of the left ulna; I3 from the right premaxillary; an incisor from the left premaxillary; Pm2 from the left maxillary; and Pm1 from the left mandible. From the upper Jackson formation on land owned in October 1929, by Horace Brown, 3 1/2 miles southeast of Fail, Choctaw County, Alabama; center of Section 35, Township 9 North, Range 4 West. No. 12261, Division of Vertebrate Paleontology, U. S. National Museum; collector, Charles Schuchert; November 5–13, 1896.


(17) A number of pieces of the skull, including the anterior end of the right premaxillary, 187 mm. in length, with I1 in place; a section of the conjoined right maxillary and premaxillary, 367 mm. in length, with alveoli for I2, C, and Pm1, the roots of the two last-mentioned teeth being in place; a section of the conjoined left maxillary and left premaxillary, 400 mm. in length, with the basal portion of the root of I1 and empty alveoli for I2, I2, C, and Pm1; the anterior three-fifths of the right mandible, measuring 725 mm. from anterior extremity to broken hinder end, with empty alveolus for I1, root of I2 in alveolus, I3 lacking most of the enamel on the crown, apex of crown of C missing, crown of Pm1 destroyed except for basal border, both roots of Pm2 in situ, and the empty alveoli for Pm3 and Pm4; the symphysial portion of the left mandible, measuring 545 mm. in length, with empty alveolus for II, enamel surface of crown destroyed on I2 and I3, and the roots for C, Pm1, and Pm2 in situ; four isolated teeth, including the right Pm3, the anterior root and corresponding portion of crown of Pm3, and two imperfectly preserved incisor teeth; eleven incomplete dorsal vertebrae, including four anterior dorsals and the ninth to the fifteenth, inclusive; portions of two anterior lumbar vertebrae; fragments of ribs; one mesosternal segment; and the proximal half of one phalanx. All of these bones were damaged by the blasting operations of quarry employes. From the Ocala limestone (Cooke and Shearer, 1918, p. 76), Georgia Limerock Products Company; about 4 miles south of Perry, Houston County, Georgia. These skeletal remains were found about 8 feet below the top of the light cream-colored limestone stratum which has an estimated thickness of 40 feet in this quarry. They were associated with Bryozoa (Rich Hill fauna) and Pertarchus lyelli (Conrad). No. 13890, Division of Vertebrate Paleontology, U. S. National Museum; collector, Leon P. Smith; August 1932.

**SKULL**

The skull (No. 4674, U. S. N. M.) of Basilosaurus cetoides (pl. 2) differs from that of Prostegolodon ipsis in having an unusually large Pm3, a broader supraoccipital shield which is less noticeably "pinched in" ventrally, the zygomatic breadth is proportionately less, the temporal fossae are relatively longer and narrower, the curvature of the anterior temporal margin of the cranium is more oblique, the combined width of the nasals posteriorly is less, and the rostrum is less depressed in the region of the nasals. The rostrum constitutes about 54 per cent of the condylobasal length of the skull.

The following portions of this skull, which were missing, have been restored: The right maxillary and premaxillary, the anterior two-thirds of both nasals, the left zygomatic process, the outer half of the supraorbital process of the left frontal, the anterior extremity of the left premaxillary, both lachrymals, the hinder inferior processes of both maxillaries, the right palatine, both pterygoids, the basi-sphenoid, the major portion of the basioccipital, and the lower portions of both lambdoidal crests.
Parietals (fig. 1) normal in relation to adjacent bones, contributing the roof for the cranium and the major portion of the intertemporal constriction, and meeting on the midline to form a high sagittal crest that extends forward almost to level of hinder ends of frontals; curvature of parietal somewhat unusual, since the portion forming the roof of the cranial cavity is slightly convex and depressed 72 mm. below level of sagittal crest, the portion forming hinder lateral surface of cranium is nearly vertical, and in the region of the intertemporal constriction, beginning at level of anterior end of the squamosal and extending forward to level of sphenorbital fissure, it is deeply indented or "dished in," forming a large quadrangular depression; vascular foramen on lateral surface of right parietal located about 175 mm. in front of hindermost edge of lambdoidal crest; dorsal profile (fig. 3) commences to rise gradually at level of hinder edge of orbit; lateral to apex of supraoccipital shield the lambdoidal crests are slightly elevated above level of sagittal crest; squamosal rather large, meeting the parietal in a dentate suture that runs downward and forward, its upper surface descending abruptly to its ventro-anterior or temporal margin, which is extended forward as a thin shelf; zygomatic process slender, not bowed outward, compressed from side to side, and truncated obliquely at extremity in region of contact with hinder end of jugal, and having a crest-like upper edge; lambdoidal crest constitutes the posterior boundary of the enormous temporal fossa; maximum zygomatic breadth equivalent to 46 per cent of condylobasal length of skull; supraoccipital shield (fig. 4) rather broad, deeply concave transversely, with vertical median ridge most prominent near apex, and with lateral portions of prominent lambdoidal crests strongly folded backward; the anterior face of the lambdoidal crest is contributed by the corresponding parietal and the posterior face by the supraoccipital; exoccipital relatively wide, with rather thick and somewhat convexly curved external edge; upper edge of exoccipital more or less free, and not confluent with lambdoidal crest of squamosal, but slightly below the latter; foramen magnum not particularly enlarged, its transverse diameter being greater than its vertical diameter; paroccipital processes not conspicuously prolonged downward; occipital condyles elliptical in outline, considerably broader above than below, slightly convex from side to side, set off from exoccipital surface by shallow grooves, and borne on distinct necks; intertemporal region rather long and narrow; lateral walls of intertemporal constriction are nearly vertical above region of sphenorbital fissure; groove for optic nerve originating at optic foramen, which on the right side is certainly situated anterior to and slightly above level of sphenorbital fissure, extends forward and upward on lateral surface of orbitosphenoid and then curves outward on ventral face of supraorbital process of frontal; parietals and frontals (fig. 1) quite thick in region of sutural union; supraorbital process of frontal broadened, extended laterally beyond level of jugal, and arched at extremity: postorbital angle of supraorbital process noticeably thicker than preorbital angle; orbit of moderate size; anterior end of laterally flattened jugal presumably mortised into outer face of maxillary as in Zygorhiza kochii; nasals apparently greatly attenuated anteriorly, strongly convex from side to side posteriorly, and attain their maximum width posteriorly near level of point of divergence; posterior extremities of nasals separated by a narrow wedge-like nasal process of the combined frontals and extended backward beyond level of hinder ends of maxillaries; anterior extremities of nasals constitute posterior border of dorsal nasal fossa, the posterior end of the fossa being above middle of interval between Pm1 and Pm2 and the anterior end being at level of anterior end of maxillary; premaxillaries contribute the floor and the lateral walls of the dorsal nasal fossa; ascending process of premaxillary is lodged in groove on upper internal border of maxillary and terminates posteriorly above center of Pm4; the narrow ascending process of maxillary overrides the supraorbital process of frontal; the large antorbital foramen lies above Pm2 and Pm3; flat oral surfaces of premaxillaries (fig. 2) extended backward as a narrow wedge-like tongue to level of Pm2,
**Fig. 1—Basilosaurus cetoides** (Owen). Skull, dorsal view, No. 4674, United States National Museum. X4; ant.f., antorbital foramen; c., occipital condyle; ex.oc., exoccipital; ju., jugal; max., maxillary; na., nasal; pa., parietal; pmx., premaxillary; s.or.pr., supraorbital process of frontal; sq., squamosal; zyg., zygomatic process of squamosal. Upper Eocene, upper Jackson formation, Alabama.

**Fig. 2—Basilosaurus cetoides** (Owen). Skull, ventral view, No. 4674, United States National Museum. X4; bo., basioccipital; c., occipital condyle; ex.oc., exoccipital; f.pt., pterygoid fossa; h.pt., hamular process of pterygoid; j.n., notch for jugular leash; ju., jugal; l.pr., lateral process of basioccipital; max., maxillary; m.e.a., groove for external auditory meatus; pal., palatine; pmx., premaxillary; pr.a.p., anterior process of pterygoid; pr.p., paroccipital process; pr.p.p., posterior process of pterygoid; pt., pterygoid; s.or.pr., supraorbital process of frontal; sq., squamosal; zyg., zygomatic process of squamosal. Upper Eocene, upper Jackson formation, Alabama.
separating anterior extremities of maxillaries; major portion of oral surface contributed by the more or less flattened horizontal plates of maxillaries; bony palate prolonged backward by elongation of palatines and adjacent thin plates of pterygoids, forming an enclosed tube for internal choanae; a V-shaped elevation is present on palatal surface of this choanal tube; the concave oval glenoid articular surface on attenuated zygomatic process extends downward upon the short curved postglenoid process; a well-defined channel for external auditory meatus, which originates on postero-in
ternal margin of ventral surface of squamosal, continues its course outward behind the base of the postglenoid process of that bone; paroccipital process is rather large, with ventral concavity for reception of stylohyoid and is separated from hinder edge of lateral descending process of basioccipital by the wide notch for jugular leash; posterior process of periotic wedged in between exoccipital and hinder end of squamosal; small hypoglossal foramen located on hinder margin of notch for jugular leash.

The damaged cranium of another individual (No. 11121, U. S. N. M.), however, has the basicranium sufficiently preserved to show
the essential structural peculiarities of the pterygoid fossæ, the basisphenoid, and the basioccipital with its lateral descending processes. Basisphenoid narrow; basioccipital with large lateral descending processes; suture between basioccipital and basisphenoid obliterated; median basicranial region bounded laterally in front by hamular plates of pterygoids, judging from the presence of sutural impressions, and behind by lateral descending plate-like processes of basioccipital; large pyriform pterygoid fossa for accessory air sinus of middle ear probably partially overspread below by pterygoid, the roof being contributed by alisphenoid and underlying thin plate of pterygoid, the outer wall by the postero-external limb of the pterygoid and the bifid anterior end of the squamosal, and the inner wall by the hamular plate of the pterygoid; mandibular branch of trigeminal nerve passes outward from cranial cavity through deep notch on posterior border of alisphenoid and reaches temporal fossa through the foramen ovale; extremity of alisphenoid exposed on outer wall of cranium and bounded by pterygoid parietal, and squamosal.

Table 1—Measurements (in millimeters) of skull

<table>
<thead>
<tr>
<th></th>
<th>No. 4674 U.S. N. M.</th>
<th>No. 13000 U.S. N. M.</th>
<th>No. 13000 U.S. N. M.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Left</td>
<td>Right</td>
<td>Right</td>
</tr>
<tr>
<td>Diastema between alveoli for I₂ and I₃</td>
<td>57</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>&quot;</td>
<td>72</td>
<td>57</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>31</td>
<td>44</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>33</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>Antero-posterior diameter of alveolus for I₃</td>
<td>47</td>
<td>47</td>
<td>.</td>
</tr>
<tr>
<td>&quot;</td>
<td>62</td>
<td>46</td>
<td>42.5</td>
</tr>
<tr>
<td>&quot;</td>
<td>47</td>
<td>45±</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>75.5</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>&quot;</td>
<td>80</td>
<td>.</td>
<td>.</td>
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</table>

For additional measurements of the skull, see table 62 (p. 246).

TYMPANIC BULLA

Two isolated left tympanic bullæ (Nos. 4677 and 6125, U. S. N. M.), both lacking the anterior pedicle, the sigmoid process, the median process (conical apophysis), as well as the posterior process, are referred to this archaeocete. The anterior end of the bulla is rounded and the tympanic cavity is rather wide. As regards its relative dimensions, the tympanic bulla of B. cetoides is quite similar to that of Dorudon osiris and Zygorhiza kochii, the transverse diameter at level of the anterior pedicle being equivalent to about 70 per cent of the antero-posterior diameter. The involucrum of this bulla is quite similar to that of the smaller archaeocetes and is strongly constricted anterior to the middle of its length, the anterior portion being gradually attenuated toward the narrow eustachian outlet. The convex surface of the hinder portion of the involucrum is ornamented on the dorsal face with a few coarse transverse grooves, but on the flattened anterior portion these grooves are finer and the surface is relatively smoother. A vertical cleft separated the hinder end of the involucrum from the thickened edge of the outer lip above the point of origin of the outer pedicle of the posterior process. The ventral surface of the bulla is

Table 2—Measurements (in millimeters) of the tympanic bullæ

<table>
<thead>
<tr>
<th></th>
<th>No. 4677 U.S. N. M.</th>
<th>No. 6125 U.S. N. M.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Left</td>
<td>Left</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter</td>
<td>90.5</td>
<td>98</td>
</tr>
<tr>
<td>Maximum transverse diameter of bulla</td>
<td>68.5</td>
<td>71+</td>
</tr>
<tr>
<td>Vertical distance from dorsal edge of median process (conical apophysis) to ventral face</td>
<td>. . .</td>
<td>62+</td>
</tr>
<tr>
<td>Maximum transverse diameter of involucrum</td>
<td>47.8</td>
<td>47.2</td>
</tr>
</tbody>
</table>
convex from end to end, although the internal half of this surface is somewhat flattened and rather rugose. The usual broad deep hollow separates the more convex postero-external angle from the more flattened postero-internal angle of the ventral surface. The hinder edge of the ventral surface coincides with the transverse sharp-edged crest on the involu-

crump.

PERIOTIC

The right and left periotics attached to the skull (No. 4674, U. S. N. M.) are partially concealed by the matrix. Fortunately, a left periotic of another individual (No. 6087, U. S. N. M.), which is in situ between the squamosal and the exoccipital, is available for study.

The periotic of this archaeocete is similar to that of Zygorhiza kochii, but is somewhat larger. It is characterized in part by the dorsal prolongation of the denser outer portion to form an inwardly curved and laterally compressed superior plate-like process, which is applied to the squamosal on the inner wall of the cranium, by the location of the foramen
*singulare* at the base of the anterior face of the *crista transversa*, by the large rugose fossa for the stapedial muscle, and by the relatively small size of the *tractus spiralis foraminosus*. The elongated posterior process is firmly wedged between the exoccipital and the squamosal, like in the Recent Mysticeti. The posterior process is compressed distally and its longitudinal axis forms an obtuse angle with the antero-posterior axis of the periotic. Rather broad grooves separated by narrow ridges are present on the ventral surface of the posterior process. Near the middle of its length this process (No. 6087, U. S. N. M.) measures 39.5 mm. antero-posteriorly. At the proximal end of the posterior process, a short inwardly projecting ledge overhangs the steep inner face that forms the outer wall of the posterior excavation for the stapedial muscle.

On the ventral side (fig. 5), the *pars cochlearis* is seen to be slightly flattened but the ventral surface as a whole curves from before backward. A raised crest is present on the outer border of the ventral face of the *pars cochlearis*, indicating the course of the internal carotid artery. The inner or cerebral border of the ventral face of the *pars cochlearis* is abruptly truncated.

The *fenestra rotunda* is circular in outline and is situated on the hinder face of the *pars cochlearis* approximately at the level of the ventral surface of the posterior process. Its transverse and vertical diameters are, respectively, 3.2 and 3 mm. On the extero-lateral surface of the *pars cochlearis* near its upper limit and behind the middle of its length, the *fenestra ovalis* is situated. The *fenestra ovalis*, which leads into the vestibule of the
osseous labyrinth, is somewhat elliptical in outline and measures 5 × 3.3 mm. The foot plate of the stapes is lodged in the *fenestra ovalis* and is held in position by a very narrow ledge which is sunk at least 2 mm. below the level of the epitympanic rim of the *fenestra*. The two small orifices of the semicircular canals are situated on the outer side of the roof of the vestibule, 5.5 mm. above the level of the epitympanic rim of the *fenestra ovalis*.

The epitympanic orifice of the Fallopian aqueduct, which opens into a deep narrow groove, about 2 mm. in width anteriorly and separated internally from the *fenestra ovalis* by the narrow elevated rim of the latter, is located on the roof of the recessus epitympanicus but anterior to the *fenestra ovalis*. This groove for the facial nerve becomes slightly narrower posteriorly and terminates at about the level of the antero-internal angle of the posterior process. Beyond this point, the facial nerve apparently followed the ventral border of the ventro-internal angle of the posterior process and then turned outward along the hinder face of that process. The rather deep rugose fossa for the attachment of the stapedial muscle begins at the level of the *fenestra ovalis* and extends backward to the level of the hinder face of the periotic. This rugose area is extended downward internally upon the outer face of the *pars cochlearis* and externally upon the nearly vertical inner face of the posterior process. The roughened surface for the attachment of the stapedial muscle is sunk below the level of the hinder end of the channel for the facial nerve.

External to the epitympanic orifice of the *aqueductus Fallopii* is a deep pit which is irregularly ovoidal in outline, but does not encroach upon the fossa for the head of the malleus like in *Zygoryx kochii* (No. 12975, U. S. N. M.). This pit constitutes the fossa *incudis* and lodges the crus breve of the incus. It is partially hidden from a ventral view by the inward projection of the free edge of that portion of the squamosal which forms the inner limit of the channel for the external auditory meatus.

The large concave fossa for the head of the malleus is placed obliquely on the protuberance in front of the epitympanic orifice of the *aqueductus Fallopii*. A short narrow fissure is present on the left periotic (No. 6087, U. S. N. M.) between the thickened inner portion of this protuberance and the *pars cochlearis*. The rather broad groove internal to this fissure presumably lodged the *tensor tympani* muscle whose hinder end was inserted upon the manubrium of the malleus.

On the external face of the periotic a deep dorso-ventrally curved furrow, which terminates at the level of the anterior face of the protuberance, seems to mark the hinder limit of the anterior process. The outer wall of the cavity formed by this groove when the periotic is *in situ* is contributed by the free inner edge of the squamosal. This cavity has been identified as the *fovea epitymbaria* and, if correctly identified, it lodges the *processus tubarius* of the tympanic bulla. The external face of the anterior process is strongly convex, a rounded crest is developed upon its ventral face, and its internal face is obliquely flattened in a ventro-dorsal direction to about the level of the entrance to the Fallopian aqueduct. Above this level the inner face of the anterior process exhibits an irregularly concave curvature; the curvature of this surface passes imperceptibly into that of the thin superior process of the periotic.

Viewed from the internal or cerebral side (fig. 6), the thin plate-like superior process of the periotic is curved from end to end but is conspicuously thickened posteriorly. Below this process is the ventrally placed *pars cochlearis*. The large internal acoustic meatus is the most prominent structure on the cerebral face. The diameters of this meatus (No. 6087, U. S. N. M.) are 8.5 × 6 mm. The internal acoustic meatus is conspicuously smaller at its *fundus* than at its cerebral rim and it is sunk about 12 mm. deep into the *pars cochlearis*. The small *tractus spiralis foraminosus* is well defined, with a minute *foramen centrale* at its anterior end, and it is located for the most part on the ventral side of the *fundus*. A thin osseous partition or *crista transversa*, which does not rise to the level of the cerebral
rim of the internal acoustic meatus, separates the fundus from the cerebral entrance to the aqueductus Fallopii. At the base of the anterior face of this thin osseous partition is the minute orifice of the foramen singulare, through which passes the vestibular branch of the acoustic nerve. The entrance to the Fallopian aqueduct for the passage of the facial nerve lies within the same cerebral rim as that which encircles the internal acoustic meatus, but it is located anterior to the foramen singulare.

The small orifice of the aqueductus cochleae is situated outside of the internal acoustic meatus (4 mm. behind on No. 6087, U. S. N. M.) and at the postero-internal angle of the pars cochlearis. Behind the cerebral rim of the internal acoustic meatus and above the orifice of the aqueductus cochleae is a deep, elongated slit-like fossa for the sacculus endolymphaticus and the small cerebral orifice of the aqueductus vestibuli for the ductus endolymphaticus is located at the bottom of this fossa.

The dorsal half of the hiatus epitympanicus is formed by the depression on the outer border of the periotic that lies between the protuberance on which the fossa for the head of the malleus is located and the basal portion of the almost vertically rising anterior face of the posterior process, while the ventral half is limited anteriorly by the sigmoid process and posteriorly by the basal portion of the posterior process of the tympanic bulla. The

<table>
<thead>
<tr>
<th>Table 3—Measurements (in millimeters) of the periotics</th>
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<tbody>
<tr>
<td><strong>No. 6087</strong></td>
</tr>
<tr>
<td>U. S. N. M.</td>
</tr>
<tr>
<td><strong>Left</strong></td>
</tr>
<tr>
<td>Maximum transverse diameter at level of fenestra ovalis</td>
</tr>
<tr>
<td>Maximum length of periotic, end of anterior process to end of posterior process</td>
</tr>
<tr>
<td>Maximum dorso-ventral depth of periotic, from most inflated portion of tympanic face of pars cochlearis to dorsal margin of superior plate-like process</td>
</tr>
<tr>
<td>Distance from fenestra rotunda to end of anterior process</td>
</tr>
<tr>
<td>Distance from fenestra rotunda to end of posterior process</td>
</tr>
<tr>
<td>Distance from epitympanic orifice of aqueductus Fallopii to end of anterior process</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of pars cochlearis</td>
</tr>
<tr>
<td>Extremity of anterior process to anterior edge of fossa for malleus</td>
</tr>
<tr>
<td>Maximum transverse diameter of pars cochlearis behind level of fenestra ovalis</td>
</tr>
<tr>
<td>Greatest length of posterior process</td>
</tr>
</tbody>
</table>

The free edge of the squamosal at the inner end of the channel for the external auditory meatus overspreads this hiatus, concealing it entirely from a ventral view when the periotic is attached in its normal position. This raises the question as to whether or not this depression is functionally equivalent to the hiatus epitympanicus which in Recent Cetacea forms the connecting passage between the cavum epitympanicum and the sinus pneumaticus squamosi.

**MANDIBLE**

The extreme anterior end and the hinder lower angle of the left mandible (No. 4674, U. S. N. M.) are missing, but it is otherwise complete. The right mandible was not found.

The mandible (fig. 3) is rather robust; total length of mandible about 1136 mm.; the edges of the alveoli for incisors and for canine are not noticeably elevated; from before backward the horizontal ramus increases in depth rather gradually up to Pm2, the vertical depth at level of hinder edge of alveolus of I2 being 71.4 mm., and at level of anterior edge of Pm2 it is 101 mm.; the interval between Pm1 and Pm2 marks the transition to the rising alveolar edge which culminates in the rather steep anterior edge of the coronoid process; the depth of the left ramus at level of anterior edge of alveolus of Pm4 is 123 mm. and at posterior margin of alveolus of M3 it is 200 mm.; external surface of horizontal ramus somewhat convex in front, becoming flattened posteriorly; several small mental foramina are located
anterior to Pm₂, those below the incisors and the canine being nearer the ventral edge, while the hinder ones are located in front of and behind Pm₃, but the latter are nearer the alveolar edge; internally (fig. 7) the flat symphysial surface extends backward to about middle of Pm₂, its maximum length being 415 mm.; coronoid process rather broad, its posterior edge is truncated obliquely, and the maximum depth of the left mandible through this process is 362 mm.; entrance to alveolar canal extraordinarily wide and situated 360 mm. anterior to hinder face of condyle; condyle convex dorso-ventrally and slightly broader than high, its upper surface being on a level with hinder rim of alveolus for M₁; a prominent rounded longitudinal swelling on outer face of mandible extends forward a short distance from condyle. Additional measurements of this mandible are as follows: Vertical height of mandible at hinder edge of alveolus for M₃, 200 mm.; anterior edge of Pm₂ to hinder edge of M₃, 400 mm.; posterior edge of M₃ to hinder face of condyle, 370 mm.; and vertical diameter of condyle, 52 mm.

The position of the mental foramina (pl. 8, figs. 1–2) does not appear to have any diagnostic significance, since no apparent uniformity exists in the distribution of these foramina in opposite mandibles of the same individual. On the external surface of the right mandible (No. 13690, U. S. N. M.) there are nine mental foramina, which are separated respectively by the following intervals from the anterior extremity: 25.5 mm., 87 mm., 139 mm., 373 mm., 412 mm., 465 mm., 542 mm., 598 mm., and 663 mm. The anteriormost or first foramen is located 6.5 mm. below rim of alveolus for Π, the second 28 mm. below rim of alveolus for I₂, the third 38.5 mm. below rim of alveolus for I₃, the fourth 32 mm. below rim of alveolus for Pm₁, the fifth 29 mm. below dorsal surface of diastema between Pm₁ and Pm₂, the sixth 36 mm. below rim of alveolus for Pm₂, the seventh 16 mm. below anterior edge of rim of alveolus for Pm₃, the eighth 11 mm. below hinder edge of rim of alveolus for hinder root of Pm₃, and the ninth 15.5 mm. below rim of alveolus for hinder root of Pm₄. The orifices of the seven anterior foramina look forward, while those of the eighth and the ninth look upward and backward.

On the external surface of the left mandible (No. 13690, U. S. N. M.) there are seven mental foramina, which are separated respectively by the following intervals from the anterior extremity: 18.5 mm., 57.5 mm., 115 mm., 187 mm., 257 mm., 404 mm., and 462 mm. The anteriormost or first foramen is located 8 mm. below rim of alveolus for Π, the second 24 mm. below rim of alveolus for I₂, the third 34 mm. below dorsal surface of diastema between I₂ and I₃, the fourth 32.5 mm. below hinder edge of rim of alveolus for I₃, the fifth 34.5 mm. below center of rim of alveolus for C, the sixth 40.5 mm. below dorsal
surface of diastema between Pm1 and Pm2, and the seventh 35 mm. below hinder edge of rim of alveolus for anterior root of Pm2. There is present in addition to the above a small foramen in the external fossa located between Pm1 and Pm2.

### Table 4—Measurements (in millimeters) of mandibles

<table>
<thead>
<tr>
<th></th>
<th>No. 4674 U.S. N.N. Left</th>
<th>No. 13690 U.S. N.N. Left</th>
<th>No. 13690 U.S. N.N. Right</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diastema between alveoli for I1 and I2.</td>
<td>11</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>&quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; I2 and I3.</td>
<td>26</td>
<td>39.5</td>
<td>34</td>
</tr>
<tr>
<td>&quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; I3 and C.</td>
<td>31</td>
<td>41.5</td>
<td>41</td>
</tr>
<tr>
<td>&quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; Pm1 and Pm2.</td>
<td>27</td>
<td>46</td>
<td>49</td>
</tr>
<tr>
<td>&quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; Pm2 and Pm3.</td>
<td>16.5</td>
<td>22±</td>
<td></td>
</tr>
<tr>
<td>Antero-posterior diameter of alveolus for I2.</td>
<td>57</td>
<td>43</td>
<td></td>
</tr>
<tr>
<td>&quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; I3.</td>
<td>71</td>
<td>46.5</td>
<td>44.5</td>
</tr>
<tr>
<td>&quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; C.</td>
<td>74</td>
<td>46.3</td>
<td>46.5</td>
</tr>
<tr>
<td>&quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; Pm1</td>
<td>61.5</td>
<td>53</td>
<td>51.5</td>
</tr>
<tr>
<td>&quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; Pm2</td>
<td>79.5</td>
<td>80±</td>
<td>78</td>
</tr>
<tr>
<td>&quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; Pm3</td>
<td>91.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; Pm4</td>
<td>100</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance from anterior extremity of mandible to hinder edge of alveolus for C.</td>
<td>265±1</td>
<td>273</td>
<td>274</td>
</tr>
<tr>
<td>Distance from anterior extremity of mandible to hinder edge of alveolus for Pm1.</td>
<td>355±1</td>
<td>379</td>
<td>383</td>
</tr>
<tr>
<td>Distance from anterior extremity of mandible to hinder edge of alveolus for Pm2.</td>
<td>384±1</td>
<td>424</td>
<td>430</td>
</tr>
<tr>
<td>Distance from anterior extremity of mandible to hinder edge of alveolus for Pm3.</td>
<td>563±1</td>
<td>605</td>
<td></td>
</tr>
<tr>
<td>Vertical height at anterior edge of alveolus for I2.</td>
<td>42</td>
<td>55</td>
<td></td>
</tr>
<tr>
<td>&quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; I3.</td>
<td>71.5</td>
<td>70</td>
<td>69</td>
</tr>
<tr>
<td>&quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; C.</td>
<td>80</td>
<td>75</td>
<td>75.5</td>
</tr>
<tr>
<td>&quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; Pm1</td>
<td>89</td>
<td>78.5</td>
<td>81.5</td>
</tr>
<tr>
<td>&quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; Pm2</td>
<td>101</td>
<td>100</td>
<td>103.5</td>
</tr>
<tr>
<td>&quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; &quot; Pm3</td>
<td>111</td>
<td></td>
<td>119.5</td>
</tr>
<tr>
<td>Length of symphysis.</td>
<td>415±1</td>
<td>477</td>
<td>478</td>
</tr>
</tbody>
</table>

1 At least 40 mm. of anterior extremity missing.

**PERMANENT DENTITION**

Dentition of upper and lower jaws heterodont and anisodont. The tooth formula is: 8.1.4.2.3.3. At the anterior end of the upper tooth row (fig. 2), the pits for the reception of the apices of the lower single rooted teeth are located on the outer side of the grasping teeth, while the larger cavities for the apices of the lower cheek teeth are on the inside of the two-rooted serrated cheek-teeth, showing that the upper and lower tooth series cross over when the jaws are closed. The distance from the anterior edge of the alveolus of the first incisor to anterior edge of alveolus of second premolar is certainly greater above than below, and conversely the length of the lower serrated cheek tooth series is much greater than that of the upper. The upper teeth hereinafter described, unless noted otherwise, are in situ in the skull (No. 4674, U.S. N.N.) on exhibition in the United States National Museum. The isolated teeth have been allocated by comparison with those that are in situ in the skull and mandible and by other structural peculiarities which reveal their position.

Although the extremities of both premaxillaries of the skull are destroyed, an incomplete left I1 (No. 4674, U.S. N.N.) was found nearby. The apex of the crown of this tooth is worn off and a considerable portion of the root is destroyed. The enamel on the laterally compressed crown is ornamented with anastomosing vertical striae and the anterior edge is carinate. Koch (1851, pl. 7, fig. 4) figures the extremity of the rostrum with both I1 in situ. The I1 in situ (pl. 8, fig. 4) in the right premaxillary (No. 13690, U.S. N.N.) has a backwardly curved and laterally compressed crown. The enamel on the crown is ornamented with rather coarse anastomosing vertical striae. The anterior carina
is not very prominent and the hinder carina is hardly more distinct than a vertical stria. The root (118 mm.) is more than twice as long as the crown (45 mm.), and is convex externally, but more or less flattened internally. A shallow median groove is present on the distal one-third of the external surface of the strongly compressed root. The maximum diameter of the root is 35 mm. and the transverse diameter is 23 mm.

An isolated left I2 (No. 4675, U. S. N. M.) has a relatively long, backwardly curved and laterally compressed crown. The crown is also curved slightly inward from base to apex. The enamel on the crown is ornamented with anastomosing vertical striae. The anterior carina is rather sharp and extends the full height of the crown, but the posterior carina is less distinct, especially on the proximal half of this edge. The root is fully three times as long as the crown. It is convex externally, somewhat flattened internally, and tends to curve slightly outward from base of crown to extremity. A broad median groove is present on the external surface of the laterally compressed distal one-third of this root. The maximum antero-posterior diameter of the root is 38 mm. and the maximum transverse diameter is 28 mm.

The third incisor in situ in the left premaxillary of the skull (No. 4674, U. S. N. M.) lacks the internal surface of the crown. An isolated right I3 of another individual (No. 12261, U. S. N. M.) furnishes the peculiarities of the root. The laterally compressed crown of I3 is larger than that of I2. The high enamel-covered crown of the isolated right I3 (No. 12261, U. S. N. M.) is compressed from side to side, striated vertically with anastomosing ridges, especially so on the internal surface, and is curved backward and also slightly inward. The anterior carina is more distinct than the hinder carina, and both extend the full height of the crown. The root is more than twice as long as the crown. A median groove, which is broader on the external than on the internal surface, extends nearly the full length of the root. The extremity of the root is strongly compressed from side to side. The maximum antero-posterior diameter of the root is 41 mm. and the maximum transverse diameter is 27.2 mm.

The right and left upper canines were found lying near the skull (No. 4674, U. S. N. M.). The right canine has the apex of the crown worn off rather squarely and the extremity of the root is complete. Considerably more of the apical portion of the crown of the left canine, however, is worn off, the abraded surface extending downward on the hinder face of the crown, and the anterior angle of the extremity of the root is broken off. The antero-posterior diameter of the laterally compressed crown of the upper canine is distinctly greater than that of the upper incisors. The rather high crown is curved backward and also slightly inward. The enamel on the crown is striated vertically with anastomosing and converging ridges. The carina on the anterior cutting edge of the right canine is denticulated for a distance of 21 mm. above its base. The carina on the hinder edge extends the full height of the crown, but is not as prominent as the anterior carina. The rather thin layer of cementum extends upward flush with the basal border of the enamel covered crown. The root is more than twice as long as the crown. The external surface of the root is convex and there is a rather shallow median longitudinal groove on the somewhat flattened internal surface. The extremity of the root is strongly compressed from side to side and is rather squarely truncated. The pulp cavity is closed. The maximum antero-posterior diameter of the root of the right upper canine is 41 mm. and the maximum transverse diameter is 28.6 mm.

Müller (1849, pl. 12, fig. 3) figures a Pm1 collected by Koch, which has a fairly large accessory denticle and a rather minute tubercle below it at the base of the hinder edge of the crown. On the laterally compressed crown of an isolated right Pm1 (No. 4675, U. S. N. M.), the enamel is ornamented with convergent vertical striae and the anterior edge is carinate. The basal borders of the crown of this tooth are incomplete, the apex is
missing, and the basal accessory denticles on the hinder edge are broken off. The root is complete and is strongly attenuated distally. A median lengthwise groove, which is much deeper on the outer than on the inner surface, characterizes the root of this tooth. The maximum antero-posterior diameter of the root is 36.5 mm. and the maximum transverse diameter is 23.3 mm.

The left Pm1 in situ in the skull (No. 4674, U. S. N. M.) has the apex of the crown worn off. The detached right Pm1 found near the skull (No. 4674, U. S. N. M.) has the crown almost entirely worn off and the internal surface of the root is weathered. The dimensions of the root and of the basal portion of the crown are similar to those of the above described right Pm1 (No. 4675, U. S. N. M.).

The left Pm2 in situ in the skull (No. 4674, U. S. N. M.) has a fairly complete crown, but the apex of the principal cusp and the apices of the anterior accessory denticles are abraded. This premolar has a high principal cusp, and three accessory denticles on both the anterior and the posterior cutting edges. The uppermost accessory denticle on the hinder cutting edge is somewhat nearer the apex of the principal cusp than the corresponding denticle on the anterior cutting edge. The basal hinder accessory denticle is bent outward and forward. The enamel on the crown of Pm2 is ornamented with anastomosing vertical striae and these striae extend over upon the surfaces of the accessory denticles. The striae on the external surface of the crown are coarser than those on the internal surface. No cingulum is developed on either the inner or the outer basal borders of the crown. The maximum transverse diameter of the anterior root is 26 mm. and the corresponding measurement of the posterior root is 35 mm.

The anterior half of the crown of the isolated left Pm2 (No. 12261, U. S. N. M.), including the principal cusp and the accessory denticles on the anterior cutting edge, as well as the anterior portion of the upper half of the anterior root are destroyed. The measurements of this tooth correspond quite closely with those of the premolar in situ in the skull. The basal accessory denticle on the hinder cutting edge of the crown has a distinctly carinate edge. This denticle is bent outward and forward. The cutting edges of the two remaining denticles on the hinder edge of the crown are creneled. The vertical anastomosing striae on the enamel of the external face of the crown extend over upon the accessory denticles. The hinder root is larger than the anterior root and is separated from the latter by a maximum interval of 12 mm. The distal ends of the two roots are strongly attenuated and are slightly divergent.

The left Pm3 in situ in the skull (No. 4674, U. S. N. M.) is complete, with the exception of the abraded apices of the principal cusp, of the three uppermost anterior accessory denticles and of the two uppermost hinder accessory denticles. This premolar is the largest of the upper cheek teeth. Pm3 has a high principal cusp, and four accessory denticles on the anterior cutting edge and a like number on the hinder cutting edge. The uppermost denticle on the anterior edge is farther removed from the apex of the principal cusp than is the corresponding denticle on the hinder edge. The enamel on the crown of Pm3 is ornamented with vertical anastomosing striae, the striae being somewhat coarser on the external than on the internal surface. No cingulum is developed. The hinder root is somewhat larger than the anterior root, the maximum transverse diameter of the former being 37 mm. and the corresponding measurement of the latter 31 mm.

The hinder upper cheek teeth, Pm2 to M2, form a closed series, and each has two roots.

The fourth upper premolar (pl. 2, fig. 1) has been artificially implanted in the skull (No. 4674, U. S. N. M.), the corresponding portion of the left maxillary having been destroyed. The apex of the crown of Pm4 does not project ventrally as far as that of Pm2, and the crown as a whole is somewhat smaller than that of the latter. The anterior cutting edge is destroyed and the apex of the principal cusp is abraded. At least two
accessory denticles were present on the anterior cutting edge. There are three denticles on the hinder cutting edge. The enamel on the crown is striated vertically with anastomosing ridges. No cingulum is developed on either the inner or the outer basal borders of the crown. The hinder root is somewhat larger and also distinctly wider transversely than the anterior root, the maximum transverse diameter of the former being 33 mm. and the corresponding measurement of the latter is 21 mm.

The left upper molar artifically implanted in the skull (No. 4674, U. S. N. M.) is not in its correct position (pl. 2, fig. 1), since it is actually M1 and not M2. The crown of M1 is noticeably smaller than that of Pm4. Although the crown of the left M1 is greatly abraded, vestiges remain of the principal cusp as well as of two accessory denticles on the hinder cutting edge and one on the anterior cutting edge. The internal surface of the upper portion of both roots is abraded. The crown of the detached right M1 (No. 4674, U. S. N. M.) is almost entirely worn off, a narrow strip of the external basal border being the only enamel preserved. The internal surface of both roots of this molar are likewise abraded for a distance of 15 mm. below the crown. Commencing at a point 18.5 mm. below the enamel crown, the two roots are separated for a distance of 17 mm. by a maximum interval of 5.5 mm. Below this interval the two roots are ankylosed together. The transverse diameter of these roots increases rather abruptly below the crown. The maximum transverse diameter of the anterior root is 20.7 mm., and the corresponding measurement of the posterior root is 22.8 mm.

The detached right M2 (No. 4674, U. S. N. M.) is almost entirely destroyed by wear. The internal surfaces of the anterior and posterior roots are worn upward for about half their length, the abraded surface of the anterior root being strongly oblique in relation to the antero-posterior axis of the crown. Commencing at a point 22.5 mm. below the enamel crown, the two roots are separated for a distance of 22 mm. by a maximum interval of 7 mm. Below this interval the two roots are ankylosed together. The maximum transverse diameter of the anterior root is 23.5 mm., and the corresponding measurement of the posterior root is 19.7 mm.

A rather small single-rooted tooth found near the skull and the left mandible (No. 4674, U. S. N. M.) is tentatively identified as the left II. The apical portion of the crown is damaged and the distal end of the root is missing. The external surface of the root is weathered and the internal surface is partially encrusted with bone. As compared with the other incisors, the crown is rather broad antero-posteriorly in proportion to its height, strongly recurved backward, and conspicuously compressed from side to side. The enamel surface of the crown is striated vertically with anastomosing ridges. The basal half of the carina on the anterior cutting edge is strongly denticulated. The root is laterally flattened and is relatively slender.

The second lower incisor has been figured by Koch (1851, pl. 7, fig. 3).

The isolated right I3 (No. 4675, U. S. N. M.) has the apex of the crown worn off, the enamel on the basal half of the anterior face of the crown is missing, and the extremity of the root is broken off. The high enamel crown is compressed from side to side, striated vertically with anastomosing ridges, and is curved backward and slightly inward. The anterior carina is better developed than the hinder carina, the latter being restricted to the apical half of the posterior edge. The basal border of the enamel crown is distinctly emarginate. The root of this tooth is much larger and is less curved than those of the upper incisors, but the crown is bent backward at a sharper angle from the root. A median longitudinal groove, which is deeper on the internal than on the external surface, is present on the opposite sides of the root. The pulp cavity of the root is completely closed. The maximum antero-posterior diameter of the root is 45.5 mm. and the maximum transverse diameter is 30.5 mm.
The lower canine does not appear to be represented among the teeth collected by Schuchert. The canine (pl. 8, fig. 2) in situ in the right mandible (No. 13690, U. S. N. M.) is incomplete; the apex of the crown is destroyed and the enamel on both sides of the hinder third of the crown is missing. The enamel is striated with vertically anastomosing ridges, the striae on the internal face being coarser than those on the external face. A prominent carina constitutes the anterior cutting edge of the crown. The maximum antero-posterior diameter of the root of this tooth is 41 mm. and the transverse diameter is 27.5 mm.

The high crown of the left Pm1 (No. 12261, U. S. N. M.) has a prominent carina on the anterior cutting edge above the two basal accessory denticles, which incline in the direction of the principal cusp. The laterally compressed crown of this tooth is curved backward, and also slightly inward, from base to apex. On the hinder edge a weak carina is present on the apical half of the crown, but no accessory denticles are developed. The enamel on the crown is striated vertically with anastomosing and converging ridges, the latter being somewhat coarser on the external than on the internal surface. The roots are united by a thin isthmus for about half their length and their distal extremities are not widely separated. The maximum transverse diameter (27.7 mm.) of the anterior root is slightly greater than that (25.5 mm.) of the hinder root.

The entire principal cusp is destroyed on the left Pm2 found near the mandible (No. 4674, U. S. N. M.). All of the anterior cutting edge is missing with the exception of a large basal accessory denticle and a minute tubercle below the latter. On the hinder cutting edge of the crown, there are at least four sharp-edged accessory denticles, the largest being near the principal cusp and the smallest at the base of this edge. When viewed from behind, the crown is seen to curve inward from base to apex. The enamel on the crown is striated vertically with anastomosing and converging ridges, the latter being somewhat coarser on the internal than on the external surface. No cingulum is developed on either the inner or the outer basal borders of the crown. The two roots of this lower premolar are not united by an osseous isthmus, but are separated by a maximum interval of 17.5 mm. Each root is noticeably expanded transversely at a level about 10 mm. below the crown and each exhibits a strong distal attenuation. The maximum transverse diameter of the anterior root is 29.6 mm. and the maximum transverse diameter of the posterior root is 34.4 mm. The hinder lower cheek teeth, Pm3 to M3, form a closed series.

The alveoli in the left mandible (No. 4674, U. S. N. M.) indicate that Pm3 is nearly as large as Pm2. An isolated Pm3 has been figured by Müller (1849, pl. 22, fig. 1). The apices of the principal cusp and of the four accessory denticles on the anterior cutting edge of the crown of this tooth are abraded. The basal and the uppermost denticles are directed upward, while the two middle ones curve more forward than upward. There are four large denticles on the hinder cutting edge. The enamel on the crown is striated vertically with anastomosing ridges. The two roots of this premolar are strongly curved, their distal ends probably being closely approximated.

The Pm5 (pl. 8, fig. 5), which was dislodged when the hinder end of the right mandible (No. 13690, U. S. N. M.) was split longitudinally, lacks the ends of both roots. The apices of the principal cusp and of three of the accessory denticles on the anterior cutting edge of the crown are abraded. Four accessory denticles, in addition to an incipient denticle at the base of the anterior edge of the principal cusp, may have been present originally on the anterior cutting edge of the crown, if the worn basal angle was occupied by a denticle. These denticles are slightly smaller than four of the five accessory denticles on the hinder cutting edge of the crown, the basal one of the latter being quite small. On the external face of the crown the enamel is almost entirely worn off on the three lower denticles on the hinder cutting edge and also on the lower two-fifths of the anterior border, including the lower one of the three large accessory denticles. The uppermost denticle on the hinder
cutting edge is fully 7 mm. nearer the apex of the principal cusp than the corresponding denticle on the anterior cutting edge. The enamel on both sides of the crown is relatively smooth and is faintly striated vertically with anastomosing ridges.

The fourth lower premolar (fig. 3) is in situ in the left mandible (No. 4674, U. S. N. M.). The lower portion of the anterior cutting edge as well as the anterior third of the outer enamel surface of this tooth are destroyed. This tooth is the largest of the lower cheek teeth. The distance from the external alveolar margin to the apex of the principal cusp is 125 mm. There are five large accessory denticles on the hinder cutting edge of Pm4, the largest denticle being near the summit of the crown and the smallest at the base of this edge. Two accessory denticles are preserved on the upper portion of the anterior cutting edge. The uppermost accessory denticle on the hinder cutting edge is somewhat nearer the apex of the principal cusp than the corresponding denticle on the anterior cutting edge. The crown curves slightly inward from base to apex. The enamel on the crown is striated vertically with anastomosing ridges and no cingulum is developed. The maximum vertical diameter of the enamel on the external surface at level of the apex of the principal cusp is 50 mm. The external groove, which is located above and between the two roots, extends upward at least 35 ± mm. above the level of a line drawn between the anterior and posterior angles of the base of the crown. Both roots are expanded transversely between the base of the crown and the alveolar margin of the mandible.

The first lower molar is not represented among the isolated teeth in the collection made by Schuchert.

The anterior portion of the crown of an isolated left M2 (No. 4675, U. S. N. M.) is greatly worn, the principal cusp and most of the uppermost accessory denticle on the hinder cutting edge are worn off, and the external face of the anterior root is worn off obliquely for a distance of 36 mm. below the enamel crown. The enamel on the crown is relatively smooth. Three accessory denticles and a minute basal tubercle are present on the hinder cutting edge. No cingulum is developed on either the inner or outer basal borders of the crown. The two roots are attenuated distally and are closely appressed throughout their length. The anterior root is at least 19 mm. longer than the posterior root and is curved backward. The groove on the anterior face of the anterior root is quite deep. The maximum transverse diameter of the anterior root is 24.9 mm. and the corresponding measurement of the hinder root is 21.6 mm.

Table 5—Measurements (in millimeters) of premaxillary and maxillary tooth

<table>
<thead>
<tr>
<th></th>
<th>M2</th>
<th>M1</th>
<th>Pm3</th>
<th>Pm2</th>
<th>Pm1</th>
<th>C</th>
<th>I3</th>
<th>I2</th>
<th>I1</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R.</td>
<td>R.</td>
<td>L.</td>
<td>L.</td>
<td>L.</td>
<td>R.</td>
<td>R.</td>
<td>L.</td>
<td>L.</td>
</tr>
<tr>
<td>Maximum length of tooth, crown plus root</td>
<td>71</td>
<td>74^1</td>
<td>86^1</td>
<td>86^1</td>
<td>156.6</td>
<td>143^1</td>
<td>152^1</td>
<td>160^1</td>
<td>149.5</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of crown at base</td>
<td>33.5</td>
<td>60</td>
<td>84.7</td>
<td>78.8</td>
<td>85^1</td>
<td>33^1</td>
<td>41.3</td>
<td>37.5</td>
<td>30.5</td>
</tr>
<tr>
<td>Maximum transverse diameter of crown at base</td>
<td>25</td>
<td>50</td>
<td>31.5</td>
<td>15</td>
<td>16.5</td>
<td>17</td>
<td>25.8</td>
<td>24</td>
<td>23</td>
</tr>
<tr>
<td>Vertical height of enamel crown, from level of line drawn between basal margins of anterior and posterior angles to apex of principal cusp</td>
<td>44</td>
<td>72^1</td>
<td>66.5^1</td>
<td>18^1</td>
<td>54^1</td>
<td>40^1</td>
<td>45^1</td>
<td>41^1</td>
<td>45</td>
</tr>
<tr>
<td>Distance from alveolar margin of jaw to apex of principal cusp</td>
<td>34±</td>
<td>63±</td>
<td>97</td>
<td>67.5</td>
<td>52</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

^1 Apex of principal cusp abraded.
^2 Apex of principal cusp abraded and extremity of root broken off.
The rather broad anterior face of the crown of the left M₃ found near the mandible (No. 4674, U. S. N. M.) is inclined obliquely upward and backward, and is grooved for the reception of the hinder edge of the crown of M₂. There are four accessory denticles and a minute basal tubercle on the hinder cutting edge and of these the uppermost one is nearly as large as the principal cusp. All of these denticles have rather sharp cutting edges. The enamel on the crown of M₃ is relatively smooth, especially on the outer surface. Indistinct vertical striæ are present on the inner surface of the crown. A vestige of the cingulum persists at the postero-internal end of the crown. The two roots of this molar are attenuated distally and are not united by an isthmus. They diverge distally. The maximum transverse diameter of the anterior root is 24 mm. and the corresponding measurement of the hinder root is 19.4 mm. The M₃ figured by Emmons (1846, pl. 2, fig. 3) likewise has, in addition to the principal cusp, five accessory denticles on the hinder cutting edge.

### Table 6—Measurements (in millimeters) of mandibular teeth

<table>
<thead>
<tr>
<th>M₃</th>
<th>M₂</th>
<th>M₁</th>
<th>Pm₃</th>
<th>Pm₂</th>
<th>Pm₁</th>
<th>C</th>
<th>M₂</th>
<th>M₁</th>
<th>H</th>
<th>I</th>
</tr>
</thead>
<tbody>
<tr>
<td>L.</td>
<td>R.</td>
<td>L.</td>
<td>R.</td>
<td>L.</td>
<td>R.</td>
<td>L.</td>
<td>R.</td>
<td>L.</td>
<td>L.</td>
<td>L.</td>
</tr>
<tr>
<td>No. 4674</td>
<td>No. 4679</td>
<td>No. 4674</td>
<td>No. 13990</td>
<td>No. 4674</td>
<td>No. 13990</td>
<td>No. 4674</td>
<td>No. 13990</td>
<td>No. 4674</td>
<td>No. 4675</td>
<td>No. 13990</td>
</tr>
</tbody>
</table>

- Maximum length of tooth, crown plus root .......... 104 105.5
- Maximum antero-posterior diameter of crown at base .......... 47.2 43.2
- Maximum transverse diameter of crown at base .......... 85 + 82 78.7 42 46 33 × 35 + 40 + 31
- Vertical height of enamel crown, from level of line drawn between basal margins of anterior and posterior angles to apex of principal cusp .......... 21.4 17 + 23.5 25.8 19 25 17 23 ± 25 23 19.3
- Distance from alveolar margin of jaw to apex of principal cusp .......... 37 83 69 + 57.5 52

¹ Apex of principal cusp abraded.
² Apex of principal cusp abraded and extremity of root broken off.

The cheek teeth of Basilosaurus cetoides differ from those of Prozeuglodon isis in the following particulars: (1) Pm₂ and Pm₃ are closely approximated; (2) the hinder upper cheek teeth, Pm₂ to M₂, form a closed series; (3) Pm₃ is the largest of the upper cheek teeth; (4) the crown of Pm₁ is more molariform than caniniform in appearance, and (5) Pm₄ is the largest of the lower cheek teeth.

**HYOID BONES**

The hyoid apparatus (No. 4674, U. S. N. M.) of Basilosaurus cetoides consists of a median hexagonal element, the basihyal, from which two pairs of cornua extend upward, outward, and backward. The ventral surface (fig. 8) of the dorso-ventrally compressed basihyal is relatively flat, while the fore and hinder borders of the dorsal surface exhibit a rather deep concave side-to-side curvature. Since the obliquely truncated posterolateral angles of the basihyal are roughened and depressed for the ligamentous attachment of the lower pair of hyoids, the thyrohyals, it is obvious that they did not come in contact with one another on the middle line of the hinder end. The left thyrohyal (fig. 9), which is complete, has a conspicuously expanded anterior end and a laterally flattened
curved shaft, but its free or laryngeal extremity is not enlarged. The right thyrohyal is restored. The upper cornua were attached to the rostral end of the basihyal. The ceratohyal, if present, were very short and probably cartilaginous. The anterior long curved bone presumably represents the fused epihyal and stylohyal. The caudal extremity of this laterally flattened bone is expanded and appears to have had a ligamentous connection with the paroccipital process of the skull.

**Table 7—Measurements (in millimeters) of the hyoid bones**

<table>
<thead>
<tr>
<th>Description</th>
<th>Measurement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Greatest length of left thyrohyal</td>
<td>225</td>
</tr>
<tr>
<td>Greatest diameter of left thyrohyal, anteriorly</td>
<td>51.5</td>
</tr>
<tr>
<td>Greatest diameter of left thyrohyal, posteriorly</td>
<td>17.5</td>
</tr>
<tr>
<td>Greatest length of basihyal</td>
<td>87</td>
</tr>
<tr>
<td>Greatest transverse diameter of basihyal near middle</td>
<td>94</td>
</tr>
<tr>
<td>Greatest length of left fused epihyal and stylohyal</td>
<td>340</td>
</tr>
<tr>
<td>Greatest diameter of left fused epihyal and stylohyal, anteriorly</td>
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</tr>
<tr>
<td>Greatest diameter of left fused epihyal and stylohyal, posteriorly</td>
<td>26</td>
</tr>
<tr>
<td>Least diameter of left fused epihyal and stylohyal, posteriorly</td>
<td>17.6</td>
</tr>
</tbody>
</table>

**Vertebrae**

The fore part of the skeleton (pl. 1, A) on exhibition in the U. S. National Museum was reconstructed from a consecutive series of 7 cervical, 15 dorsal, and 1 lumbar vertebrae belonging to one individual (No. 4675, U. S. N. M.), and the hinder part from a consecutive series consisting of 12 lumbar, 2 sacral, and 21 caudal vertebrae belonging to another
individual (No. 12261, U. S. N. M.) of approximately the same size. As mounted, the skeleton, including the skull, measures 54 feet or 16.46 meters in a straight line and 55 feet following the curvature of the vertebral column. That this species occasionally attained a somewhat larger size is shown by the occasional occurrence of unusually large lumbar vertebrae approximating 18 inches (457 mm.) in length (Buckley, 1846, p. 128). The largest lumbar vertebrae in the first collection made by Koch measured 16 inches 6 lines (419 mm.) according to Müller (1849, p. 22). The largest lumbar vertebra (No. 12261, U. S. N. M.) in the mounted skeleton, however, measures 405 mm. in length. The conspicuous elongation of the centra of the six hinder dorsals, all of the lumbar, and the anterior caudals, as well as the separation of the post- and pre-zygapophyses of successive vertebrae by increasing intervals proportional to the length of the centrum serve to emphasize the aberrant specialization of this genus.

Cervical Vertebrae

A consecutive series of seven cervical vertebrae (fig. 10) belonging to one individual (No. 4675, U. S. N. M.), as well as the atlas, axis, and third cervical associated with the skull (No. 4674, U. S. N. M.) were available for study. The five anterior cervical vertebrae are curiously interlocked. A strong hypapophysis projecting backward from the ventral portion of the atlas almost touches the under surface of the axis. The neural spine of the axis overhangs the atlas in front and projects backward above the neural spines of the third and fourth cervicals. The ventral transverse processes (parapophyses) of the third, fourth, and fifth cervicals have a slender ventral projection which is directed downward and forward. The sixth cervical has elongated ventral transverse processes that are directed more downward than outward. These processes are not developed on the seventh cervical. The neck is shortened and the transition between the lengths of the centra of the hinder cervicals and the anterior dorsals is less abrupt than in Zugorhiza kochii. The cervical series comprised approximately 2.4 per cent of the total length of the skeleton. This computation is based on the mounted skeleton, in which the vertebrae are separated by intervals arbitrarily assumed to represent the original amount of intervertebral substance. There is thus an unknown degree of error.

Before taking up the peculiarities of the cervical vertebrae, it is important to note that the three cervical vertebrae and the manubrium associated with the skull (No. 4674, U. S. N. M.) are considerably larger than the corresponding portions of the skeleton (No. 4675, U. S. N. M.) utilized in the reconstruction. For instance the measurements of the third cervical vertebra of Nos. 4674 and 4675 U. S. National Museum are, respectively: Transverse diameter of anterior face of centrum, 107 and 88.9 mm., and vertical diameter of anterior face of centrum, 101 and 90 mm.

Atlas—Transverse processes (fig. 11) broad, directed strongly backward and perforated at base by large vertebrarterial canal; upper and lower outer angles of each process thickened, dorsal edge thin, and ventral edge thickened; dorsal foramen for first cervical nerve smaller than vertebrarterial foramen at base of transverse process; hypapophysis (fig. 12) long and pointed; anterior articular facets for occipital condyles sloping obliquely forward and upward; and vertical diameter of right posterior articular facet, 68 mm. One atlas (No. 4675, U. S. N. M.) is complete, but the other atlas (No. 4674, U. S. N. M.) is weathered.

The large size of the vertebrarterial foramina on all of the cervical vertebrae may indicate that the vertebral arteries have already taken over the function of supplying the brain. Boeninghaussen (1903, pp. 152-155) has shown that the arterial blood-supply reaches the brain in Phocaena phocaena and presumably also in the other odontocetes solely through the pair of enormously enlarged arteriae meningeae spinalae. Since these arteries enter the cranium through the non-compressible spinal canal, the blood-supply of the brain is not affected by any pressure disturbance while submerged.
Fig. 10—*Basilosaurus cetoides* (Owen). Lateral view of cervical series and of 1st dorsal vertebra, No. 4675, United States National Museum. ×1. *af*, anterior demifacet for capitulum of rib; *ct*, facet for tuberculum of rib; *h yp.*, hypapophysis; *nz.*, neural spine; *pf.*, posterior demifacet for capitulum of rib; *pz.*, postzygapophysis; *tr.*, transverse process. Upper Eocene, upper Jackson formation, Alabama.
Axis—Transverse processes short, directed more backward than outward, quite thin distally, and perforated at base by large vertebrarterial canal; anterior articular facets (fig. 13) slope obliquely upward and backward; odontoid process blunt and rounded; neural spine unusually large, conspicuously thickened at the base, and has concave posterior face, a crest-like anterior edge, and an obliquely flattened ventro-anterior angle; and rather small postzygapophyses. The greatest diameter of the vertebrarterial canal in left transverse process is 18.5 mm. One axis (No. 4675, U. S. N. M.) is complete except for restored left transverse process, but the other axis (No. 4674, U. S. N. M.) is damaged.

Fig. 11—*Basilosaurus cetoides* (Owen). Anterior view of atlas, No. 4675, United States National Museum. ×§. hyp., hypapophysis; tr., transverse process. Upper Eocene, upper Jackson formation, Alabama.

Fig. 12—*Basilosaurus cetoides* (Owen). Lateral view of atlas, No. 4675, United States National Museum. ×§. Upper Eocene, upper Jackson formation, Alabama.

Fig. 13—*Basilosaurus cetoides* (Owen). Anterior view of axis, No. 4675, United States National Museum. ×§. Upper Eocene, upper Jackson formation, Alabama.

Third Cervical—Articular facets of prezygapophyses convex, sloping obliquely inward; postzygapophysial facets concave; prezygapophysis supported by oblique external buttress; neural spine vestigial; transverse process (fig. 10) rather long, perforated at base by a very large vertebrarterial canal, the upper bar being very thin and the lower bar thick; upper and lower outer angles of transverse process slightly thickened; a narrow projection arises near base of ventral edge of lower transverse process and slopes obliquely forward and downward; four longitudinal ridges on ventral face of centrum; and neural canal low. The third cervical in the consecutive series (No. 4675, U. S. N. M.) is complete, and the other one (No. 4674, U. S. N. M.) lacks most of its processes.

Fourth Cervical—Transverse process (fig. 10) long, thin, perforated at base by a very large vertebrarterial canal, the upper bar being very thin and the lower bar thick, the
upper outer angle thin and the lower outer angle slightly thickened; a broad plate-like projection arises from middle of lower edge of transverse process, and slopes obliquely forward and downward; neural spine quite short; postzygapophyses larger than prezygapophyses; and prezygapophysis supported by oblique external buttress. The fourth cervical (No. 4675, U. S. N. M.) is complete except for the restored left transverse process.

Fifth Cervical—Lower transverse process (fig. 10) rather long and with a broad and acute-angled projection extending forward and outward from its lower edge; the small flattened tongue-like remnant of upper transverse process apparently not connected distally with extremity of lower transverse process; prezygapophysis robust, projecting distinctly forward and supported by oblique external buttress; postzygapophysis large; neural canal somewhat higher than that of fourth cervical vertebra; and neural spine quite short. The fifth cervical (No. 4675, U. S. N. M.) is complete except for the restored right transverse process.

Sixth Cervical—Upper transverse process (fig. 10) a short broad plate, directed obliquely forward and continuous with oblique external buttress which supports prezygapophysis; outer edge of this process curved forward and united ventrally with lateral oblique crest of lower transverse process; vertebrarterial canal large; lower transverse process very long, directed more downward than outward, and has an antero-posteriorly expanded distal end; neural spine slender; and antero-posterior diameter of centrum greater than that of fifth cervical. The sixth cervical (No. 4675, U. S. N. M.) is complete except for restored right lower transverse process.

Seventh Cervical—Transverse process (fig. 10) quite robust, relatively short, directed obliquely outward and forward, continuous dorsally with oblique external buttress which supports prezygapophysis, perforated at base by large vertebrarterial canal, and has the lower outer end very thick and rounded; antero-posterior diameter of centrum slightly greater than that of sixth cervical; a small posterio-superior facet on lateral face of centrum for capitulum of first rib; pre- and post-zygapophyseal facets large and slope obliquely; neural canal higher than that of sixth cervical; and neural spine probably higher and thicker. The seventh cervical (No. 4675, U. S. N. M.) complete except for the restored roof of the neural arch and the neural spine.

| Table 8—Measurements (in millimeters) of cervical vertebra (No. 4675, U. S. N. M.) |
|-----------------------------------------------|---|---|---|---|
| Maximum vertical diameter of vertebra, tip of neural spine to ventral face of centrum | 140 | 236.5 | 133.5 | 131.5 | 133.5 | 133.5 | 133.5 |
| Antero-posterior diameter of centrum | 104 | 56 | 42 | 40.2 | 46.5 | 58.5 | 66.5 |
| Vertical diameter of centrum anteriorly | 87 | 83.5 | 90 | 93 | 87 | 97.5 | 100 |
| Transverse diameter of centrum anteriorly | 90.5 | 86.9 | 94 | 91 | 92.5 | 38.5 |
| Maximum vertical diameter of neural canal anteriorly | 69 | 45 | 35.5 | 35 | 40.5 | 53.5 | 53.5 |
| Maximum transverse diameter of neural canal anteriorly | 67.5 | 45.5 | 43 | 44.5 | 42± | 43 | 61.5 |
| Antero-posterior diameter of neural spine at base (anterior margin to hinder margin of postzygapophysis) | 98.5 | 31 | 32.5 | 33 | 38 | 38 |
| Maximum distance between outer surfaces of diapophyses | 218 | 224± | 202 | 202 |
| Maximum distance between outer surfaces of parapophyses | 306 | 173.5 | 221 | 227 | 213 | 235 | 246 |
| Least antero-posterior diameter of right pedicle of neural arch | 54 | 26.6 | 16.4 | 16.3 | 25 | 25 |
| Maximum distance between outer margins of postzygapophyses | 86± | 119 | 120.5 | 138 | 136.5 | 165 |
| Distance between tip of right postzygapophysis and tip of right prezygapophysis | 44 | 48.5 | 59.5 | 63.5 | 80.5 |

1 Posteriorly.

Dorsal Vertebrae

There are fifteen vertebrae (pl. 3) in the dorsal series (No. 4675, U. S. N. M.). Although the centrum of the fifteenth dorsal is fully four times as long as that of the first,
no marked tendency toward elongation is apparent in the seven anterior dorsals, and furthermore the centrum of the eighth dorsal is only slightly longer than that of the seventh. The centrum of the ninth dorsal, however, is conspicuously lengthened. A marked increase in the length of the centrum occurs again at the eleventh in the series. Well-developed ribs articulate with all the dorsal vertebrae with the exception of the hindermost one. On the fifteenth dorsal, however, which resembles somewhat a lumbar vertebra, the rudimentary rib seems to have been attached to the posterior angle of the extremity of the transverse process.

Anterior and posterior facets for articulation with the ribs are present on the lateral surfaces of the centra of the seven anterior dorsals, the anterior facet articulating with a portion of the head of its own rib and the hinder one with a portion of the head of the succeeding rib. The seventh dorsal is the hindermost one in the series that has a posterior facet for reception of the head of the succeeding rib. Behind the eighth in the dorsal series, the ribs articulate only with their corresponding vertebrae.

The diapophyses of the anterior dorsals arise rather high up on the side of the neural arch and gradually increase in size from the first to the eighth dorsal, being replaced behind the latter by the metapophyses (mamillary processes). On the first and second dorsals these diapophyses are directed almost horizontally outward, but on the third to eighth dorsals, inclusive, the extremities of these processes are bent upward. The diapophysis on the ninth dorsal is reduced to a small tuberosity on the side of the neural arch, while simultaneously a similar low tuberosity, the parapophysis, rises from the side of the centrum, the two providing the capitular attachment of the corresponding rib. On the tenth, eleventh, and twelfth dorsals the capitular attachment of the rib to the lateral face of the centrum is restricted to the concavity in the swollen protuberance, which on the thirteenth dorsal becomes serially homologous with the transverse processes of the lumbar vertebrae. These transverse processes progressively increase in length on the fourteenth and fifteenth dorsals.

All of the dorsal vertebrae have an unusually low and broad neural canal, which becomes progressively larger toward the hinder end of this series. The neural canals of the first and second dorsals are somewhat triangular in outline, but on the remaining dorsals the contour is transversely oval. The third, fourth, and fifth dorsals have the longest neural spines, and all of the ten anterior dorsals have relatively narrow neural spines. The antero-posterior diameter of the neural spine of the eleventh dorsal, however, is fully one-third greater than that of the neural spine of the tenth dorsal. The large metapophyses, which gradually increase in height from the ninth to the hinder end of the dorsal series, arise anteriorly from the side of the neural arch, from which they project forward and upward. Furthermore, the outward inclination of these metapophyses becomes progressively more oblique from the ninth to the posterior end of the dorsal series. It is quite obvious that the pre- and post-zygapophyses of the dorsal vertebrae behind the eighth in the dorsal series can not articulate with one another, and it is possible also that the eighth does not articulate with the ninth dorsal. The prezygapophyseal facets are represented on the anterior dorsals by a flattened surface on the angle formed by the junction of the pedicle, the roof of the neural arch, and the base of the diapophysis.

On the first to twelfth dorsals, inclusive, well-developed flattened articular surfaces corresponding in position to postzygapophyseal facets are formed at the base of the neural spine on the hinder angles of the roof of the neural arch, and these surfaces are separated by a notch that is progressively reduced toward the hinder end of the series. On the thirteenth dorsal, these flattened surfaces have lost their distinctive character, although they persist in reduced condition on the fifteenth dorsal. Behind the seventh in the dorsal series, the postzygapophyseal facets are not embraced by the prezygapophyseal facets. Even in the case of the seven anterior dorsals, where the postzygapophyses project back-
ward above the prezygapophyses and lie within the lateral protuberances formed by the diapophyses, the articular connections appear to be very poorly coadjusted, as compared with those of most terrestrial mammals.

The dorsal series comprised approximately 19.4 per cent of the total length of the skeleton.

First Dorsal—Low neural arch (fig. 10) inclined forward, its pedicles being unusually thick transversely and having a concave anterior edge and a concave posterior edge; diapophysis projects outward and very little forward, but is extended forward beyond level of anterior end of centrum; an unusually large facet on lateral and under surface of diapophysis for tuberculum of first rib; antero-posterior diameter of distal end of diapophysis is 59.5 mm.; upper portion of neural arch and entire neural spine missing; centrum distinctly wider than long; anterior and posterior ends of centrum slightly concave; and a distinct facet for capitulum of first rib on lateral face of centrum at antero-superior angle and a similar one for capitulum of second rib at postero-superior angle.

Second Dorsal—Pedicles of neural arch rather thick transversely; hinder edge of each pedicle slopes obliquely forward from posterior end of centrum while the abruptly rising anterior edge is set back at base 19 mm. from anterior end of centrum; antero-posterior diameter of upper portion of neural arch unusually great in proportion to height of spine; diapophysis projected forward and outward, expanded distally and extended forward beyond level of anterior end of centrum; distal expansion of diapophysis furnished with lateral articular surface for tuberculum of second rib; antero-posterior diameter of distal end of diapophysis, 45 + mm.; neural spine (distal portion missing) probably low and rapidly attenuated distally; prezygapophysial facets merely elongated flattened areas, depressed below convexly curved upper surfaces of diapophyses; postzygapophyses widely separated and project backward beyond level of hinder end of centrum; a large deep-pitted facet for capitulum of second rib on lateral face of centrum at antero-superior angle and a similar one for capitulum of third rib at postero-superior angle; and anterior end of centrum concave and posterior end flat.

Third Dorsal—Pedicles of neural arch quite thick transversely, very little inclined forward; anterior edge of each pedicle set back at base farther from anterior end of centrum than hinder edge is from posterior end of centrum; diapophysis projected forward and slightly outward, extended forward beyond level of anterior end of centrum and has a large expanded lateral facet for tuberculum of third rib; antero-posterior diameter of distal end of diapophysis, 64, mm.; neural spine quite high, slender, and inclined slightly backward; prezygapophysial facets concave and depressed below level of strongly concave curvature of inner face of diapophyses; postzygapophyses project backward barely to level of posterior end of centrum, but distance between their outer margins is reduced; antero-superior facet on lateral surface of centrum for capitulum of third rib and postero-superior facet for capitulum of fourth rib rather large; lateral surface of centrum concave; and anterior and posterior ends of centrum slightly concave.

Fourth Dorsal—Pedicles of neural arch relatively thin transversely, but widened antero-posteriorly and set back at base from anterior end of centrum; diapophysis projected strongly outward and forward, expanded distally, and extended forward beyond level of anterior end of centrum; distal expansion of diapophysis, which is furnished with an unusually long lateral facet for tuberculum of fourth rib, is twisted obliquely inward and looks more forward than outward; antero-posterior diameter of distal end of diapophysis, 60 mm.; neural spine quite high, even more slender than that of third dorsal; distal half of neural spine bowed forward and extremity rounded; antero-posterior diameter of neural spine distally, 39.5 mm.; prezygapophysial facets slightly concave and slightly depressed below strongly curved inner surface of diapophyses; postzygapophyses terminate on a
level with posterior end of centrum; a large deep antero-superior facet on lateral surface of centrum for capitulum of fourth rib and a smaller postero-superior facet for capitulum of fifth rib; and anterior and posterior ends of centrum concave.

Fifth Dorsal—Pedicles of neural arch relatively thin transversely, widened antero-posteriorly, and set back at base from anterior end of centrum; diapophysis projected forward and very little outward, and has a large antero-posteriorly expanded extremity, which extends forward beyond anterior end of centrum; antero-posterior diameter of distal end of diapophysis, 82 mm.; distal expansion of diapophysis not twisted obliquely and its lateral articular surface for tuberculum of fifth rib is more rounded; neural spine rather high and inclined slightly backward, its antero-posterior width being greater than that of the fourth dorsal; prezygapophyseal facets relatively flat, reduced in extent, and apparently continuous with curved inner surface of diapophyses; postzygapophyses project backward to level of posterior end of centrum; antero-superior facet on lateral surface of centrum for capitulum of fifth rib rugose and smaller than that on fourth dorsal; and postero-superior facet for capitulum of sixth rib reduced.

Sixth Dorsal—Pedicles of neural arch relatively thin transversely, inclined slightly forward, widened antero-posteriorly, and set back at base from anterior end of centrum; diapophysis projected forward beyond level of anterior end of centrum and but very little outward; large expanded extremity of diapophysis not twisted obliquely and furnished with convex lateral articular surface for tuberculum of sixth rib; antero-posterior diameter of distal end of diapophysis, 76 mm.; distal two-thirds of neural spine missing; prezygapophyseal facets not sharply defined, but apparently continuous with curved inner surface of diapophysis; postzygapophyses project backward beyond level of posterior end of centrum; antero-superior facet on lateral surface of centrum for capitulum of sixth rib rugose and larger than postero-superior facet for capitulum of seventh rib.

Seventh Dorsal—Pedicles of neural arch widened antero-posteriorly and set back at base from anterior end of centrum; diapophysis projected forward beyond level of anterior end of centrum and but very little outward; large expanded extremity of diapophysis twisted somewhat obliquely and furnished with rounded lateral articular surface for tuberculum of seventh rib; antero-posterior diameter of distal end of diapophysis, 82 mm.; distal three-fourths of neural spine destroyed; prezygapophyseal facets reduced, not sharply defined and apparently continuous with curved inner surface of diapophyses; postzygapophyses project backward beyond level of posterior end of centrum; antero-superior facet on lateral surface of centrum for capitulum of seventh rib deep, pitted, and larger than postero-superior facet for capitulum of eighth rib.

Eighth Dorsal—Pedicles of neural arch widened antero-posteriorly and set back at base from anterior end of centrum; diapophysis projected forward beyond level of anterior end of centrum and but very little outward; lateral articular surface on large expanded extremity of diapophysis for tuberculum of eighth rib roughened and nearly vertical; antero-posterior diameter of distal end of diapophysis, 94 mm.; distal two-thirds of neural spine (apex missing) abruptly constricted above basal third; prezygapophyseal facets narrow, elongate, and slightly depressed below curved inner surface of diapophyses; postzygapophyses project backward beyond level of posterior end of centrum; antero-superior facet on lateral surface of centrum for capitulum of eighth rib rather large, quite deep, and rugose; and no postero-superior facet for capitulum of ninth rib.

Ninth Dorsal—Pedicles of neural arch, as compared with those of eighth dorsal, abnormally widened antero-posteriorly, very slightly set back at base from anterior end of centrum; metapophysis large, projected forward and strongly upward, and extended forward beyond level of anterior end of centrum; inner surface of metapophysis curves obliquely upward; diapophysis reduced to a rounded tuberosity on lateral surface of
neural arch and the paraphysis to a rugose depression on lateral surface of centrum, these two facets being separated by an interval about equivalent to transverse diameter of the rib; distal half of neural spine destroyed; prezygapophysial facets greatly reduced, possibly missing; hinder ends of postzygapophyses do not come within 55 mm. of level of posterior end of centrum; and no antero-superior facet for rib on lateral surface of centrum.

*Tenth Dorsal*—Pedicles of neural arch unusually widened antero-posteriorly and slightly set back at base from anterior end of centrum; metapophysis large, projected forward and upward, but not extended forward beyond level of anterior end of centrum; inner surface of metapophysis slopes obliquely upward; vestigial diapophysis on lateral surface of right pedicle of neural arch and rudimentary parapophysis on lateral surface of centrum coalesced, the raised margins of the combined processes encircling an irregular deep hollow in which the head of the tenth rib is lodged; on the left side the vestigial diapophysis is separated from the rudimentary parapophysis by an interval of 13 mm.; distal expansion of neural spine extended forward; maximum antero-posterior diameter of neural spine below distal expansion is 64.5 mm.; prezygapophysial facets not developed; hinder ends of postzygapophyses do not come within 60 mm. of posterior end of centrum.

*Eleventh Dorsal*—Pedicles of neural arch relatively short at base in proportion to length of centrum and not set back so far from anterior end of centrum as from posterior end; neural canal low and broad; metapophysis large and broad, projected forward and upward, but not extended forward to level of anterior end of centrum; neural spine very broad and nearly vertical, its expanded distal end being extended forward; antero-posterior diameter of neural spine at distal end is 105 mm.; no prezygapophysial facets; postzygapophysial facets reduced and their hinder ends do not come within 75 mm. of level of posterior end of centrum; transverse process (parapophysis) barely projects beyond level of lateral face of centrum, and head of eleventh rib is lodged in the deep pit in its center.

*Twelfth Dorsal*—Pedicles of neural arch widened antero-posteriorly, but relatively short in proportion to length of centrum, and placed slightly nearer the anterior than the posterior end of the centrum; neural canal very low and broad; metapophysis large and broad, projected forward and upward, but not extended forward to level of anterior end of centrum; neural spine very broad, nearly vertical, and less expanded distally than on the eleventh dorsal; antero-posterior diameter of neural spine at distal end is 97 mm.; no prezygapophysial facets; postzygapophysial facets reduced and their hinder ends do not come within 100 mm. of level of posterior end of centrum; transverse process (parapophysis) forms low tuberosity on lateral surface of centrum and head of twelfth rib is lodged in deep cavity in its center.

*Thirteenth Dorsal*—Neural arch, neural spine, and metapophyses destroyed; base of right pedicle shows that it was relatively short in proportion to length of centrum; transverse process (parapophysis) projects distinctly beyond lateral surface of centrum.

*Fourteenth Dorsal*—Pedicles of neural arch relatively short in proportion to length of centrum and set back at base from anterior end of centrum; neural spine and metapophyses destroyed; transverse process (parapophysis) relatively long, wide, flattened dorso-ventrally, and furnished with distal facet for head of fourteenth rib.

*Fifteenth Dorsal*—Pedicles of neural arch relatively short in proportion to length of centrum and placed approximately in middle of centrum; metapophysis projects forward and upward, but does not reach level of anterior end of centrum; neural spine very broad antero-posteriorly, rather short, without any indication of distal expansion; antero-posterior diameter of neural spine at distal end, 112 \( \pm \) mm.; distance from hinder edge of right pedicle of neural arch at base to tip of right metapophysis, 212 mm.; hinder ends of postzygapophysial facets do not come within 80 mm. of level of posterior end of centrum; transverse process (parapophysis) relatively long, directed outward, obliquely downward,
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<td>182+</td>
<td>186.5</td>
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<tr>
<td>Maximum vertical diameter of neural canal, anteriorly</td>
<td>47±5</td>
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<td>52</td>
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<td>Maximum transverse diameter of neural canal, anteriorly</td>
<td>58</td>
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<td>89</td>
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<td>Vertical height of neural spine, ventral margin of posterior angle of roof of neural arch to distal end of neural spine</td>
<td>211</td>
<td>217</td>
<td>211</td>
<td>186±186±</td>
<td>164</td>
<td>148±175.5</td>
<td>175</td>
<td>178.5</td>
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<td>Maximum distance between outer surfaces of diapophyses</td>
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<td>Maximum distance between outer surfaces of metapophyses</td>
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<td>56.5</td>
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<td>61.5</td>
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<td>115</td>
<td>101</td>
<td>108</td>
<td>103+130+</td>
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<td>Least antero-posterior diameter of right pedicle of neural arch</td>
<td>51</td>
<td>25.5</td>
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<td>32</td>
<td>33</td>
<td>46</td>
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<td>47.5</td>
<td>50</td>
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<tr>
<td>Transverse diameter of right pedicle of neural arch</td>
<td>89</td>
<td>68</td>
<td>78.5</td>
<td>70</td>
<td>64</td>
<td>68</td>
<td>71.5</td>
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and slightly forward, flattened dorso-ventrally, and furnished with small facet for head of fifteenth rib at hinder angle of distal end.

**Lumbar and Sacral Vertebrae**

The lumbar vertebrae shown in the reconstructed skeleton (pl. 1, A) include the first lumbar (No. 4675, U. S. N. M.) associated with the dorsal series of vertebrae, and twelve consecutive lumbar vertebrae of another individual (No. 12261, U. S. N. M.). Gidley (1913, p. 650) states that:

"The bones in each of these skeletons when found were lying nearly in their natural positions, so that there was little or no chance for error in again placing the elements of the vertebral column after removal from their original bed. Moreover, the specimens admirably supplement each other, the one comprising the anterior portion [No. 4675, U. S. N. M.] of the skeleton ending just behind the thoracic region includes but one lumbar vertebra which differs in the character of the transverse processes sufficiently to indicate that it is not duplicated by the first vertebra, a lumbar, of the second specimen [No. 12261, U. S. N. M.]. Hence, if any error has been made in the total number of elements included in the vertebral column, it is that they are too few rather than too many."

The fifteen vertebrae (pls. 4–5) in the lumbar-sacral series comprise approximately 36.6 per cent of the total length of the mounted skeleton. The lengthening of the centra of the hinder dorsals, of the entire lumbar-sacral series, and of the anterior caudals, materially alters the general appearance of the skeleton as compared with that of *Zygorhiza kochii* (pl. 1, B). The relatively small head, short neck, comparatively small thorax (proportionately the same length as in *Zygorhiza kochii*), and very greatly lengthened lumbar-sacral region distinguish this skeleton from those of most Recent Cetacea. The elongation of the centra of the lumbar vertebrae is quite unusual.

The lumbar vertebrae have exceedingly long, heavy centra, and proportionately short neural arches. All of these lumbars exhibit a remarkable similarity to one another, both in form and dimensions. The centra of the largest lumbar vertebrae average about 400 mm. in length, as compared with 92 mm. for the first dorsal vertebra. The centra of these lumbar vertebrae increase very slightly in length from the anteriormost one to the eighth in the series, and from there on to the hinder end of this series they decrease slightly in length, the disparity in the lengths of the longest and the shortest centra not exceeding 20 mm. One of the most characteristic peculiarities of these lumbars is found on the ventral face of the centrum. About midway of its length, the under surface of the centrum becomes distinctly concave, and in the center of this concavity is a deep elongate fossa that is divided longitudinally by an osseous partition. This fossa is formed by the two orifices of the vascular canals that pierce the centrum in a vertical direction. No ventral keel is developed. The lateral surfaces of the centra, between the pedicle of the neural arch and the base of the transverse process, are flattened on the first to sixth lumbars, inclusive, but beginning with the seventh these areas become progressively more concave toward the hinder end of the lumbar series.

The transverse processes are relatively narrow in comparison to the length of the centrum, projecting outward, downward, and slightly forward, and distally are dorso-ventrally flattened, except in the case of the first lumbar where the distal extremities of these processes are turned upward. These transverse processes increase in length from the first to the eighth in the series. On the four anterior lumbars the fore-edge of these processes curves from the base outward and forward, while the hinder-edge is more nearly straight. On the seventh to twelfth lumbars, inclusive, these processes are rather strongly contracted near the middle of their length, noticeably widened at their distal extremities, and both edges are curved.
The pedicles of the neural arches become gradually narrower antero-posteriorly from the anteriormost lumbar to the eighth in the series, and then increase in width up to the second sacral. The neural canals of the hinder lumbars are somewhat lower than those of the anterior lumbars. When the lumbar vertebrae are arranged in serial sequence, the neural spines increase in height from the first to the seventh and then decrease in height to the thirteenth in the series. Viewed from the side, these neural spines are greatly flattened, slightly rugose at their extremities, and more or less vertical in position. The decrease in the antero-posterior diameter of the neural spine is barely perceptible in the five anterior lumbars, but behind the seventh in the lumbar series these spines become somewhat narrower.

Neither pre- nor post-zygapophyses are developed on any of the lumbars. Like in other archaeocetes, the metapophyses are large, well-developed processes, that project upward, outward, and forward from the neural arch. They do not embrace the postero-basal angle of the neural spine of the antecedent vertebra, but are separated from the latter by intervals ranging from 160 to 225 mm., and are apparently modified for the attachment of strong back muscles. One peculiarity that distinguishes these metapophyses from those of Recent Cetacea is the indentation of their anterior edges and their gradual elevation on the neurapophyses in passing from before backward. On the second lumbar the metapophyses arise mainly from the pedicles of the neural arch below the level of the top of the neural canal, and the dorsal edge of each process is at least 105 mm. above the dorsal surface of the centrum; on the hindermost lumbar they arise from the roof of the neural arch and the fore part of the pedicles, and their dorsal edges are 120 mm. above the dorsal surface of the centrum. The antero-posterior diameter of the dorsal ends of these metapophyses increases from the anteriormost to the hindermost lumbar.

The lumbars thus articulated only by the nearly circular ends of their centra, which are probably separated by somewhat thickened intervertebral cartilaginous disks. This mechanical condition must have permitted the long, slender body to move perfectly free in almost any direction, and doubtless enabled the animal to dive and turn at will.

First Lumbar—Neural arch, neural spine, both metapophyses, and left transverse process restored (pl. 4, fig. L.1); lateral surfaces of centrum eroded near each end (No. 4675, U. S. N. M.). Transverse process (parapophysis) relatively long, directed outward, obliquely downward, and slightly forward, its distal end being turned slightly upward; antero-posterior diameter of right transverse process at distal end 65 mm., and minimum antero-posterior diameter near base 104 mm.; maximum distance between outer ends of transverse processes, estimated, 440 mm.; centrum elongated, contracted near the middle and expanded at both ends; and a thin partition separates the elongated and laterally compressed ventral orifices of the dorso-ventral vascular canals.

Second Lumbar—Left transverse process restored and lateral surfaces of centrum eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch (pl. 4, fig. L.2) relatively narrow antero-posteriorly (minimum diameter of right pedicle, 104 mm.), being equivalent to less than one-third of length of centrum and placed slightly anterior to middle of centrum; elongated and laterally compressed metapophysis (mammillary process) projecting upward and slightly outward and extending forward to within 30 mm. of level of anterior end of centrum; neural spine rather broad antero-posteriorly, with rounded distal end; maximum antero-posterior diameter of neural spine near middle of its length, 133 mm.; postero-basal angle of neural spine does not come within 85 mm. of level of posterior end of centrum; relatively long transverse process (parapophysis) noticeably flattened dorso-ventrally, directed outward, obliquely downward, and rather strongly forward; antero-posterior diameter of right transverse process at distal end 108+ mm., and minimum antero-posterior diameter near base 82.5 mm.; centrum elongated, con-
tracted near the middle and expanded at both ends; and a low partition separates the laterally compressed ventral orifices of the two dorso-ventral vascular canals.

Third Lumbar—Left transverse process as well as distal half and posterior border of neural spine restored (pl. 4, fig. L 3); lateral surfaces of centrum eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch narrower antero-posteriorly than on second lumbar (minimum diameter of left pedicle, 95 mm.); laterally flattened metapophysis projecting more strongly upward and more elongated than that of second lumbar, but not extending as far forward (end of metapophysis to level of anterior end of centrum, 55 mm.), and having a nearly straight anterior edge; neural spine corresponding apparently in general outline to that of preceding lumbar; dorso-ventrally flattened transverse process (parapophysis) projecting in same direction as on preceding lumbar, but having the antero-distal angle projected farther forward; antero-posterior diameter of right transverse process at distal end 120 mm., and minimum antero-posterior diameter near base 82.5 mm.; centrum cylindrical; and a low partition separates the large ventral orifices of the two dorso-ventral vascular canals.

Fourth Lumbar—Left transverse process and distal half of neural spine restored (pl. 4, fig. L 4); lateral surfaces of centrum eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch placed nearer the middle of centrum than on the third lumbar (minimum antero-posterior diameter of left pedicle 107 mm.); elongated and laterally flattened metapophysis projecting upward and slightly outward, but not extending forward as far as that on the third lumbar (end of metapophysis to level of anterior end of centrum 80 mm.), and having a strongly concave anterior edge; neural spine nearly vertical and noticeable widened antero-posteriorly; postero-basal angle of neural spine does not come within 80 mm. of level of posterior end of centrum; transverse process (parapophysis) thin, strongly flattened dorso-ventrally, relatively long, directed outward, more forward than downward, and noticeably expanded distally; antero-posterior diameter of right transverse process at distal end, 135 mm., and minimum antero-posterior diameter near base 83 mm.; hinder end of centrum wider than that of third lumbar; and a thick partition separates the large ventral orifices of the two dorso-ventral vascular canals.

Fifth Lumbar—Left transverse process restored; lateral surfaces of centrum eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch (pl. 4, fig. L 5) relatively narrow (minimum antero-posterior diameter of left pedicle, 99 mm.); elongated and laterally flattened metapophysis projecting more upward than outward and extending farther forward than on fourth lumbar (end of metapophysis to level of anterior end of centrum, 65 mm.), and having a slightly convex dorsal edge and a deeply indented anterior edge; neural spine rather broad antero-posteriorly, inclined slightly more backward than that of the fourth lumbar and having its distal end rounded; maximum antero-posterior diameter of neural spine near middle of its height, 131 mm.; postero-basal angle of neural spine does not come within 100 mm. of level of posterior end of centrum; direction of dorso-ventrally flattened transverse process (parapophysis) approximately the same as on preceding lumbars, but less expanded distally; antero-posterior diameter of right transverse process at distal end, 112 mm., and minimum antero-posterior diameter near base, 79 mm.; centrum more cylindrical but expanded at both ends; and a thick partition separates the ventral orifices of the two dorso-ventral vascular canals.

Sixth Lumbar—All of the left and the distal half of the right transverse process restored (pl. 4, fig. L 6); lateral surfaces of centrum eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch placed almost at middle of centrum (minimum antero-posterior diameter of right pedicle, 96 mm.); elongated and laterally flattened metapophysis projecting more upward than outward, but not extending as far forward as on fifth lumbar (end of metapophysis to level of anterior end of centrum, 95 mm.), and having a slightly
convex dorsal edge and an emarginate anterior edge; neural spine not so broad anteroposteriorly as that of fifth lumbar, but has distal end truncated and posterior profile more curved; antero-posterior diameter of neural spine near middle of its height is 126 mm.; postero-basal angle of neural spine does not come within 82 mm. of level of posterior end of centrum; centrum elongated and expanded at both ends; and a thick partition separates the ventral orifices of the two dorso-ventral vascular canals.

**Seventh Lumbar**—Left transverse process and left metapophysis (pl. 4, fig. L. 7) restored; lateral surfaces of centrum eroded near each end (No. 12261, U. S. N. M.); pedicles of neural arch strongly constricted medially (minimum antero-posterior diameter of right pedicle, 91 mm.); elongated and laterally flattened metapophysis (fig. 14) projecting more upward than outward, extending forward to within 75 mm. of level of anterior end of centrum and having a convex dorsal edge and a concave anterior edge; neural spine somewhat higher and narrower antero-posteriorly than that of sixth lumbar and has a rounded distal end; antero-posterior diameter of neural spine near middle of its height, 115 mm.; postero-basal angle of neural spine does not come within 130 mm. of level of posterior end of centrum; dorso-ventrally flattened transverse process (parapophysis) relatively long, directed outward, obliquely downward, and strongly forward, and conspicuously expanded distally; antero-posterior diameter of right transverse process at distal end 134 mm., and minimum antero-posterior diameter near base 84 mm.; centrum elongated and less noticeably expanded at both ends than preceding vertebra; and a short osseous bridge separates the ventral orifices of the two dorso-ventral vascular canals.

**Eighth Lumbar**—Left transverse process restored (pl. 4, fig. L. 8); lateral surfaces of centrum eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch similar to those of seventh lumbar (minimum antero-posterior diameter of left pedicle, 93 mm.); elongated and laterally flattened metapophysis projecting more upward than outward, extending forward to within 70 mm. of level of anterior end of centrum and having a convex dorsal edge and a deeply indented anterior edge; dorso-ventrally flattened transverse process (parapophysis) similar to that of seventh lumbar; antero-posterior diameter of right transverse process at distal end, 138 mm., and minimum antero-posterior diameter near base, 78 mm.; maximum distance between outer ends of transverse processes, estimated, 480 mm.; centrum cylindrical but expanded at hinder end; and an osseous bridge separates the ventral orifices of the two dorso-ventral vascular canals.

**Ninth Lumbar**—Right and left transverse processes restored (pl. 5, fig. L. 9); lateral surfaces of centrum eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch wider antero-posteriorly than on preceding lumbar (minimum diameter of right pedicle, 102 mm.); elongated and laterally flattened metapophysis projecting more upward
than outward, extending farther forward than on the eighth lumbar (end of metapophysis to level of anterior end of centrum, 30 mm.), and having a nearly straight dorsal edge and an emarginate anterior edge; neural spine resembles that of seventh lumbar, but is truncated at distal end; antero-posterior diameter of neural spine at distal end, 101 mm.; postero-basal angle of neural spine does not come within 138 mm. of level of posterior end of centrum; centrum elongated and slightly contracted near the middle; and region of ventral orifices of dorso-ventral vascular canals destroyed.

Tenth Lumbar—Left transverse process restored; lateral surfaces of centrum eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch (pl. 5, fig. L. 10) proportionately rather short (minimum antero-posterior diameter of right pedicle, 90+ mm.); elongated and laterally flattened metapophysis projecting upward and outward, extending forward to within 70 mm. of level of anterior end of centrum, and having a nearly straight dorsal edge and a slightly curved anterior edge; neural spine quite similar to that of ninth lumbar, but having an obliquely truncated distal end; antero-posterior diameter of neural spine near middle of its height, 105 mm.; postero-basal angle of neural spine does not come within 110 mm. of level of posterior end of centrum; dorso-ventrally flattened transverse process (parapophysis) directed more outward and downward than forward, strongly contracted near the base and conspicuously expanded at the distal end; antero-posterior diameter of right transverse process at distal end, 132 mm., and minimum antero-posterior diameter near base, 86 mm.; centrum elongated and cylindrical; and region of ventral orifices of dorso-ventral vascular canals destroyed.

Eleventh Lumbar—Right and left transverse process as well as posterior end of centrum restored (pl. 5, fig. L. 11); lateral surfaces of centrum eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch wider antero-posteriorly (minimum diameter of right pedicle, 102 mm.) than those on preceding lumbar; elongated and laterally flattened metapophysis projecting upward and outward, extending forward to within 65 mm. of level of anterior end of centrum and having a slightly convex dorsal edge and a deeply concave anterior edge; neural spine shorter and somewhat broader antero-posteriorly than that of the tenth lumbar, and has a rounded distal end; antero-posterior diameter of neural spine near middle of its length, 115 mm.; postero-basal angle of neural spine does not come within 130 mm. of level of posterior end of centrum; centrum elongated, contracted near the middle, and expanded at both ends; and region of ventral orifices of dorso-ventral vascular canals destroyed.

Twelfth Lumbar—Right and left transverse processes restored (pl. 5, fig. L. 12); lateral surfaces of centrum eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch placed nearer anterior end of centrum than on the two preceding lumbars (minimum antero-posterior diameter of right pedicle, 100 mm.); elongated and laterally flattened metapophysis projecting upward and outward, extending forward to within 45 mm. of level of anterior end of centrum and having a convex dorsal edge and a deeply indented anterior edge; neural spine somewhat shorter and broader than that of eleventh lumbar, its distal end rounded and the antero-posterior contraction near its base more pronounced; maximum antero-posterior diameter of neural spine near middle of its height, 118 mm.; postero-basal angle of neural spine does not come within 128 mm. of level of posterior end of centrum; centrum elongated, contracted near the middle, and expanded at both ends; and region of ventral orifices of dorso-ventral vascular canals destroyed.

Thirteenth Lumbar—Right and left transverse processes restored (pl. 5, fig. L. 13); lateral surfaces of centrum eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch rather low (minimum antero-posterior diameter of right pedicle, 100 mm.); elongated and laterally flattened metapophysis projecting upward and outward, extending forward to within 30 mm. of level of anterior end of centrum, and having a slightly convex
dorsal edge and a straight anterior edge; neural spine rather short, very broad antero-posteriorly below rounded extremity, and contracted antero-posteriorly above its base; maximum antero-posterior diameter of neural spine near middle of its height, 138 mm.; postero-basal angle of neural spine does not come within 135 mm. of posterior end of centrum; centrum elongated, contracted near middle and expanded at both ends; and region of ventral orifices of dorso-ventral vascular canals destroyed.

First Sacral—Extremity of neural spine (pl. 5, fig. L. 14), left transverse process and portion of left metapophysis restored; lateral surfaces of centrum eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch (fig. 15) narrow in proportion to length of centrum (minimum antero-posterior diameter of right pedicle, 103 mm.); laterally flattened and conspicuously elongated metapophysis projecting upward and outward, extending forward almost to level of anterior end of centrum, and having a convex

![Fig. 15—Basilosaurus cetoides (Owen). Lateral view of 1st sacral vertebra, No. 12261, United States National Museum. X4. mp., metapophysis; tr., transverse process. Upper Eocene, upper Jackson formation, Alabama.](image1)

![Fig. 16—Basilosaurus cetoides (Owen). Lateral view of 2nd sacral vertebra, No. 12261, United States National Museum. X4. mp., metapophysis; tr., transverse process. Upper Eocene, upper Jackson formation, Alabama.](image2)

dorsal edge and an emarginate anterior edge; neural spine restored; transverse process (parapophysis) thickened dorso-ventrally, relatively long, directed outward, strongly downward, and somewhat forward; upper surface of distal end of transverse process noticeably thicker and rougher than those of preceding lumbar; antero-posterior diameter of right transverse process at distal end, 121 mm., and minimum antero-posterior diameter near middle of its length, 91 mm.; maximum distance between outer ends of transverse processes, 496± mm.; centrum elongated, contracted near middle and expanded at both ends; lateral limits of the single ventral orifice for the two rather small dorso-ventral vascular canals sharply defined; a short groove leads forward and backward from this orifice; and ventral surface of centrum concave between this median orifice and the ventral face of base of each transverse process.

Second Sacral—Left transverse process restored; lateral surfaces of centrum (pl. 5, fig. S. 2) eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch (fig. 16)
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<td>and dorsal surface of centrum</td>
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similar to those of first sacral (minimum antero-posterior diameter of right pedicle, 107 mm.); elongated and laterally flattened metapophysis projecting upward and outward, extending forward almost to level of anterior end of centrum, and having a convex dorsal edge and a nearly straight anterior edge; neural spine rather short, quite broad antero-posteriorly, and has a truncated distal end; maximum antero-posterior diameter of neural spine near distal end, 132 mm; postero-basal angle of neural spine does not come within 132 mm. of posterior end of centrum; transverse process (parapophysis) thickened dorso-ventrally, broader than that of first sacral but otherwise quite similar, and its somewhat thickened distal end is trihedral in outline; maximum antero-posterior diameter of right transverse process at distal end, 140 mm., and minimum antero-posterior diameter near base, 110 mm.; maximum distance between outer ends of transverse processes, 458 ± mm.; centrum elongated, contracted near the middle, and expanded at both ends; and a single ventral orifice for the two dorso-ventral vascular canals (transverse diameter, 22.5 mm.).

Caudal Vertebrae

Twenty-one consecutive caudal vertebrae (No. 12261, U. S. N. M.) comprise the tail of this skeleton. The hinder six caudals are relatively small, antero-posteriorly compressed, and agree so closely in general appearance with the corresponding vertebrae of Recent Cetacea (Ryder, 1887, pp. 456-459) that there is reason to believe that they were imbedded in a caudal fluke. The centra of the nine anterior caudals exhibit a very slight progressive decrease in length. From the tenth to the hinder end of this series, the centra rapidly decrease in length, the reduction in length being most obvious between the fifteenth and sixteenth caudals. The twenty-one vertebrae in the caudal series comprise approximately 34 per cent of the total length of the skeleton.

These caudal vertebrae differ from one another in the peculiarities of their processes. The anteriormost caudal differs but slightly from the hinder sacral. Of these twenty-one caudals, the anterior fourteen may have had chevron bones attached to their ventral surfaces, although but four of these bones were found associated with the skeleton.

On the anterior caudals, the transverse processes project outward and downward, with a slight inclination forward, and their origin is slightly below the middle of the side of the centrum. The second and fourth in the caudal series have unusually broad transverse processes. The transverse processes of the anteriormost caudal are approximately the same size as those of the hinder sacral. These processes diminish in length from the anteriormost caudal to the tenth in the series. The transverse processes of the sixth to tenth caudals, inclusive, are pierced at the base by a foramen. On the twelfth caudal these processes are reduced to a thin longitudinal ridge. On the thirteenth caudal, these processes have disappeared and their place is taken by a low rounded prominence. The lateral surfaces of these centra, between the pedicle of the neural arch and the base of the transverse process, are concave, the concavity becoming progressively deeper from the fifth to the twelfth caudal.

The neural spine rapidly decreases in height from the first to the fifth in the series and is represented solely by a sagittal ridge on the sixth to the ninth caudals. The neural arch is complete as far backward as the thirteenth caudal. On the fourteenth, although the pedicles of the arch are present, the neural arch is not roofed over. The pedicles of the neural arches on all of the caudals are placed nearer the anterior than the posterior end of the centrum.

On the first caudal, the metapophyses are prominent wing-like processes, projecting upward and forward from the pedicles and the anterior border of the roof of the neural arch. These metapophyses increase in prominence from the first to the seventh in the
series, their dorsal edges becoming progressively thicker and rougher, and then diminish in size to the thirteenth in the series. On the three anterior caudals, the height of the dorsal edges of the metapophyses above the centrum remains very nearly the same, but the neural spines decrease in height. On the thirteenth caudal the truncated metapophyses are separated by a narrow groove for which the roof of the neural arch forms the floor. On the first caudal, the metapophyses project 130 mm. above the level of the dorsal surface of the centrum, on the seventh caudal, 110 mm., and on the twelfth caudal, 57 mm.

First Caudal—All of right and distal end of left transverse process restored (pl. 5, fig. Ca. 1); lateral surfaces of centrum eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch relatively narrow antero-posteriorly (minimum diameter of right pedicle, 104 mm.), being equivalent to less than one-third of length of centrum, and placed much nearer the anterior than the posterior end of the centrum; laterally flattened metapophysis conspicuously elongated and widened antero-posteriorly, projected upward and and slightly outward, and extended forward almost to level of anterior end of centrum; dorsal end of metapophysis thickened and roughened; neural spine quite short, with truncated distal end, and projecting slightly above level of dorsal edges of metapophyses; vertical height of neural spine, 107 mm.; maximum antero-posterior diameter of neural spine near distal end, 116 mm.; postero-median angle of roof of neural arch elongated, forming a pointed process which terminates 145 mm. in front of level of posterior end of centrum; dorso-ventrally flattened transverse process (parapophysis) longer than that of second sacral, directed outward, downward and somewhat forward, and probably expanded distally; minimum antero-posterior diameter of right transverse process near base, 122 mm.; centrum elongated and constricted ventrally near the middle; lateral surfaces of centrum between pedicle of neural arch and base of transverse process shallowly concave; dorso-ventral vascular canals open into a large deep fossa on ventral surface of centrum; and hæmaphysial facets destroyed.

Second Caudal—Hinder border and postero-basal angle of neural spine restored (pl. 5, fig. Ca. 2); lateral surfaces of centrum eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch similar to those of first caudal (minimum antero-posterior diameter of left pedicle, 94 mm.); laterally flattened and antero-posteriorly widened metapophysis conspicuously elongated, projected upward and slightly outward, and extended forward to level of anterior end of centrum; dorsal edge of metapophysis thickened and roughened; neural spine quite short, barely projecting above level of dorsal edges of metapophyses; vertical height of neural spine, 90 + mm.; dorso-ventrally flattened transverse process (parapophysis) much broader than that of first caudal and directed outward and downward, but not forward; maximum antero-posterior diameter of right transverse process at distal end, 157 mm., and minimum antero-posterior diameter near base, 134 mm.; centrum elongated, similar to that of first caudal; dorso-ventral vascular canals open into large elongated fossa near middle of ventral surface of centrum; and hæmaphysial facets destroyed.

Third Caudal—Distal border of right and of left transverse process restored (pl. 6, fig. Ca. 3); lateral surfaces of centrum eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch placed anterior to middle of centrum (minimum antero-posterior diameter of left pedicle, 107 mm.); elongated and laterally flattened metapophysis conspicuously widened antero-posteriorly, projected upward and slightly outward, and extended forward beyond level of anterior end of centrum; dorsal edge of metapophysis roughened; neural spine rather short, with obliquely truncated distal end and not projecting above level of dorsal edges of metapophyses; vertical height of neural spine, 92 mm.; maximum antero-posterior diameter of neural spine near distal end, 74 mm.; backward projecting process of roof of neural arch destroyed; dorso-ventrally flattened transverse process (parapophysis)
relatively long, directed outward and downward, and expanded distally; maximum antero-posterior diameter of right transverse process at distal end, 142 ± mm., and minimum antero-posterior diameter near base, 118 mm.; centrum elongated, each of its lateral surfaces below pedicles of neural arch being hollowed out, forming an elongate shallow concavity; ventral orifices of dorso-ventral vascular canals open into an elongated fossa; and hemaphysial facets destroyed.

Fourth Caudal—Distal border of left transverse process restored (pl. 6, fig. Ca. 4); lateral surfaces of centrum eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch similar to those of preceding caudal (minimum antero-posterior diameter of left pedicle, 88 mm.); laterally flattened metapophysis conspicuously elongated, projected upward and slightly outward and extended forward to within 10 mm. of level of anterior end of centrum; dorsal edge of metapophysis thickened and roughened; neural spine reduced to a low sagittal ridge; backward projecting hinder angle of roof of neural arch forms a pointed process which terminates 138 mm. in front of level of posterior end of centrum; dorso-ventrally flattened transverse process (parapophysis) very broad and relatively long, conspicuously expanded distally and directed outward and downward; maximum antero-posterior diameter of right transverse process at distal end, 157 mm., and minimum antero-posterior diameter near base, 128 mm.; centrum elongated, similar to that of third caudal; ventral orifices of dorso-ventral vascular canals open into an elongated fossa; and hemaphysial facets destroyed.

Fifth Caudal—Lateral surfaces of centrum (pl. 6, fig. Ca. 5) eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch rather low (minimum antero-posterior diameter of right pedicle, 97 mm.), and placed slightly nearer the anterior than the posterior end of the centrum; laterally flattened metapophysis conspicuously elongated, projected upward and slightly outward, and extended forward almost to level of anterior end of centrum; dorsal edge of metapophysis thickened and roughened; neural spine reduced to a low sagittal ridge; backward projecting process of roof of neural arch elongated and pointed, terminating 100 mm. in front of level of posterior end of centrum; dorso-ventrally flattened transverse process (parapophysis) much narrower than that of fourth caudal, directed outward and downward and inclined somewhat forward; maximum antero-posterior diameter of right transverse process at distal end, 124 mm., and minimum antero-posterior diameter near base, 106 mm.; centrum elongated, contracted near the middle ventrally, expanded at both ends; lateral surfaces of centrum between pedicle of neural arch and base of transverse process hollowed out, forming a shallow concavity; ventral orifices of dorso-ventral vascular canals open into an elongated fossa; and hemaphysial facets destroyed.

Sixth Caudal—Lateral surfaces of centrum (pl. 6, fig. Ca. 6) eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch rather thick transversely (minimum antero-posterior diameter of left pedicle, 97 mm.); laterally flattened metapophysis conspicuously elongated, projected upward and outward and extended forward to within 50 mm. of level of anterior end of centrum; dorsal edge of metapophysis thickened and roughened; neural spine vestigial; backward projecting process of roof of neural arch elongated and pointed, terminating 98 mm. in front of level of posterior end of centrum; dorso-ventrally flattened transverse process (parapophysis) considerably shorter than that of fifth caudal, directed outward and downward, and notched at base near anterior border by a large foramen (actually located almost at level of middle of centrum); maximum antero-posterior diameter of right transverse process at distal end, 110 mm., maximum diameter near the middle, 130 mm., and minimum antero-posterior diameter near base, 97 mm.; centrum elongated, contracted near the middle ventrally, but less expanded at both ends than that of fifth caudal; lateral surfaces of centrum between pedicle of neural arch and base of
transverse process hollowed out, forming a large concavity; ventral orifices of dorso-ventral vascular canals open into an elongated fossa; and hæmapophysial facets destroyed.

Séventh Caudal—End of left transverse process restored; lateral surfaces of centrum (pl. 6, fig. Ca. 7) eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch very thick transversely (minimum antero-posterior diameter of right pedicle, 90 mm.); laterally flattened metapophysis conspicuously elongated, projected upward and outward and extended forward to within 40 mm. of level of anterior end of centrum; dorsal edge of metapophysis thickened and roughened; neural spine reduced to a low sagittal ridge; extremity of backward projecting process of neural arch destroyed; dorso-ventrally flattened transverse process (parapophysis) somewhat shorter than that of sixth caudal, directed outward and downward, and pierced at base, but near anterior margin, by a small foramen; maximum antero-posterior diameter of right transverse process at distal end, 124 mm., and minimum antero-posterior diameter near base, 122 mm.; centrum similar to that of sixth caudal; ventral orifices of dorso-ventral vascular canals open into an elongated fossa, bounded laterally by a prominent longitudinal elevation; and hæmapophysial facets destroyed.

Eighth Caudal—Lateral surfaces of centrum (pl. 6, fig. Ca. 8) eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch relatively narrow antero-posteriorly (minimum diameter of right pedicle, 87 mm.), and placed nearer the anterior than the posterior end of the centrum; laterally flattened metapophysis elongated, projected upward and outward and extended forward to within 35 mm. of level of anterior end of centrum; dorsal edge of metapophysis thickened and roughened; neural spine vestigial, represented by sagittal ridge; extremity of backward projecting process of roof of neural arch destroyed; dorso-ventrally flattened transverse process (parapophysis) relatively short, directed outward and downward and pierced at base by a small foramen; maximum antero-posterior diameter of right transverse process at distal end, 127 mm., and minimum antero-posterior diameter near the middle of its length, 120 mm.; centrum very thick in proportion to its length and contracted near the middle ventrally; lateral surfaces of centrum between pedicle of neural arch and base of transverse process hollowed out, forming a deep concavity; ventral orifices of dorso-ventral vascular canals open into an elongated fossa; and hæmapophysial facets destroyed.

Ninth Caudal—Ends of right and of left transverse processes restored (pl. 6, fig. Ca. 9); lateral surfaces of centrum eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch very low (minimum antero-posterior diameter of right pedicle, 86 mm.); neural canal about twice as wide as high; laterally flattened and elongated metapophysis projecting more upward than outward, terminating 60 mm. behind level of anterior end of centrum and having dorsal edge thickened and roughened; a low sagittal ridge constitutes sole vestige of neural spine; extremity of backward projecting process of roof of neural arch destroyed; dorso-ventrally flattened transverse process (parapophysis) subtriangular in outline, the hinder edge extending obliquely forward to the antero-distal angle, directed outward and downward, and pierced at base by a small foramen; centrum somewhat shorter than that of eighth caudal and rather thick in proportion to its length; lateral surfaces of centrum between pedicle of neural arch and base of transverse process hollowed out, forming a deep concavity; ventral orifices of dorso-ventral vascular canals open into an elongated fossa; and hæmapophysial facets destroyed.

Tenth Caudal—End of left transverse process restored; lateral surfaces of centrum (Pl. 6, fig. Ca. 10) eroded near each end (No.12261, U. S. N. M.). Pedicles of neural arch very low (minimum antero-posterior diameter of right pedicle, 97 mm.); laterally flattened metapophysis rather short, projecting more upward than outward, terminating 70+ mm. behind level of anterior end of centrum, and having dorsal edge thickened and roughened;
backward projecting process of roof of neural arch bluntly pointed, terminating 112 mm. in front of level of posterior end of centrum; dorso-ventrally flattened transverse process (parapophysis) very short and rather wide, directed outward and downward, and pierced at base by a large oval foramen (25 × 17 mm.); centrum shorter than that of ninth caudal, but otherwise quite similar; ventral orifices of dorso-ventral vascular canals open into an elongated fossa; and hemapophysial facets damaged.

Eleventh Caudal—Lateral surfaces of centrum (pl. 6, fig. Ca. 11) eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch very low (minimum antero-posterior diameter of right pedicle, 96 mm.), and placed nearer the anterior than the posterior end of the centrum; neural arch complete; neural canal very small, about twice as wide as high; laterally flattened metapophysis conspicuously reduced in size, projected more upward than outward, terminated 68 + mm. behind level of anterior end of centrum, and has upper edge thickened and roughened; backward projecting process of roof of neural arch elongated and bluntly pointed, terminating 93 + mm. in front of level of posterior end of centrum; transverse process (parapophysis) greatly reduced, the anterior portion being relatively short and narrow, the posterior portion being reduced to a low projecting ridge, and separating them is the deep notch for a large blood-vessel; maximum antero-posterior diameter of anterior portion of right transverse process at distal end, 70 mm.; centrum somewhat shorter than that of tenth caudal, contracted near the middle and expanded at both ends; lateral surfaces of centrum between pedicle of neural arch and base of transverse process hollowed out, forming a deep concavity; ventral orifices of dorso-ventral vascular canals open into a narrow fossa; and hemapophysial facets low, separated by a shallow longitudinal groove, and located at hinder end of ventral face of centrum.

Twelfth Caudal—Posterior end of centrum (pl. 6, fig. Ca. 12) destroyed (No. 12261, U. S. N. M.). Pedicles of neural arch very low (minimum antero-posterior diameter of right pedicle, 84.5 mm.) and placed nearer the anterior than the posterior end of the centrum; laterally thickened metapophysis greatly reduced, projected upward and slightly outward, and has dorsal edge roughened; neural arch complete; neural canal very small, but much wider than high; backward projecting process from roof of neural arch very short and bluntly pointed, terminating 96 mm. in front of level of posterior end of centrum; anterior portion of transverse process (parapophysis) reduced to a low projecting ridge, but barely a vestige of posterior portion persists; maximum antero-posterior diameter of anterior portion of right transverse process, 82 ± mm.; centrum shorter and narrower than that of the eleventh caudal and contracted near the middle; lateral surfaces of centrum more strongly excavated below than above level of transverse processes; ventral orifices of dorso-ventral vascular canals closed; and hemapophysial facets destroyed.

Thirteenth Caudal—Posterior end of centrum (pl. 6, fig. Ca. 13) damaged; lateral surfaces of centrum eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch rather thick (minimum antero-posterior diameter of left pedicle, 93 mm.) and placed much nearer the anterior than the posterior end of the centrum; laterally thickened metapophysis reduced, projected more upward than outward, and extended very slightly forward; neural arch complete though greatly reduced; neural canal very small; backward projecting process of roof of neural arch vestigial, terminating 116 ± mm. in front of level of posterior end of centrum; anterior portion of transverse process (parapophysis) barely visible; centrum shorter than that of twelfth caudal, constricted near middle and expanded at both ends; ventral orifices of dorso-ventral vascular canals open into a short narrow fossa; and hemapophysial facets destroyed.

Fourteenth Caudal—Lateral surfaces of centrum (pl. 6, fig. Ca. 14) eroded near each end (No. 12261, U. S. N. M.). Both pedicles of neural arch retained (minimum antero-posterior diameter of left pedicle, 77 ± mm.) and placed much nearer the anterior than the
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<td>358</td>
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<td>273+</td>
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<td>66.5</td>
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<td>194+</td>
<td>183+</td>
<td>207</td>
<td>194+</td>
<td>205</td>
<td>209</td>
<td>205</td>
<td>188+</td>
<td>177+</td>
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<td>151</td>
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<td>42</td>
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<td></td>
</tr>
<tr>
<td>Least antero-posterior diameter of right pedicle of neural arch</td>
<td>104</td>
<td>104</td>
<td>100</td>
<td>100</td>
<td>97</td>
<td>106</td>
<td>90</td>
<td>87</td>
<td>87</td>
<td>92</td>
<td>95</td>
<td>85</td>
<td>75</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance between dorsal margin of right metapophysis and dorsal surface of centrum</td>
<td>130</td>
<td>128</td>
<td>127</td>
<td>120</td>
<td>121</td>
<td>106</td>
<td>110</td>
<td>106</td>
<td>94</td>
<td>78</td>
<td>64</td>
<td>57</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
posterior end of the centrum; narrow neural canal not roofed over; metaphysis not differentiated from pedicle of neural arch; centrum much shorter than that of thirteenth caudal and distinctly constricted near middle of its length; ventral orifices of dorso-ventral vascular canals open into a narrow fossa; and hemapophysial facets destroyed.

Fifteenth Caudal—Lateral surfaces of centrum (pl. 6, fig. Ca. 15) eroded near each end (No. 12261, U. S. N. M.). Pedicles of neural arch reduced to low nodosities; centrum greatly shortened, less than half the length of first caudal, constricted near middle of its length and also encircled by narrow groove for vascular vessel; ventral orifices of dorso-ventral vascular canals open into narrow fossa; and hemapophysial facets absent.

Sixteenth Caudal—Essentially complete (pl. 6, fig. Ca. 16), with exception of a small section of hinder end (No. 12261, U. S. N. M.). Centrum strongly compressed antero-posteriorly, encircled near middle of its length by a narrow irregular groove, and has an elongate depression near center of lateral surface; no remnants of neural arch persist; vestigial transverse process represented by small osseous nodule; a single small ventral orifice for dorso-ventral vascular canals; and posterior face of centrum convex and anterior face concave.

Seventeenth Caudal—Essentially complete (No. 12261, U. S. N. M.). Centrum (pl. 6, fig. Ca. 17) strongly compressed antero-posteriorly; a deep fossa on lateral face of centrum bounded above and below by longitudinal osseous nodules; an irregular transverse groove on dorsal and ventral surfaces of centrum near middle of its length; and ventral orifices of dorso-ventral vascular canals open into a small fossa.

Eighteenth Caudal—Essentially complete (No. 12261, U. S. N. M.). Centrum (pl. 6, fig. Ca. 18) strongly compressed antero-posteriorly; except for its lesser dimensions, this caudal differs very slightly from the preceding caudal.

Nineteenth Caudal—Essentially complete (No. 12261, U. S. N. M.). Centrum (pl. 6, fig. Ca. 19) strongly compressed antero-posteriorly and characterized by its very irregular configuration.

Twentieth Caudal—Essentially complete (No. 12261, U. S. N. M.). Centrum (pl. 6, fig. Ca. 20) asymmetrical and characterized by presence of a number of rugose protuberances or nodosities.

Twenty-first Caudal—Essentially complete (No. 12261, U. S. N. M.). Centrum (pl. 6, fig. Ca. 21) of this terminal caudal reduced to a small asymmetrical nodular mass, covered with a number of irregularly placed nodosities.

**Hemaphyses**

Four chevron bones (No. 12261, U. S. N. M.) were associated with the vertebral column, which was found near Fall, Alabama. One of these was found in close proximity to the second sacral vertebra, and the other three near the third caudal vertebra. It is obvious that three of these chevrons had in some fortuitous manner been moved subsequent to the disintegration of the fleshy portions of the carcase.

In case of a number of Recent odontocetes, the two arms of the first chevron are not ankylosed ventrally. It would seem that the two arms of the first chevron of this archaeocete likewise were not ankylosed ventrally. The right arm of a chevron (fig. 17), measuring 64 mm. in length, which was found near the third caudal vertebra, belongs certainly at the anterior end of the series and is tentatively identified as the first chevron, as there is no indication of ankylosis with the opposite arm. It tapers from the upper to the lower end, its antero-posterior diameter at the proximal end being 22 mm. and at the distal end 10 mm. The maximum transverse diameter of this arm is 6 mm. The upper articular end is destroyed.

In so far as our present knowledge goes, the anterior chevrons of all cetaceans are characterized by their peculiar shape. The second and third chevrons of Recent odonto-
cetes have unusually high haemal canals, long arms, and a very short haemal spine. It is therefore reasonable to assume that the slightly bowed left arm of the chevron found associated with the third caudal vertebra belongs either with that caudal or with the preceding one. This chevron has a haemal canal at least 65 mm. in height. The upper end of this arm is eroded and it is broken ventrally at its union with the opposite arm. The minimum antero-posterior diameter of the left arm is 25 mm. Posteriorly this arm is strongly compressed from side to side, forming a hinder crest. The anterior edge is relatively thick and conspicuously roughened on its upper half. The ventral end is distinctly rugose and there is no evidence of the existence of a haemal spine.

The two remaining chevrons probably belong behind the middle of the series. One of them is crushed laterally and its haemal spine is destroyed. The measurements of this chevron are as follows: Minimum antero-posterior diameter of right arm, 36.5 mm.; distance from mid-line of union of opposite arms to upper end of right arm, 47 mm.; antero-posterior diameter of right articular facet, 44.5 mm.

The right arm of the chevron (fig. 18), which was found near the second sacral vertebra, is fairly well preserved, but the left arm is eroded and a portion of the haemal spine on the left side is destroyed. The two arms of this chevron are constricted medially and inclose a broad V-shaped haemal canal, and below their union is a short thick haemal spine. The ventral face of this haemal spine is flattened transversely and slopes obliquely downward from anterior to hinder margin. The upper end of each arm is conspicuously elongated and the articular surface is convex antero-posteriorly and transversely. The measurements of this chevron are as follows: Maximum vertical diameter, 69 mm.; vertical diameter of haemal canal, 32 mm.; minimum antero-posterior diameter of right arm, 28.7 mm.; maximum antero-posterior diameter of right articular facet, 48 mm.; maximum antero-posterior diameter of haemal spine, 38.5 mm.; and transverse diameter of haemal spine, 27 mm.

**FORELIMB**

The scapula has elongated acromial and coracoidal processes and is thoroughly cetaceanlike in appearance, although the supraspinous fossa is much less reduced in area than in any known fossil or Recent mysticete or odontocete. Assuming that the restoration of
the manus (fig. 19) is approximately correct and that the functional length of the arm consists of the distance from the tip of the longest digit to the proximal end of the radius, plus the length of the humerus from trochlea to head, the humerus comprises about 38 per cent of the arm length. Nevertheless, the humerus is very short in proportion to the size of the animal, comprising about 0.03 per cent of the total length of the skeleton. The well-developed deltoid crest of the humerus, reaching well below the middle of the shaft, provides a greater leverage for the deltoid muscle. Structurally, the humerus is not at all cetaceanlike. The bones of the forearm are flattened laterally and are quite short in proportion to the length of the humerus. The radius and ulna are so articulated with one
another and with the humerus as to permit flexion and extension only. Thus a hinged and non-rotary type of elbow joint is formed. The olecranon process of the ulna is large, wide, and flat. The arrangement of the carpal elements and the relative lengths of the individual digits shown in the reconstructed manus are highly conjectural, since Gidley (1913) used the corresponding parts of whale and sea-lion flippers as a guide in modeling them.

**Scapula**

The scapula (fig. 20) is relatively broad, the average ratio of height to maximum breadth being approximately 10 to 13. It has a strongly convex vertebral edge, a cavelly curved posterior edge, and a slightly convex anterior edge. The area between the anterior edge and the low spinous crest of the scapula, corresponding to the suprascapular fossa, is fairly broad, shallow, and flattens out dorsally. The external surface of the scapula is depressed behind the spinous crest, forming a shallow infraspinous fossa. In area the supraspinous fossa is equivalent to one-third or at most to two-fifths of that of the infraspinous fossa. A narrow fossa for a strong teres muscle extends along the dorsal half of the posterior border of the scapula. The elongated acromion is thin, flat, and attenuated very slightly toward the distal end. It is bent inward near the end of the basal fourth of its length, and is also directed forward and slightly downward. The thick anterior border of the scapula turns slightly inward above the level of the acromion and terminates ventrally at the base of the coracoid process. The slender finger-like coracoid process is
directed downward and inward from the anterior face of the head of the scapula. On one (No. 11783, U. S. N. M.) of these scapulae, the coracoid process projects about 38 mm. beyond the head. The neck is relatively narrow in contrast to the breadth of the scapula. Viewed from below, the shallowly concave articular head is ovoid in outline. The posterior margin commences to curve upward and backward at about the level of the lower edge of the acromion. The costal surface of the scapula is relatively flat, smooth, and devoid of conspicuous ridges.

### Table 12—Measurements (in millimeters) of the scapula

<table>
<thead>
<tr>
<th></th>
<th>No. 4675</th>
<th>No. 4675</th>
<th>No. 4674</th>
<th>No. 11783</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>U. S. N. M.</td>
<td>U. S. N. M.</td>
<td>U. S. N. M.</td>
<td>U. S. N. M.</td>
</tr>
<tr>
<td>Greatest antero-posterior diameter</td>
<td>512</td>
<td>490±</td>
<td>530±</td>
<td>465</td>
</tr>
<tr>
<td>Greatest vertical diameter, articular head to vertebral margin</td>
<td>378</td>
<td>375</td>
<td>400</td>
<td>368±</td>
</tr>
<tr>
<td>Length of acromion, superior margin at base to distal end</td>
<td>135±</td>
<td>145</td>
<td>132</td>
<td>147</td>
</tr>
<tr>
<td>Greatest diameter of acromion near distal end</td>
<td>40.5</td>
<td>38.5±</td>
<td>137</td>
<td>40.5</td>
</tr>
<tr>
<td>Posterior face of articular head to distal end of coracoid process</td>
<td>135±</td>
<td></td>
<td>104</td>
<td>137</td>
</tr>
<tr>
<td>Greatest antero-posterior diameter of articular head</td>
<td>100</td>
<td>100</td>
<td>102</td>
<td></td>
</tr>
<tr>
<td>Greatest transverse diameter of articular head</td>
<td>79.5</td>
<td>75±</td>
<td>85</td>
<td>79.5</td>
</tr>
</tbody>
</table>

### Humerus

Considerable individual variation not only in the relative lengths of the shafts, but also in the development of the deltoid crest exists between humeri of different individuals. Some of these differences may be attributable possibly either to age or to sex.

The following specimens were examined: The plaster cast of the left humerus described by Harlan in 1835 (No. 840, U. S. N. M.); the crushed left humerus (No. 4674, U. S. N. M.) associated with the skull; the left humerus (No. 4675, U. S. N. M.) associated with the consecutive series of cervical and dorsal vertebrae lacks the proximal fifth of the shaft though the proximal end is preserved; the distal half of a right humerus (No. 6087, U. S. N. M.); and the head of the left humerus (No. 12261, U. S. N. M.) associated with the consecutive series of caudal and lumbar vertebrae.

Two of these humeri (Nos. 4674 and 4675, U. S. N. M.) have much slenderer shafts than the others and the backward swelling of the distal portion of the shaft is less pronounced. Viewed from behind, the proximal three-fourths of the shaft is strongly bent inward. The distal rounded angle of the deltoid crest (fig. 21) is about 145 mm. distant from the center of the distal face of the trochlear surface, while the posterior face of the shaft commences to swell backward immediately above the trochlea on two of these humeri (Nos. 840 and 6087, U. S. N. M.). On the other two humeri, the posterior face of the

### Table 13—Measurements (in millimeters) of the humerus

<table>
<thead>
<tr>
<th></th>
<th>No. 4673</th>
<th>No. 4674</th>
<th>No. 12261</th>
<th>No. 6087</th>
<th>No. 840</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>U. S. N. M.</td>
<td>U. S. N. M.</td>
<td>U. S. N. M.</td>
<td>U. S. N. M.</td>
<td>U. S. N. M.</td>
</tr>
<tr>
<td>Greatest length</td>
<td>490±</td>
<td>510</td>
<td>...</td>
<td>245±</td>
<td>420</td>
</tr>
<tr>
<td>including greater tuberosity</td>
<td>133.5</td>
<td>143.5</td>
<td>135</td>
<td>...</td>
<td>138.7</td>
</tr>
<tr>
<td>Greatest antero-posterior diameter of head</td>
<td>105</td>
<td>120</td>
<td>105</td>
<td>...</td>
<td>113.7</td>
</tr>
<tr>
<td>Greatest transverse diameter of head</td>
<td>99</td>
<td>93.5</td>
<td>89.5</td>
<td>...</td>
<td>110</td>
</tr>
<tr>
<td>Antero-posterior diameter of shaft through lower end of deltoid crest</td>
<td>116</td>
<td>116</td>
<td>...</td>
<td>146.7</td>
<td>135</td>
</tr>
<tr>
<td>Transverse diameter of shaft at same level</td>
<td>46</td>
<td>43.5</td>
<td>66</td>
<td>...</td>
<td>52</td>
</tr>
<tr>
<td>Antero-posterior diameter of outer condyle</td>
<td>67</td>
<td>67</td>
<td>62.8</td>
<td>...</td>
<td>56.6</td>
</tr>
<tr>
<td>Antero-posterior diameter of inner condyle</td>
<td>64</td>
<td>...</td>
<td>76.7</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Transverse diameter of combined trochlea and capitulum</td>
<td>54.5</td>
<td>54</td>
<td>...</td>
<td>58.7</td>
<td>52</td>
</tr>
</tbody>
</table>

1 Proximal half of shaft missing.
shaft (fig. 22b) commences to swell backward about 100 mm. above the center of the distal face of the trochlear surface. The shallow coronoid fossa (fig. 22a) is situated above the trochlea on the distal end of the anterior face of the shaft. A circular and rather deep olecranon fossa is present on the hinder face of the shaft (fig. 22c) above the trochlear surface. The trochlear surface on the distal end of the shaft is bounded by inner and outer condyles. The outer condyle projects distally beyond the level of the inner condyle. The capitulum is not sharply differentiated from the trochlea, the combined surfaces being shallowly concave transversely and describe a semicircle antero-posteriorly. The outer portion of this trochlear surface, which corresponds to the capitulum, is extended upward posteriorly on the rather large triangular protuberance; its maximum width here does not exceed 21 mm. The inner trochlear surface is likewise extended upward posteriorly and almost forms a right angle with the corresponding portion of the hinder capitular surface. This constitutes a mechanical safeguard against the elbow joint being dislocated.

The smooth articular surface of the head is convex from side to side and also in a fore and aft direction. It is so placed on the proximal end of the shaft that it looks somewhat outward and backward, and projects posteriorly beyond the level of the hinder face of the shaft. The articular head of the humerus is separated from the tuberosity by a broad shallow furrow. Below the head, the antero-posterior diameter of the shaft gradually increases to the level of the lower end of the deltoid crest. The deltoid crest (fig. 22b) is unusually long, reaching well below the middle of the shaft, quite thin, and curved inward distally. The hinder face of the shaft is quite thick and is either rounded or slopes obliquely from external to internal faces of the shaft (Nos. 6087 and 4675, U. S. N. M.). The internal face of the shaft is flattened and the external face is convex.

Aside from its larger size, the humerus of *Basilosaurus cetoides* differs from that of *Zygorhiza kochii* very slightly. The ratio between length of shaft and greatest antero-posterior diameter through lower end of deltoid crest is approximately the same in both. The backward swelling of the hinder face of the distal end of the shaft is more accentuated and the olecranon fossa on the hinder face of the shaft above the trochlear surface is deeper in *Basilosaurus cetoides* than in *Zygorhiza kochii*. The trochlear surface is prolonged upward posteriorly on the humeri of both of these archaeocetes, but the angle between the outer capitular and the inner trochlear surfaces is not so acute in *Zygorhiza kochii* as in *Basilosaurus cetoides*.

**Radius**

The shaft of the radius (fig. 23) is flattened laterally, although the external and internal faces are somewhat convex, and the anterior and posterior edges are fairly sharp. The pronounced antero-posterior expansion of the shaft below the head is the most obvious
peculiarity of this radius. An elliptical rugose area, presumably for the insertion of the *m. pronator teres*, covers the antero-internal surface of the angle thus formed. The broad shallow groove, which extends downward from the anterior face of the proximal end across the internal surface of the radius, may have marked the course of a muscle and tendon. A fairly large tuberosity is developed on the antero-internal angle of the proximal end of the shaft.

The proximal end of this radius is occupied by a large articular surface which is considerably wider transversely than antero-posteriorly. It is strongly concave antero-posteriorly and slightly convex transversely. The outer area for articulation with the capitulum of the humerus is considerably larger than the inner area for the trochlea. The trochlear facet, however, does not extend over on the internal surface of the proximal epiphysis as in *Zalophus* and hence the elbow joint is not so well-perfected mechanically. The entire circumference of the proximal epiphysis is either deeply grooved or else pitted, which in turn suggests the presence of a capsular cartilage enveloping the elbow joint. The postero-distal angle of the shaft is twisted outward. The distal epiphysis is missing on both the right and the left radius (No. 4675, U. S. N. M.).
The radius of *Basilosaurus cetoides* differs from that of *Zygorniza kochii* in the more pronounced expansion of the proximal portion of the shaft, the more proximal position of the anterior angle, the relatively greater width of the shaft throughout its length, and the development of a posterior prominence for the attachment of a muscle, presumably the *biceps*.

**Table 14—Measurements (in millimeters) of the radius**

<table>
<thead>
<tr>
<th></th>
<th>No. 4675 U.S. N.M. Left</th>
<th>No. 4675 U.S. N.M. Right</th>
</tr>
</thead>
<tbody>
<tr>
<td>Greatest length</td>
<td>250</td>
<td>253</td>
</tr>
<tr>
<td>Antero-posterior diameter of proximal facet at middle</td>
<td>...</td>
<td>39</td>
</tr>
<tr>
<td>Transverse diameter of proximal articular surface</td>
<td>75.5</td>
<td>75</td>
</tr>
<tr>
<td>Antero-posterior diameter of shaft at level of angle</td>
<td>53.5</td>
<td>58.5</td>
</tr>
<tr>
<td>Least antero-posterior diameter of shaft near distal end</td>
<td>53.5</td>
<td>58.5</td>
</tr>
<tr>
<td>Transverse diameter of shaft at same level</td>
<td>25</td>
<td>25</td>
</tr>
<tr>
<td>Antero-posterior diameter of distal end</td>
<td>54</td>
<td>59.5</td>
</tr>
<tr>
<td>Transverse diameter of distal end</td>
<td>28.5</td>
<td>28</td>
</tr>
</tbody>
</table>

**Ulna**

The shaft of the ulna (fig. 24) is laterally flattened and faintly bowed outward from end to end. The anterior edge of the shaft is slightly thinner than the hinder edge. The olecranon process (fig. 23) is quite broad; its anterior face slopes obliquely backward and upward, and its slightly curved upper or hinder edge is distinctly rugose. The transverse diameter of the greater sigmoid cavity is much greater distally than proximally. The external margin of this cavity presents a concave curvature from end to end, but the internal
margin is deeply notched. The rather broad and deep groove, extending at least half-way across the greater sigmoid cavity, is directed inward and upward and disappears on the internal face of the olecranon process near the level of the upper end of the greater sigmoid cavity. It is possible that the capsular ligamentous structures associated with a hyper-extended position of the elbow joint may have lain in this groove. The roughened triangular area on the anterior face of the shaft for the presumed *brachialis* attachment is depressed below the level of the projecting distal border of the greater sigmoid cavity. A broad groove, originating in this area, extends obliquely downward on the internal face of the shaft for a distance of approximately 20 mm. The distal epiphysis is missing on the right ulna and the distal half of the shaft of the left ulna is destroyed (No. 4675, U. S. N. M.).

The following specimens were examined: The right and left ulnae (No. 4675, U. S. N. M.) associated with the consecutive series of cervical and dorsal vertebrae, and the proximal portion of the left ulna (No. 12261, U. S. N. M.) associated with the consecutive series of caudal and lumbar vertebrae.

**Table 15—Measurements (in millimeters) of the ulna**

<table>
<thead>
<tr>
<th></th>
<th>No. 4975</th>
<th>No. 4975</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>U. S. N. M.</td>
<td>U. S. N. M.</td>
</tr>
<tr>
<td>Greatest length</td>
<td>105+</td>
<td>334</td>
</tr>
<tr>
<td>Greatest dorso-ventral diameter of olecranon process</td>
<td></td>
<td>120</td>
</tr>
<tr>
<td>Length of anterior edge of olecranon process, dorso-posterior angle to dorsal margin of greater sigmoid cavity</td>
<td></td>
<td>90</td>
</tr>
<tr>
<td>Greatest diameter of greater sigmoid cavity</td>
<td>52.5</td>
<td>52</td>
</tr>
<tr>
<td>Greatest transverse diameter of distal portion of greater sigmoid cavity</td>
<td>41.2</td>
<td>43</td>
</tr>
<tr>
<td>Greatest length of anterior face of shaft below greater sigmoid cavity</td>
<td></td>
<td>220</td>
</tr>
<tr>
<td>Greatest antero-posterior diameter of shaft at distal end</td>
<td></td>
<td>65.5</td>
</tr>
<tr>
<td>Greatest transverse diameter of shaft at distal end</td>
<td></td>
<td>36</td>
</tr>
<tr>
<td>Least antero-posterior diameter of shaft below greater sigmoid cavity</td>
<td></td>
<td>60</td>
</tr>
</tbody>
</table>

**Manus**

In 1895, Lucas published a short statement in regard to portions of two skeletons (Nos. 4674 and 4675, U. S. N. M.) found by Schuchert in Alabama, and mentioned the presence of some carpal elements. Lucas (1895, p. 746) states that “two or three small bones of irregular form are very likely carpals, and if so they too were largely cartilaginous.” These bones can not now be found. It is quite likely that the carpals of *Basilosaurus cetoides* are similar in most respects to those of *Zygorhiza kochii*.

Koch (1851, p. 62) reports that wrist and finger bones were found associated with the skeleton which he discovered on February 7, 1848, in Choctaw County, Alabama. Müller (1851, p. 246) published a very brief description of the finger bones mentioned by Koch. One of these, which was not complete, measured $2\frac{1}{2}$ inches in length; the transverse diameter of the largest end was $1\frac{3}{4}$ inches and the dorso-plantar diameter 11 lines. Another very long finger bone exhibited a great similarity to the largest metacarpal of the sea-lion. Müller did not find any terminal phalanges in Koch’s collection.

The fact that the known metacarpals and phalanges of the related *Zygorhiza kochii* (No. 4679, U. S. N. M.) retain a limited ball and socket type of articulation indicates that the digits of both of these archaeocetes were similar in construction to those of the sea-lion, and also that *Basilosaurus* did not have flattened phalanges like those of whales. This evidence, therefore, seems to justify the inclusion of sea-lion rather than whale-like characters by Gidley in restoring the fore flipper (fig. 19). The first finger, however, is shortened in accordance with conditions existing in most of the Cetacea, and digits II and III are made the longest and heaviest of the fingers. The construction of the carpus is unknown, but judging from the modifications of the radius and ulna in conjunction with the
elongation of the more or less cylindrical, slender metacarpals and phalanges, the fore flipper was evidently highly specialized.

**INNOMINATE BONES**

The right innominate bone (fig. 25a) was found near the twenty-second vertebra (second sacral), counting forward from the posterior end of the series, and the left one (fig. 25b) near the twenty-first vertebra (first caudal). Inasmuch as little or no evidence was found by Schuchert to indicate that the series of vertebrae (No. 12261, U. S. N. M.), with which these bones were associated, had been washed about after deposition, it is quite likely that the pelvis was located somewhere near these vertebrae. A description accompanied by photographs of these bones was published by Lucas (1900a).

Abel (1906) has contended that these bones were the coracoids of a large bird to which he gave the name *Alabamornis gigantea*. Gidley (1913, pp. 651–652) restudied these elements and concluded that there can be no doubt as to their mammalian characteristics.

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**Fig. 25—Basilosaurus cetoides** (Owen). Innominate bones, No. 12261, United States National Museum. a, external view of right innominate bone; b, external view of left innominate bone. × 4. ac., acetabulum; f. ob., obturator or thyroid foramen; il., ilium; is., ischium; p., pubis. Upper Eocene, upper Jackson formation, Alabama.
and that there is no reason to assume that they do not belong to the skeleton with which they were found associated. Stromer (1908b, p. 146) had reached the same conclusion some time previously.

Neither of these bones is quite complete, the right one lacking the vestigial iliac process and the left one the postero-superior angle of the ischium. The iliac, ischial, and pubic elements are all present, although these parts are so completely fused that their respective boundaries can not be distinguished. All three bones may meet in the acetabulum. As regards the relative proportions of the preacetabular and the postacetabular portions, the resemblance of the innominate bone of Basilosaurus to that of Phoca hispida is much closer than to that of any known cetacean.

The anterior end of the right innominate bone is exceptionally well preserved; the surfaces are rather smooth and there is not the slightest indication that an elongated ilium was originally present. It is quite probable that the ilium is limited to the small forward projecting process above and in front of the acetabulum. Stromer (1921, pp. 54–56) was mislead by the photographs published by Lucas (1900a, pls. 5–6) into concluding that the ilium had been broken off. He therefore restored the ilium as a rod- or club-like process similar to that of Halitherium schinzii.

As a result of the atrophy of the ilium, the acetabulum is situated at the anterior end of the innominate bone. The acetabular depression is about as wide and deep as that of a full-grown female sea-lion, Enmetopias stelleri. Traces of the cotyloid notch are retained at the hinder end of the acetabulum. There is an irregular, roughened depression at the bottom of the acetabulum, apparently for insertion of a ligamentum teres, although as Lucas has observed it is a little difficult to see the necessity for a ligament in so degenerate a pelvis as that under consideration. This round ligament seems to have been present in the Miocene pinniped, Allodesmus kernensis (Kellogg, 1931, p. 267), but is absent according to Owen (1866, p. 507) in the Recent eared and earless seals, although both groups have large depressions in the acetabulum. The innominate bone is considerably thickened in the region of the acetabulum.

The obturator or thyroid foramen is bounded by the rather broad ischium above and by the pubis below. This foramen lies behind and not below the acetabulum like in the Eocene sirenians, Eostren and Prolotherium. Although the pubis does not meet its fellow in a ventral symphysis, the pubic border of the innominate bone is distinctly roughened below the obturator foramen, a condition that may indicate the retention of a ligament connecting the opposite bones across the middle line. The ischial portion of the innominate bone is rather broad, flattened, and rather thin. The outer or gluteal surface of both innominate bones is rather smooth, while the inner or sacral surface of the right one is slightly roughened by the accidental presence of irregularly spaced small pits. The obliquely truncated posterior end of the right innominate bone (fig. 25a) has every appearance of being natural and there is no evidence of a fracture at this level. This nearly straight edge is distinctly roughened; it may have been capped by cartilage. The ischial tuberosity does not appear to have been developed.

The flattened and rather broad innominate bone of Basilosaurus is less simplified in some respects than in any known fossil or Recent cetacean. The presence of a relatively large acetabulum and the retention of a distinct thyroid foramen are heritages from a more generalized precursor. The extreme atrophy of the ilium, however, and the vestigial condition of the femur seem to be directly correlated with the functional disuse of the hindlimb. This reduction in the length of the ilium, as Howell (1930, pp. 305–306) points out, may be attributed to the atrophy of the hip muscles and the ensuing relinquishment of the iliocostalis and multifidus attachment. A less-marked reduction of the preacetabular portion of the innominate bone may be seen in the pinnipeds, but in no other marine or
terrestrial mammal does the shortening of the ilium even approximate the advanced stage found in Basilosaurus. It is quite likely that these innominate bones were not attached directly to the sacral vertebrae, and that they lay free in the flesh as in the Recent mysticetes.

<table>
<thead>
<tr>
<th>Table 16—Measurements (in millimeters) of the innominate bone</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>No. 12261</strong></td>
</tr>
<tr>
<td>Greatest length</td>
</tr>
<tr>
<td>Greatest vertical diameter of anterior end</td>
</tr>
<tr>
<td>Greatest vertical diameter at level of obturator foramen</td>
</tr>
<tr>
<td>Vertical diameter of acetabulum</td>
</tr>
<tr>
<td>Transverse diameter of acetabulum</td>
</tr>
<tr>
<td>Vertical diameter of obturator foramen</td>
</tr>
<tr>
<td>Transverse diameter of obturator foramen</td>
</tr>
<tr>
<td>Greatest diameter of hinder end</td>
</tr>
<tr>
<td>Distance between anterior margin of obturator foramen and notch in front of acetabulum</td>
</tr>
</tbody>
</table>

**FEMUR**

According to Lucas (1900a, p. 330) the shaft of the slender right femur (No. 12261, U. S. N. M.) was found near the nineteenth vertebra (third caudal) counting forward from the posterior end of the series. No articular surface was preserved at either end of the shaft (fig. 26), the slightly weathered lower end having been capped apparently with cartilage. A small piece of the upper end disintegrated while the bone was being removed from the matrix. There was also found near the twenty-second vertebra (second sacral), however, a rounded fragment of bone which proved to be a proximal epiphysis. A natural contact was found to exist between this proximal epiphysis and the shaft of the right femur, as is shown in figure 26.

The elongated shaft of the femur is quite slender and somewhat curved. The proximal third of the shaft is distinctly flattened, the medial portion is more or less cylindrical, and the distal third is curved inward and slightly forward. The crest-like lesser trochanter on the inner or medial face of the shaft is placed considerably lower than in the creodons. This process was identified as the third trochanter by Lucas. The greater tuberosity seems to be partially destroyed, but is separated from the atrophied and flattened head by a broad shallow groove. With respect to the direction of the transverse axis of the shaft at the level of the lesser tuberosity, the proximo-external angle, including the greater tuberosity, is strongly twisted backward. No trace of a trochanteric fossa was found on the hinder face of the proximal end. A small cavity is present on the head, but one can not be certain whether it represents a vestigial pit for the *ligamentum teres* or an accidental breakage. The ends of the femur, as figured by Gidley (1913, fig. 3), are reversed.

**RIBS**

The whole or portions of twelve ribs (No. 4675, U. S. N. M.) were utilized in reconstructing the skeleton on exhibition in the U. S. National Museum. The positions to
which these ribs were allocated by Gidley have been accepted tentatively. On the left side, the proximal two-thirds of the first rib is destroyed, the second is complete with the exception of a small piece of the distal extremity, the sixth and the tenth ribs are complete, and the distal half of the shaft of the twelfth rib is destroyed. On the right side, the fourth and seventh ribs are complete, the ninth is essentially complete with the exception of the head, the upper halves only remain of the eleventh and twelfth ribs, the thirteenth rib is complete, and the distal one-fourth of the fourteenth rib is missing. In addition to these, there are in the reference collection several incomplete ribs belonging to this individual (No. 4675, U. S. N. M.) as well as other fragmentary ribs belonging to two other individuals (Nos. 4674 and 6087, U. S. N. M.).

The seven anterior pairs of ribs have the upper portions of the shafts more conspicuously flattened antero-posteriorly and widened transversely than on the middle and hinder ribs. The necks of the seven anterior pairs of ribs are bent rather sharply downward from the curvature of the rest of the shaft, while the necks of the ninth pair of ribs conform rather closely with the curvature of the shaft. The ribs near the middle of the thorax are more strongly bowed outward than the anterior and posterior ribs. The first rib, which is obviously shorter than the second, has the distal end of the shaft abruptly expanded, forming a pestile-like extremity. The ribs attached to the second to ninth dorsal vertebrae inclusive have large club-like distally expanded extremities, those of the fourth to the seventh in the series being especially large. The distal end surfaces of these ribs are quite rugose. The upper halves of the shafts of the posterior ribs (eleventh to fourteenth) are nearly circular in cross-section. The five hinder ribs are single headed. The thirteenth and the fourteenth pairs of ribs have a large expanded head conspicuously larger than the slender shaft. The shafts of the fifteenth pair of ribs are reduced presumably to a vestigial condition.

**Table 17—Measurements (in millimeters) of right femur**

<table>
<thead>
<tr>
<th>Greatest length, as preserved</th>
<th>197.5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Greatest transverse diameter of proximal end</td>
<td>37+</td>
</tr>
<tr>
<td>Least transverse diameter of head and level of lesser tuberosity</td>
<td>27</td>
</tr>
<tr>
<td>Least antero-posterior diameter of shaft at same level</td>
<td>13.3</td>
</tr>
<tr>
<td>Greatest transverse diameter of shaft through lesser tuberosity</td>
<td>29.5</td>
</tr>
<tr>
<td>Least transverse diameter of shaft below lesser tuberosity</td>
<td>18</td>
</tr>
</tbody>
</table>

**Table 18—Measurements (in millimeters) of the ribs**

<table>
<thead>
<tr>
<th></th>
<th>1st Left</th>
<th>2nd Left</th>
<th>4th Right</th>
<th>6th Left</th>
<th>7th Right</th>
<th>9th Left</th>
<th>10th Left</th>
<th>13th Right</th>
</tr>
</thead>
<tbody>
<tr>
<td>Greatest length, in a straight line</td>
<td>640±</td>
<td>790</td>
<td>820±</td>
<td>870</td>
<td>840±</td>
<td>820±</td>
<td>730</td>
<td></td>
</tr>
<tr>
<td>Posterior face of tuberculum to extremity of capitulum</td>
<td>125.5</td>
<td>158</td>
<td>132</td>
<td>137</td>
<td>103</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Greatest antero-posterior diameter of distal club</td>
<td>80.5</td>
<td>90.5</td>
<td>94</td>
<td>103.5</td>
<td>88.5</td>
<td>79</td>
<td>57.5</td>
<td>54.5</td>
</tr>
<tr>
<td>Greatest transverse diameter of distal club</td>
<td>68</td>
<td>51.5</td>
<td>76.5</td>
<td>75.5</td>
<td>88</td>
<td>48</td>
<td>41</td>
<td>37</td>
</tr>
</tbody>
</table>

**Sternum**

The sternum of this archaeocete appears to have consisted of five or six segments, including a large presternum or manubrium, three or four segments of the mesosternum, and a short posteriorly bifurcated xiphisternum. Two large rugose nodular masses (No. 4675, U. S. N. M.) found with one of the skeletons may represent halves of a mesosternal segment, in which case each segment ossifies from two centers and these unite in most instances to form a continuous osseous element. The descriptions that follow are based on four sternal elements, including the manubrium, and two nodular masses belonging to one
individual (No. 4675, U. S. N. M.), the manubrium and the second mesosternal segment associated with the skull (No. 4674, U. S. N. M.), and two isolated prester nal segments (Nos. 12064 and 13681, U. S. N. M.). Four sternal elements are figured by Müller, including three inverted prester nal segments (1849, pl. 9, figs. 3, 4, 5) and one that may represent the xiphisternum (1849, pl. 8, fig. 8, and pl. 9, fig. 6).

The manubrium or presternum is elongated, wider dorsally than ventrally, shield-like in outline as viewed from the dorsal face (fig. 27), deeply notched medially in front, and has prominent antero-external angles which seemingly are turned or rolled downward; hinder half of dorsal surface distinctly flattened; lateral surfaces (fig. 27c) concavely curved from end to end and slope obliquely from dorsal to ventral surface; ventral surface (fig. 27b) is concave from end to end, and convex from side to side; and the two oblique surfaces comprising the bluntly pointed hinder end are very rugose. Very little variation in form was observed in the prester nal segments, although they belong to indi viduals differing considerably in size (see table 19, p. 74). The manubrium of *Basilosaurus cetoides* in comparison to that of *Prozeuglodon isis* (Stromer, 1908b, pl. 6, figs. 2–3) is more deeply bifurcated anteriorly, not expanded near the middle of its length, and relatively narrower in proportion to its length.

![Fig. 27—*Basilosaurus cetoides* (Owen). Manubrium of ster num, No. 13681, United States National Museum. a, dorsal view; b, ventral view; c, lateral view. X4. Upper Eocene, upper Jackson formation, Alabama.](image-url)
The arrangement of the segments of the mesosternum (pl. 7) is highly conjectural, since it is not known whether or not they were found in natural sequence. The sternal element tentatively designated as the first segment of the mesosternum (pl. 7, fig. 6) is broadly oval in outline, transversely widened and antero-posteriorly shortened; dorsal surface quite flat, but depressed medially near posterior end; lateral surfaces slope obliquely from dorsal to ventral surface; saddle-shaped ventral surface very narrow as compared to dorsal surface, concave from end to end, and convex from side to side; and anterior and posterior surfaces are strongly rugose.

On the pentagonal sternal element (pl. 7, fig. 11) identified as the second segment of the mesosternum, the dorsal surface is rather flat, but is depressed medially near the posterior end; lateral surfaces slope obliquely from dorsal to ventral surface; ventral surface quite narrow, concave from end to end, and convex from side to side; the two oblique surfaces comprising the obtusely pointed anterior end are very rugose; and the slightly curved posterior surface is likewise rugose.

The third segment of the mesosternum (pl. 7, fig. 12) is also pentagonal in outline, but is smaller than the second segment; transverse diameter greater than the antero-posterior diameter; dorsal surface flat; lateral surfaces very rugose, but slope less obliquely from dorsal to ventral surface than on preceding sternal segment; ventral surface small but relatively larger than on preceding segment, concave from end to end, and convex from side to side; anterior end squarely truncated but very rugose; and the two rugose oblique surfaces comprising the hinder end meet medially in a blunt prominence.

The two nodular masses (No. 4675, U. S. N. M.), which are assumed to represent halves of a mesosternal segment, are quite similar in general appearance, but one (pl. 7, figs. 1–2) is somewhat larger than the other (pl. 7, figs. 3–4). These nodular masses (Lucas, 1904, p. 436), although more or less ovoidal in general shape, are somewhat compressed in one direction and widened in the other. Both of these bones are rather rugose on all sides, but one of the flattened convex surfaces is less roughened than the others. They are rather thick at one end and slightly less so on one side, but the other end and the adjacent side are compressed to such an extent that the irregular excrescences form a continuous thick ridge. The measurements of these nodular masses are, respectively, as follows: Length, 123 and 112 mm.; width, 102 and 88 mm.; and maximum thickness, 82 and 77 mm.

A short posteriorly bifurcated bone figured by Müller (1849, pl. 9, fig. 6) may represent the terminal sternal segment. The measurements given by Müller (1849, p. 30) for this bone, converted into millimeters, are as follows: Length, 76 mm.; breadth, 93 mm.; and thickness anteriorly, 38 mm. Should subsequent discoveries show that this is actually the xiphisternum, then Basilosaurus cetoides possessed a quite different hinder sternal element than that of Prozeuglodon isis (Stromer, 1905b, pl. 6, fig. 4), which consists of a quadrangular anterior portion and a long posteriorly attenuated backward projecting process which is bifurcated at the extremity.

<table>
<thead>
<tr>
<th></th>
<th>No. 4675</th>
<th></th>
<th>No. 4674</th>
<th></th>
<th>No. 13904</th>
<th></th>
<th>No. 13981</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>U. S. N. M.</td>
<td></td>
<td>U. S. N. M.</td>
<td></td>
<td>U. S. N. M.</td>
<td></td>
<td>U. S. N. M.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Manubrium</td>
<td>Meosternum I</td>
<td>Meosternum II</td>
<td>Meosternum III</td>
<td>Manubrium</td>
<td>Meosternum I</td>
<td>Meosternum II</td>
<td>Meosternum III</td>
</tr>
<tr>
<td>Antero-posterior diameter, medially</td>
<td>198</td>
<td>132.5</td>
<td>153</td>
<td>128</td>
<td>202</td>
<td>145</td>
<td>171</td>
<td>158</td>
</tr>
<tr>
<td>Transverse diameter, anteriorly</td>
<td>130.8</td>
<td>.</td>
<td>156</td>
<td>80±</td>
<td>215</td>
<td>147±</td>
<td>161.8</td>
<td>121±</td>
</tr>
<tr>
<td>Transverse diameter, posteriorly</td>
<td>151</td>
<td>150</td>
<td>143</td>
<td>138</td>
<td>171.5</td>
<td>170+</td>
<td>126</td>
<td>128</td>
</tr>
<tr>
<td>Dorso-ventral diameter, medially</td>
<td>94</td>
<td>77</td>
<td>85</td>
<td>66.5</td>
<td>101</td>
<td>83</td>
<td>84</td>
<td>83</td>
</tr>
<tr>
<td>Dorso-ventral diameter, posteriorly</td>
<td>75</td>
<td>79</td>
<td>77</td>
<td>73</td>
<td>85</td>
<td>77</td>
<td>71.8</td>
<td>55</td>
</tr>
</tbody>
</table>

1 Medially.
PROZEUGLODON


Permanent dental formula, I \( \frac{1\sqrt{3}\times}{3} \), C\( \frac{1\sqrt{3}\times}{3} \), Pm \( \frac{4\sqrt{3}\times}{3} \), M \( \frac{4\sqrt{3}\times}{3} \); deciduous dental formula, D\( \frac{1\sqrt{3}\times}{3} \), Dpm \( \frac{4\sqrt{3}\times}{3} \).

Pm\( \sqrt{2} \) separated from Pm\( \sqrt{3} \) by a wide interval; Pm\( \sqrt{3} \) may or may not be closely approximated to Pm\( \sqrt{4} \); Pm\( \sqrt{4} \) to M\( \sqrt{2} \) form a closed series; crowns of Pm\( \sqrt{2} \) and Pm\( \sqrt{3} \) approximately equal in size; Pm\( \sqrt{2} \) to M\( \sqrt{2} \), inclusive, have two roots; crown of Pm\( \sqrt{1} \) more caniniform than molariform in appearance; Pm\( \sqrt{3} \) and Pm\( \sqrt{4} \) approximately equal in size; Dpm\( \sqrt{3} \) and Dpm\( \sqrt{4} \) possess an enamel-covered buttress, which seemingly is a remnant of the postero-internal cusp, and have three roots; rostrum equivalent to 58 per cent of condylobasal length of skull; greatest width of supraoccipital shield equivalent to less than 85 per cent of distance from dorsal margin of foramen magnum to apex of shield; forelimb slender; scapula unusually high in proportion to length, the greatest vertical diameter being approximately equal to greatest antero-posterior diameter, with anterior angle rounded and posterior angle not markedly produced, and with slender coracoidal and greatly elongated acromial processes, both directed forward and downward; head of humerus normal, and greater and lesser tuberosities sharply differentiated; elbow hinged; radius has convex anterior profile, viewed from the side; shaft of ulna not conspicuously narrower than olecranon process; manus not known; pelvis unknown.

Vertebral formula presumably similar to that of Basilosaurus; cervical vertebrae have compressed centra and no ankylosis of consecutive centra; atlas has a bifurcated hypophysial process, and the vertebrarterial foramen at base of transverse process is smaller than the transverse foramen in neural arch for first spinal nerve and transverse artery; axis has short but broad transverse processes and shortened neural spine; transverse processes of third cervical have no narrow process projecting forward from near base of ventral edge; lower transverse processes of sixth cervical conspicuously expanded antero-posteriorly; trunk and tail elongated; anterior dorsals have a vestigial backward projecting anapophysis which arises from hinder face of base of diaphysis; the posterior dorsals, all of the lumbarss, and the sacrals have elongated centra, relatively short, thin and rather wide neural spines, as well as relatively short transverse processes, and have the postzygapophysial portion of neural arch separated from succeeding vertebra by increasing intervals proportional to length of centrum; sacral vertebra has ends of transverse processes slightly upturned; the manubrium, the largest of the sternal elements, is expanded transversely near middle of its length; the xiphisternum consists of a quadrangular anterior portion and a long backward projecting attenuated xiphoïd process which is bifurcated at extremity.

PROZEUGLODON ISIS (Andrews)


Type locality.—Birket-el-Qurun beds west of the lake (Birket-el-Qurun), Fayum, Egypt. Lower upper Eocene.

Type specimen.—An imperfect right mandible, which lacks the coronoid process, the condyle, and the hinder lower angle; the serrated cheek teeth have more or less imperfect crowns; and alveoli for three incisors and the canine are present. No. 10208, Geological Museum, Cairo; collector, H. J. L. Beadnell.

Referred specimens.—(1) Skull and right mandible. Palatal region and base of skull imperfectly preserved; incisors and canine missing; Pm1 erupting; Dpm2, Dpm3, Dpm4 and M1 have high crowns; posterior molars missing; distal extremity as well as condyle and hinder lower angle of mandible missing. From the lower part of the Birket-el-Qurun beds in a valley about 12 kilometers west-south-west of a hill called Gar-el-Gehannem lying to the west of the lake, Fayum, Egypt. No. 9319, Geological Museum, Cairo; cast of type skull in Zoological Department, British Museum (Natural History). This is the type of Prozeuglodon atrox Andrews (1906).

(2) Isolated vertebrae, “presumably associated and perhaps belonging to the same animal as the portions of the skull” (No. M-9266, Brit. Mus.). Atlas, No. 9329; axis, No. 9330; and (?) third cervical vertebra, No. 9332, Geological Museum, Cairo. [Stromer (1908b, pp. 121, 136) referred these cervical vertebrae to Dorudon osiris.]


(4) Portions of a somewhat disarticulated skull of an immature individual, comprising the cranium and the major portion of the rostrum; nasals destroyed; Dpm3, Dpm4, and M1 are in situ. An incomplete right mandible. From the lower part of the Birket-el-Qurun beds in a valley about 12 kilometers west-south-west of a hill called Gar-el-Gehannem lying to the west of the lake, Fayum, Egypt. No. M-9266, Geological Department, British Museum (Natural History); and artificial endocranial cast of this skull, No. M-9265. This is the para type skull of Prozeuglodon atrox (Andrews, 1906).

(5) Several fragments of a composite skull, lacking several parts, and also both mandibles, of which the hinder ends are missing and only the basal portions of the crowns of the deciduous teeth are preserved. From a yellow sandstone belonging to the Birket-el-Qurun stage; Qasr-Qurun, 26 meters above the level of the lake, Fayum, Egypt. No. 11234, Württembergische Naturaliensammlung, Stuttgart; collector, Richard Markgraf; 1904 (St. 1, Stromer, 1908b, p. 136).

(6) An incomplete skull with three incisors and second premolar in place, as well as the basal portion of the crowns of Pm3 and Pm4. Associated with this skull are an atlas, the centrum of an axis, and a number of trunk vertebrae which lack well-preserved processes. From a yellow sandstone belonging to the Birket-el-Qurun stage, Fayum, Egypt. No. 11413, Württembergische Naturaliensammlung, Stuttgart (St. 8, Stromer, 1908b).

(7) Right and left mandibles, which lack the anterior extremities; both are laterally crushed and belong to two different individuals. Five cheek teeth (Pm2 to M3, except Pm4) are preserved in the right mandible, and three (Pm2 to Pm4) in the left mandible. Found at a site west of Dimê, Fayum, Egypt, and belonging perhaps to the Qasr-el-Sagha stage. No. 11417, Württembergische Naturaliensammlung, Stuttgart; collector, Richard Markgraf; 1905 (St. 5a, 5b, Stromer, 1908b).

(8) An isolated humerus and a slightly crushed and eroded right ulna lacking the distal epiphysis. Fayum, Egypt. No. 11417a, Württembergische Naturaliensammlung, Stuttgart; collector, Richard Markgraf (St. 15, Stromer, 1908b).

(9) A nearly complete skeleton. Skull almost complete and very slightly crushed, with five cheek teeth (Pm2 to M2, all with enamel on crowns) in place; two slender hyoid
bones; hinder end of left mandible with basal portions of crowns of Pm3 and Pm4; atlas; third, fifth and sixth cervical vertebrae; thirteen dorsal vertebrae; eight large lumbar vertebrae; one anterior and two quite small posterior caudal vertebrae; many ribs; the manubrium and three other sternal segments, one of which is probably the xiphisternum; the left scapula and the articular head of the right scapula; the left humerus and the distal end of the right humerus; a laterally compressed left ulna without distal end and the distal half of the right ulna. From a yellow sandstone belonging to the Birket-el-Qurun stage; Fayum, Egypt. No. 11787, Württembergische Naturwissenschaftliche Sammlung, Stuttgart; collector, E. Fraas; 1906 (St. 9, Stromer, 1908b).

(10) An incomplete cranium that lacks supraorbital and zygomatic processes; right maxillary, premaxillaries, and nasals missing; and supraoccipital shield incomplete. From a very fine-grained sandstone at Uadi Rojan1 on the northern steep cliff of the Fayum basin, belonging either to the Birket-el-Qurun or the Qasr-el-Sagha stage. No. 11951a, Württembergische Naturwissenschaftliche Sammlung, Stuttgart; collector, Richard Markgraf; December 1906–January 1907 (St. 10, Stromer, 1908b).

(11) A fractured right mandible, with tooth series from C. to and including M3 in place, and the alveoli of I2 and I3; three isolated conical crowned teeth; a fragment of a right maxillary, with four cheek teeth (Pm2 to M1, all with enamel on crowns) in place; the atlas; the third and the fifth cervical vertebrae; six anterior and five posterior dorsal vertebrae; four caudal vertebrae, mostly without epiphyses; one whole and several incomplete ribs; an anterior segment of the sternum; a right scapula which is damaged dorsally; and a left humerus that lacks the head. From a fine-grained yellow sandstone belonging to the Birket-el-Qurun stage, Fayum, Egypt. No. 1904. XII. 135, Paläontologische Sammlung, Alte Akademie, München; collector, Richard Markgraf; 1904 (Mn. 13, Stromer, 1908b).

(12) Rostral fragment, consisting of portions of right and left premaxillaries and of left maxillary; the second incisor is in place. From a very fine-grained gray sandstone containing white mollusk remains and belonging to the Birket-el-Qurun stage, Fayum, Egypt. No. 1904. XII. 135a, Paläontologische Sammlung, Alte Akademie, München; collector, Richard Markgraf; 1904 (Mn. 15, Stromer, 1908b).

(13) Right and left mandibles. The right mandible is essentially complete, except for a short section in the region of the canine which is missing; it lacks also the extreme distal end the hinder lower angle; six cheek teeth (Pm1 to M3, with exception of Pm3) are in place. Only the hinder half of the left mandible is preserved and it is broken off anteriorly in front of alveolus for Pm2; five cheek teeth (Pm3 to M3) are in place, although the hinder half of crown of Pm4 is destroyed. The enamel is preserved on the crowns of all of these teeth. From a very fine-grained grayish-yellow sandstone containing white mollusk remains and belonging to the Birket-el-Qurun stage, Fayum, Egypt. No. 1904. XII. 135b, Paläontologische Sammlung, Alte Akademie, München; collector, Richard Markgraf; 1904 (Mn. 14, Stromer, 1908b).

(14) Isolated skeletal remains found in a yellow sandstone belonging to the Birket-el-Qurun stage, Fayum, Egypt. Two single rooted teeth; No. 1904. XII. 135c. The upper end of a left humerus without the head and the upper half of a right radius; No. 1904. XII. 135d. The sixth cervical vertebra which lacks the neural arch, a thoracicolumbalis vertebra with long centrum, three lumbar vertebrae, two caudal vertebrae, a two-headed rib, and a hinder sternal segment; No. 1904. XII. 135e, Paläontologische Sammlung, Alte Akademie, München; collector, Richard Markgraf; 1904 (Mn. 16, Stromer, 1908b).

(15) Anterior end of right mandible, without the teeth. From the Birket-el-Qurun

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stage, northern Fayum, Egypt. No. 1904. XII. 135f, Paläontologische Sammlung, Alte Akademie, München; collector, Richard Markgraf; 1904.

(16) Several anterior ribs. From the Birket-el-Qurun stage, 6 kilometers west of Dimé, Fayum, Egypt. No. 1922. IX. 7, Paläontologische Sammlung, Alte Akademie, München; collector, Richard Markgraf; 1914.

(17) An imperfect axis. From the western island (Geziret-el-Qorn) of the lake (Birket-el-Qurun), Fayum, Egypt; Birket-el-Qurun stage (fide, Andrews, 1906, p. xi). No. M-17, Geologisch-Paläontologisches Institut und Museum der Universität Berlin; collector, Georg Schweinfurth; 1879.

(18) An incomplete skull that lacks the anterior ends of the premaxillaries, the ascending process of right premaxillary, most of the upper surfaces of both maxillaries, the palatines and pterygoids in the region of the internal choanal tube, both jugals, the anterior end of the right zygomatic process, I3 on both sides, the left C, Pm1 on both sides, and the right M1 and M2. The left I1 and I2 have been artificially implanted in the restored end of the rostrum, but on the right side I1 and I2 are missing. The crowns of all the cheek teeth are strongly abraded. The outer orbital border is incomplete on both supraorbital processes. The pars cochlearis is incomplete on both periotics, which are in place, but both tympanic bullae are missing. The hinder face of the cranium as well as most of the basi-craniat region are fairly well preserved. From a yellow sandstone belonging to the Birket-el-Qurun stage, near Qasr-Qurun in the Fayum Basin, Egypt. No. 14381, Department of Vertebrate Palaeontology, American Museum of Natural History; collector, Richard Markgraf.

SKULL

The distinguishing features of *Prozeuglodon isis*, as compared with the skull of *Basilosaurus cetoides*, are the separation of the posterior extremities of the nasals by the long larial process of the combined frontals, the unusually wide interval between the crowns of Pm2 and Pm3, the more abrupt rise of the dorsal profile at the level of the middle of the orbit, the more strongly backward folded lambdoidal crests, and a narrower intertemporal constriction. Otherwise, the general conformation and proportions of the skull of *P. isis* are somewhat similar to *B. cetoides*. The rostrum constitutes about 58 per cent of the condylobasal length of the skull.

Parietals normal in relation to adjacent bones, contributing the roof for the cranium and the major portion of the intertemporal constriction, and meeting on the mid-line to form a high sagittal crest that extends forward to hinder edges of frontals; foramen on lateral wall of cranium in left parietal located 103.5 mm: anterior to hindermost edge of lambdoidal crest (No. 14381, A. M. N. H.); dorsal profile rises abruptly behind level of middle of orbit; each parietal contributes a portion of the rather steep lateral cranial wall and meets the squamosal in a dentate suture that extends downward and forward; squamosal rather large, the upper surface of its anterior border sloping steeply to the temporal edge; ventro-anterior or temporal edge of squamosal extended forward as a thin shelf or projecting ledge; zygomatic process slender, tapering anteriorly, and with its ridge-like upper edge continued backward and upward to join with low lambdoidal crest along outer and hinder edges of squamosal, and forming with the latter the posterior boundary of the enormous temporal fossae; maximum zygomatic breadth equivalent to 50 per cent of condylobasal length of skull; supraoccipital shield higher than broad, strongly concave transversely, with vertical median ridge, and bounded laterally by the prominent lambdoidal crest, of which the anterior face is contributed by the corresponding parietal and the posterior face by the supraoccipital; middle portion of lambdoidal crest strongly folded backward; width of supraoccipital shield (pl. 9) greater in proportion to its height than in
*Dorudon stromeri*, its maximum width being about 0.84 of its maximum vertical diameter above the foramen magnum; exoccipital of moderate width (fig. 28), with sinuous and fairly thick external edge; upper edge of exoccipital free externally, and not in contact with lambdoidal crest of squamosal dorso-internally; foramen magnum small; occipital condyles semi-elliptical in outline, considerably broader at the apex than at base, slightly convex from side to side and set off from exoccipital surface by shallow grooves; paroccipital process large, but not prolonged downward; intertemporal region narrow and relatively shorter than in *Dorudon osiris*; lateral walls of intertemporal constriction are nearly vertical above elongated sphenorbital fissure; groove for optic nerve originating at optic foramen, which is situated anterior to and above level of sphenorbital fissure, extends upward and forward on lateral surface of orbitosphenoid and then curves outward on ventral face of supraorbital process of frontal; parietals and frontals quite thick in region of sutural union; forehead slightly depressed behind nasals; supraorbital process of frontal broadened, extended laterally beyond level of jugal and arched at extremity; postorbital projection of supraorbital process noticeably thickened and preorbital angle relatively thin; orbit of moderate size; breadth of skull across supraorbital processes relatively greater than in *Dorudon osiris*; lachrymal wedged in between preorbital end of supraorbital process and the jugal, forming part of anterior wall of orbit, and abutting against hinder border of maxillary; anterior end of jugal mortised into outer face of maxillary as in *Dorudon osiris* and ankylosed with lachrymal; an open groove for lachrymal duct present; lateral surface of maxillary grooved below anterior extremity of jugal; rostrum increases in width rather abruptly behind level of anterior extremities of nasals; nasals elongated, strongly attenuated anteriorly, slightly
convex from side to side, and attain their maximum width posterior to hinder ends of ascending processes of premaxillaries; posterior extremities of nasals widely divergent and separated by long wedge-like narial process of combined frontals; anterior extremities of nasals constitute posterior border of dorsal narial fossa, which they overhang to some extent, the posterior end of this fossa being on a level with the interval between Pm1 and Pm2 and the anterior end being between I3 and C; the premaxillaries contribute the floor and the lateral walls of the rather small dorsal narial fossa; ascending process of premaxillary lodged in groove on upper internal border of maxillary and ending above hinder edge of crown of Pm3; emarginate proximal end of maxillary abuts against supraorbital process of frontal superiorly, and inferiorly projects backward below the latter to accommodate the posterior molars; the large antorbital foramen lies above interval between Pm2 and Pm3; flat oral surfaces of premaxillaries prolonged backward as a narrow tongue-like wedge to behind level of Pm1, separating anterior extremities of maxillaries; major portion of oral surface contributed by the more or less flattened horizontal plates of maxillaries; molar series set off from palatal surface by a deep excavation; bony palate prolonged backward by elongation of palatines and by adjacent thin plates of pterygoids, forming an inclosed tube for the internal choanae; a V-shaped elevation present on palatal surface of this choanal tube; suture between basioccipital and basisphenoid obliterated; median basiscranial region bounded laterally in front by hamular plates of pterygoids and behind by lateral descending plate-like processes of basioccipital, which are truncated distally and transversely furrowed on ventral face; pterygoid fossa for accessory air sinus of middle ear bounded internally by thin hamular plate of pterygoid, anteriorly by pterygoid, and externally by the postero-external limb of the pterygoid and the bifid anterior end of the squamosal; large foramen ovale for exit of mandibular branch of trigeminal nerve located in the bifurcated anterior end of the squamosal which contributes part of outer wall of pterygoid fossa; zygomatic processes slender, attenuated anteriorly and rather strongly bowed outward; ventral surface of zygomatic process of squamosal furnished with broad concave glenoid articular surface and a short, thin, curved postglenoid process, which is not as strongly curved as in *Dorudon osiris*; a well-defined channel for external auditory meatus, which originates on postero-internal surface of squamosal, continues its course outward behind the base of the postglenoid process of that bone; paroccipital process short, broad, and separated from hinder edge of lateral descending process of basioccipital by the deep notch for the jugular leash; a rugose cavity present on paroccipital process for reception of stylohyoid; posterior process of periotic wedged in between exoccipital and hinder border of squamosal.

On the left side of the type skull of *Prozeuglodon atrox* (No. 9319, Geol. Mus., Cairo) the squamosal, exoccipital, and occipital condyle are destroyed; the outer border of the left supraorbital process is incomplete and the left jugal is missing. The right tympanic bulla is crushed into the tympano-periotic recess. The right lachrymal is quite distinct though small, and is correctly figured by Andrews (1906, pl. 21). Both nasal bones are incomplete anteriorly. The relations of the bones in the temporal region are very clearly shown on this skull. The alisphenoid forms part of the outer wall of the cranium in the temporal fossa and is bounded by pterygoid, parietal, and squamosal; its anterior border forms the outer lip of the posterior end of the deep groove for the maxillary division of the trigeminal nerve; and anteriorly the orbitosphenoid is pierced by a foramen for the optic nerve. The skull of an adult individual of *Zygorkiza kochii* shows that Andrews (1906, pl. 21, figs. 1B, 1D) has misidentified the sphenorbital fissure and labeled it the optic foramen. The optic foramen should be located in the circular enlargement that is indicated at the anterior end of this groove. The distinctness of the sutures between the several bones, which comprise the skull, show that this individual had not reached physical maturity. The enamel crowns of the upper cheek teeth are well preserved. The first
upper premolar is erupting; Pm2 is the largest of the cheek teeth and Pm4 is slightly larger than M1. The second upper molars, if originally present, are unknown.

It is obvious that the paratype skull of *Prozeuglodon atrax* (No. M-9266, Brit. Mus.) belongs to an immature individual because (1) the sutures between the opposite parietals and frontals along the mid-line of the cranium are still open; (2) the ventral surface of the basioccipital is incompletely ossified; (3) the suture between the supraoccipital and the adjoining parietals is open along the lambdoidal crest; (4) the outer end of the exoccipital is rather loosely connected with the adjoining squamosal and the posterior process of the periotic is not wedged in tightly; (5) the maxillaries are rather loosely attached to anterior projections of frontals; (6) the anterior extremity of the right jugal is missing from the groove in which it is lodged in the maxillary; (7) the posterior mandibular molar has not entirely erupted, inasmuch as a portion of the crown and the basal posterior cusp are below alveolar surface of the ramus; (8) the alveoli are much larger than the roots of the corresponding teeth; and (9) the rims of the alveoli are incompletely ossified.

On the paratype skull as now exhibited the posterior ends of the maxillaries (superior surface) are separated from the frontals by an interval of 17.5 mm., and, with the exception of M1, the molars and the corresponding portion of the inferior backward projection of the maxillary are missing. The posterior margins of the sutural grooves on the frontals for the nasals are 56.5 mm. behind the distal ends of the median projections of the frontals which ordinarily are concealed by these overlying bones. Both nasal bones are missing. The position of the wide groove on the maxillary clearly shows that the outer margin of the nasal underlaps the superior internal edge of the maxillary posterior to the hinder end of the premaxillary. The fore wall of the braincase is destroyed in the region of the sphenoidal fissure and the optic foramen. Both jugals are missing and the postero-external angle of the supraorbital process is destroyed. The right occipital condyle is missing and the left one is eroded; the upper margin of the foramen magnum is incomplete; and the basioccipital is broad, with large lateral roughened tuberosities. The crowns of all the cheek teeth are either fractured or else broken off near the base.

Stromer (1908b, pp. 136–138) has described another skull (No. 11951a, Stuttgart), belonging likewise to a young individual, on which the exoccipital is already ankylosed to the basioccipital; the basisphenoid and supraoccipital, however, are free, but the parietals and frontals are ankylosed in the mid-line.

Skulls of juvenile and subadult individuals of this large archaeocete are readily distinguishable from the skull of the smaller *Dorudon intermedius* by (1) the relatively stouter rostrum, (2) the relatively shorter intertemporal region, (3) the less widely spreading zygomatic arches, (4) the shorter nasals, (5) the lower braincase, and (6) the wider supraoccipital shield.

For measurements of the skulls, see table 62 (p. 246).

**TYMPANIC BULLA**

Both of the tympanic bullae, which belong to the Stuttgart skull (No. 11787), have the anterior end damaged. Although its dimensions are slightly greater, the general conformation of the bulla of this species is remarkably like that of *Dorudon intermedius*. In proportion to the dimensions of the skull, however, the bulla of this species is relatively small. The left tympanic bulla, which is incomplete anteriorly, measures 83 + mm. antero-posteriorly and 58.2 mm. transversely.

**PERIOTIC**

The periotic bones of the Stuttgart skull (No. 11787) were not studied critically. The right and left periotic bones are attached to the skull (No. 14381) in the American Museum of Natural History. On both of these periotics, unfortunately, the ventral portion of the
pars cochlearis is destroyed, but otherwise they are complete. In general conformation, the periotic of P. isis is similar to that of Zygorhiza kochii. The outer denser portion is prolonged dorsally to form an inwardly curved and laterally compressed superior plate-like process, which is applied to the squamosal on the inner wall of the cranium. The elongated posterior process is wedged between the squamosal and the exoccipital. The ventral face of the posterior process is faintly grooved longitudinally and its extremity is narrowed dorsally. A thin osseous crest, which constitutes the hinder boundary of the groove for the external auditory meatus, overlaps the anterior border of this process. Near the middle of its length, the antero-posterior diameter of the posterior process of the left periotic is 26.5 mm. The rather large fenestra rotunda is situated on the hinder face of the pars cochlearis somewhat above the level of the ventral surface of the posterior process.

On the extero-lateral surface of the pars cochlearis, near its upper limit and behind the middle of its length, is situated the fenestra ovalis. The small epitympanic orifice of the Fallopian aqueduct, which opens into the narrow groove for the facial nerve, is located on the roof of the recessus epitympanicus and above the level of the rim of the fenestra ovalis. The groove for the facial nerve becomes slightly wider posteriorly and curves outward around the postero-internal angle of the posterior process. Internal to this groove and behind the fenestra ovalis is a rather large fossa for the stapedial muscle. The small fossa incudis for lodging the crus breve of the incus is located opposite and external to the epitympanic orifice of the Fallopian aqueduct. The boundaries of this fossa are not as sharply delimited as on the periotic of Zygorhiza kochii. The large fossa for the reception of the head of the malleus is situated on a protuberance in front of the epitympanic orifice of the aquaeductus Fallopii. A prominent crest is developed on the ventral face of the laterally compressed anterior process. A deep obliquely curved groove on the external face of the periotic seems to mark the hinder limit of the anterior process, since it terminates ventrally opposite the fossa for the head of the malleus. The depression thus formed at the ventral termination of the above-mentioned groove is bounded externally by the ventro-internal rim of the squamosal. This small cavity is assumed to represent the fovea epitubaria which lodges the processus tubarius of the tympanic bulla.

**Table 20—Measurements (in millimeters) of the left periotic**

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance from tip of anterior process to tip of posterior process</td>
<td>110</td>
</tr>
<tr>
<td>Distance from anterior end of anterior process to posterior face of pars cochlearis</td>
<td>47.6</td>
</tr>
<tr>
<td>Distance from foramen rotundum to extremity of posterior process</td>
<td>70</td>
</tr>
<tr>
<td>Distance from epitympanic orifice of Fallopian aqueduct to anterior end of anterior process</td>
<td>35</td>
</tr>
</tbody>
</table>

MANDIBLE

Eight mandibles of this archaeocete were examined. The right and left mandibles in the collection at Munich (No. 1904. XII. 135b) were selected as being typical, and the following diagnosis is based largely on them.

Mandible rather long, with slender and comparatively narrow horizontal ramus; total length about 1100 mm.; horizontal ramus terminates anteriorly in a rounded end in which is located the alveolus of the first incisor; edges of alveoli of the four anterior single-rooted teeth slightly raised; from before backward the horizontal ramus increases in depth rather gradually up to Pm², the depth at level of I² being 80 mm. and at level of Pm² at least 112 mm.; the interval between Pm² and Pm³ marks the transition to the somewhat steeply rising convex anterior edge of the coronoid process; the depth of the right ramus at level of Pm⁴ is 133 mm. and at posterior margin of M³ it is 212.5 mm.; outer face of horizontal ramus somewhat convex in front, but becoming flattened posteriorly; the small mental foramina are placed anterior to Pm²; internally the flat symphysial surface extends backward to about the middle of Pm², its maximum length being about 460 mm.; coronoid
process rather broad and thin, the maximum depth of the right mandible through this process being 337 mm. and its posterior edge is truncated almost vertically; entrance to alveolar canal extraordinarily wide; condyle convex dorso-ventrally and slightly broader than high, its upper surface being on a level with alveolar margin of M1; and a prominent longitudinal swelling on outer surface of mandible extends forward a short distance from condyle.

The right mandible of the type of Prozeuglodon atrox lacks the condyle and the hinder border of the coronoid process; the anterior extremity of this mandible is likewise missing. Three premolars are in place in this mandible, but their crowns are not complete. The right mandible associated with the paratype skull of Prozeuglodon atrox is incomplete. It possesses alveoli for four single-rooted teeth, as well as five damaged two-rooted cheek teeth. Of the latter, the posterior molar is the most complete, although it is in the process of eruption and only a portion of the crown has pushed its way above the alveolar surface of the ramus. Except for their smaller dimensions, these mandibles are essentially similar to those of adults.

Table 21—Measurements (in millimeters) of mandibles

<table>
<thead>
<tr>
<th>No. 1904. XII. 135b Munich Right</th>
<th>No. 1904. XII. 135b Munich Left</th>
<th>No. 1904. XII. 135b Munich Right</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of mandible, from hinder face of condyle to extremity</td>
<td>1140±</td>
<td>1085±</td>
</tr>
<tr>
<td>Vertical height of mandible through coronoid process</td>
<td>337</td>
<td>325</td>
</tr>
<tr>
<td>Vertical diameter of condyle</td>
<td>50.5</td>
<td>52</td>
</tr>
<tr>
<td>Antero-posterior diameter of symphysis</td>
<td>460±</td>
<td>460±</td>
</tr>
<tr>
<td>Vertical height of mandible at level of I2</td>
<td>60</td>
<td>80</td>
</tr>
<tr>
<td>Vertical height of mandible at level of C</td>
<td>91</td>
<td>93.2</td>
</tr>
<tr>
<td>Vertical height of mandible at level of Pm3</td>
<td>108</td>
<td>111.8</td>
</tr>
<tr>
<td>Vertical height of mandible at level of Pm4</td>
<td>133</td>
<td>136</td>
</tr>
<tr>
<td>Vertical height of mandible at level of M3</td>
<td>195</td>
<td>212.5±</td>
</tr>
<tr>
<td>Anterior edge of Pm2 to hinder edge of M3</td>
<td>385</td>
<td>420</td>
</tr>
<tr>
<td>Posterior edge of M3 to hinder face of condyle</td>
<td>250</td>
<td>275</td>
</tr>
<tr>
<td>Diastema between Pm2 and Pm3</td>
<td>40</td>
<td>38</td>
</tr>
</tbody>
</table>

1 At posterior edge of M3. 2 At anterior edge of I3.

Permanent Dentition

The tooth formula is \( \frac{3}{3}, \frac{1}{1}, \frac{4}{4}, \frac{2}{2} \). All of the anterior upper single-rooted teeth, including the three incisors, the canine, and the first premolar have dropped out of their respective alveoli on the Stuttgart skull (No. 11787). Judging from the alveoli, the first incisor is directed somewhat forward, while the crowns of I2 and I3 are directed downward and are curved slightly backward. One damaged I2 indicates that the incisors have the enamel on the inside of the crown strongly wrinkled, and in addition anterior and posterior vertical carinate edges are present. The carinate on the cutting edges of the canine are more strongly developed than on the incisors, and vertical striæ extend upward to apex of the crown. The alveoli of the anterior teeth (I1 to Pm3) are separated by interspaces of varying width; the interspaces between C and Pm1, and between Pm1 and Pm2 are approximately equal; and the minimum interspace is between Pm2 and Pm3.

The hinder upper cheek teeth (Pm3 to M2) do not form a closed series. Pm1 has one root and its alveolus is narrower than that of the canine. The hinder cheek teeth, Pm2 to M2 inclusive, have two roots, and the hinder roots of Pm3 and Pm4 are thickened on the inside. On the three hinder premolars, the apex of the crown is worn and the cingulum on the anterior half of the crown is weak when present. There are three or four accessory denticles on the steep anterior edge of Pm2 and four larger ones on the posterior edge; the enamel on the internal face of the crown of this premolar is strongly wrinkled. The
crown of Pm3 is furnished with three accessory denticles on the anterior and on the posterior cutting edges. These sharp cutting edges are finely denticulated. In the right maxillary of the Stuttgart skull (No. 11787) the antero-posterior diameter of the crown of Pm3 is slightly greater than that of Pm2, while in the left maxillary the conditions are reversed. The enamel on the crown of Pm3 is striated vertically and these striae are coarser on the internal than on the external face of the crown. As compared with Pm2 and Pm3, the entire crown of Pm4 is smaller. The three accessory denticles on the anterior cutting edge of Pm4 are smaller and farther removed from the apex of the principal cusp than the three on the posterior edge, but the posterior edge is steeper than the anterior. The enamel on the crown of this premolar is weakly wrinkled. No cingulum is developed at the base of the crown.

The crowns of the two molars are considerably smaller than that of Pm4, and the hinder molar has a slightly greater antero-posterior diameter than M1. The apex of the principal cusp of M1 is missing; the crown is furnished with two accessory denticles on the anterior and on the posterior cutting edges. The enamel on the crown is rather smooth and a very weak cingulum is present. The cingulum of M2 is stronger than on M1, and the anterior edge is steeper than the posterior edge. Each cutting edge is furnished with two accessory denticles, of which the basal one on the anterior edge is distinctly smaller than the others.

In so far as our present knowledge goes, the mandibular dentition of this species is distinguished from that of the smaller Fayum species not only by the larger size of the individual teeth, but also by the presence of serrated cutting edges on crown of Pm1 and by the larger number of accessory denticles on Pm3. None of the incisors are preserved in situ on any of the mandibles examined. The canine (No. 1904. XII. 135, Munich) has a simple conical crown covered with wrinkled enamel.

Pm1 is a single rooted tooth with a high laterally compressed crown which curves somewhat backward; its sharp anterior and posterior cutting edges are serrated, the serrations on the hinder edge being somewhat coarser than those on anterior edge; the enamel, especially on the inner surface of the crown, is ornamented with a series of fine and more or less vertical ridges, which anastomose at intervals; these striae do not extend over upon the serrations on the posterior edge, the surfaces of which are quite smooth; and a vertical median furrow is present on outer surface of root.

Pm2 is a two-rooted tooth with very slightly backward curved crown, whose anterior cutting edge is furnished with two larger basal accessory denticles, above which are several smaller denticles that extend upward to near the apex of the principal cusp; there are three large accessory denticles on the hinder cutting edge.

From Pm3 to M3 the lower cheek teeth form a closed series and all have two roots. Pm3 has four or five accessory denticles on the steep anterior cutting edge and a like number of accessory denticles on the posterior cutting edge; a cingulum is present on the hinder half of the crown. It is the largest cheek tooth in the mandible.

Pm4 differs from Pm3 in having the anterior and posterior cutting edges of the principal cusp crenelated; there are five accessory denticles on the anterior cutting edge of the crown and four on the posterior cutting edge, of which the two uppermost are the largest; a cingulum is present on the hinder half of the crown.

Immediately behind Pm4 are the three closely crowded molars, which differ from the premolars in having no accessory denticles on the anterior cutting edge, and the antero-posterior diameter of the crown of M2 is usually shorter than that of M1 or M3. These molars are so closely crowded that the hinder edges of the crowns of M1 and M2 fit into a groove on the anterior face of the succeeding tooth; the enamel on the crowns of these molars is rather smooth. The posterior cutting edge of M1 is furnished with four accessory
### Table 22—Measurements (in millimeters) of premaxillary and maxillary teeth

<table>
<thead>
<tr>
<th></th>
<th>M3</th>
<th>M1</th>
<th>Pm4</th>
<th>Pm3</th>
<th>Pm2</th>
<th>Pm1</th>
<th>C</th>
<th>I3</th>
<th>I2</th>
<th>I1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Antero-posterior diameter at base of enamel crown (No. 11787, Stuttgart)</td>
<td>32.7</td>
<td>31</td>
<td>51.7</td>
<td>54.5</td>
<td>58.6</td>
<td>60</td>
<td>56.8</td>
<td>62.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum transverse diameter at base of enamel crown (No. 11787, Stuttgart)</td>
<td>14</td>
<td>27</td>
<td>25</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>M3</th>
<th>M1</th>
<th>Pm4</th>
<th>Pm3</th>
<th>Pm2</th>
<th>Pm1</th>
<th>C</th>
<th>I3</th>
<th>I2</th>
<th>I1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Antero-posterior diameter at base of enamel crown (No. 14381, A. M. N. H)</td>
<td>23+</td>
<td>28+</td>
<td>53.5</td>
<td>51.3</td>
<td>60.3</td>
<td>62.5</td>
<td>70.5</td>
<td>69</td>
<td>33.7</td>
<td></td>
</tr>
<tr>
<td>Maximum transverse diameter at base of enamel crown (No. 14381, A. M. N. H)</td>
<td>13.8</td>
<td>25</td>
<td>27</td>
<td>24</td>
<td>24.8</td>
<td>25.8</td>
<td>19.8</td>
<td></td>
<td></td>
<td>22.2</td>
</tr>
</tbody>
</table>

### Table 23—Measurements (in millimeters) of mandibular teeth

<table>
<thead>
<tr>
<th></th>
<th>M3</th>
<th>M2</th>
<th>M1</th>
<th>Pm4</th>
<th>Pm3</th>
<th>Pm2</th>
<th>Pm1</th>
<th>C</th>
<th>I3</th>
<th>I2</th>
<th>I1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Antero-posterior diameter at base of enamel crown (No. 1904 XII. 135, Munich)</td>
<td>45.2</td>
<td>48.3</td>
<td>40±</td>
<td>72.2</td>
<td>83.3</td>
<td>65.8</td>
<td>35.5</td>
<td>40</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum transverse diameter at base of enamel crown (No. 1904 XII. 135, Munich)</td>
<td>18</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>M3</th>
<th>M2</th>
<th>M1</th>
<th>Pm4</th>
<th>Pm3</th>
<th>Pm2</th>
<th>Pm1</th>
<th>C</th>
<th>I3</th>
<th>I2</th>
<th>I1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Antero-posterior diameter at base of enamel crown (No. 1904 XII. 135a, b, Munich)</td>
<td>45.4</td>
<td>46</td>
<td>39.2</td>
<td>41</td>
<td>43</td>
<td>43.2</td>
<td>77.5</td>
<td>79</td>
<td>55.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum transverse diameter at base of enamel crown (No. 1904 XII. 135a, b, Munich)</td>
<td>19</td>
<td>20</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vertical height of enamel crown, from center of outer face to apex of crown (No. 1904 XII. 135a, b, Munich)</td>
<td>32.6</td>
<td>41.8</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>57</td>
<td>48+</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
denticles, of which the two uppermost are the largest. There are three accessory denticles on the posterior cutting edges of M2 and three large and a minute basal one on M3.

At the anterior end of the upper tooth row (1 to C), the pits for the reception of the lower teeth are located chiefly on the outer surface of the premaxillary; between C and Pm1, and also between Pm1 and Pm2, these pits are situated between the alveoli; and on the inside of the two-rooted cheek teeth these pits are progressively enlarged. On the mandible, however, the pits for the reception of the upper teeth are located entirely on the outer side of the tooth row, the hindermost one being between Pm3 and Pm4. The position of these pits shows that in this species also the upper and lower tooth series cross over when the jaws are closed.

DECIDUOUS DENTITION

The deciduous dental formula is Di $\frac{1}{1}$-$\frac{2}{2}$-$\frac{3}{3}$ Dc $\frac{1}{1}$ Dpm $\frac{1}{1}$-$\frac{2}{2}$-$\frac{3}{3}$-$\frac{4}{4}$. The milk dentition is not replaced until the animal attains adult size. The crowns of the deciduous cheek teeth possess certain peculiarities which are morphologically intermediate between those of Protocetus atavus and those of an adult Prozeuglodon isis. These deciduous cheek teeth, however, have the serrated cutting edges which are so characteristic of the archaeocetes from later geological horizons, but Dpm3 and Dpm4 have retained a third root, supporting a postero-internal enamel-covered buttress. This remnant of the postero-internal cusp is more protuberant on Dpm3 than on Dpm4.

The teeth in the type and paratype skulls of Prozeuglodon atrox supplement one another to some extent. On the type skull of Prozeuglodon atrox the crowns of Di1 and Di2 are broken off, but Di3 is essentially complete. The alveoli of these deciduous incisors decrease in diameter from the first to the third. The enamel at the base of the crown of Di3 is striated, forming fine ridges, the crown is somewhat compressed from side to side, and there is a slight carina on the anterior and posterior edges. Behind and external to the alveoli of Di2 and of Di3 there are small pits for the reception of the tips of the lower incisors. Judging from the diameters of the alveoli, the deciduous canines were somewhat larger than any of the deciduous incisors.

The first upper premolar on the type skull of Prozeuglodon atrox is erupting and is replacing the deciduous tooth, which is missing. The contour of the alveolus for Dpm1 in the left maxillary of the paratype skull of Prozeuglodon atrox indicates that this tooth was single rooted. There is a deep pit on the outer border of the maxillary between Dmp1 and Dmp2 for the apex of the corresponding tooth in the mandible. Dpm2 is a two-rooted tooth and it is also the largest tooth in the upper cheek tooth series. This deciduous premolar has a high crown, which is compressed from side to side; on its anterior cutting edge are four small denticles, while the hinder edge has two large accessory denticles and a small basal one.

On the inner side and a little behind the middle of the crown of Dpm3 is a prominent enamel-covered buttress which apparently is a remnant of a postero-internal cusp; this buttress is supported by a third root. The high crown of Dpm3 is furnished with three large accessory denticles on its anterior and posterior cutting edges. Adjacent to and on the inner side of the anterior root of Dpm3 is a deep fossa for the apex of the mandibular tooth. A similar fossa is present on the inner side of Dpm4.

Dpm4 differs from Dpm3 in having a lower principal cusp and furthermore the three accessory denticles on its anterior cutting edge are larger than the three on the posterior cutting edge. The enamel-covered buttress on the postero-internal face of the crown is much less conspicuous than on Dpm3, but seemingly it is supported by a third root.

The anterior upper molar on the type and paratype skulls of Prozeuglodon atrox belongs to the permanent dentition. It is considerably smaller than Dpm4. The crown
of M1 consists of a low principal cusp, one large and a very small basal accessory denticle on its anterior cutting edge, and two large accessory denticles on its posterior cutting edge. Andrews (1906, p. 244) states that the postero-internal buttress is present on M1. The structure referred to is very much reduced, and it is not clear whether it is supported by a third root or by the inner portion of the transversely widened posterior root which when viewed from behind seems to be imperfectly divided by a vertical groove.

It is quite certain that M2 was not present on the type skull of Prozeuglodon atrox.

The deciduous lower incisors, which are not represented in the known material, were presumably similar to the upper ones. The deciduous canine and Dpm1 are likewise unknown.

Dpm2 has a strongly compressed crown and rather steep cutting edges; there are four small denticles on its anterior edge and two large and one small basal accessory denticles on its posterior edge.

In the mandible, Dpm3 is the largest tooth in the deciduous cheek tooth series. It is a two-rooted tooth, with serrated anterior and posterior cutting edges. As the crown is imperfectly preserved, accurate description is difficult; the remnants of the accessory denticles, however, indicate that there were at least four on each cutting edge, and that the hinder ones were larger than the anterior ones.

Although the crown of Dpm4 is damaged, there remain remnants of two large and one small basal accessory denticles on the posterior cutting edge and two smaller accessory denticles on the lower portion of the anterior cutting edge.

On the right mandible associated with the type skull of Prozeuglodon atrox there are alveoli for two molars, the diameter of the anterior one being four-fifths as large as that of Dpm4. In the second alveolus the crown of M2, which is erupting, can be seen, and on the hinder edge of this alveolus is a slight swelling which may represent the developing permanent M3.

Stromer (1908b, pp. 136, 137) has described the deciduous dentition in the left maxillary of a skull (No. 11951a, Stuttgart) and in a mandible (No. 11234, Stuttgart), both of which are unquestionably young animals.

ENDOCRANIAL CAST

Perhaps the most obtrusive features of the artificial endocranial cast taken from the paratype skull of Prozeuglodon atrox are the abrupt elevation of the cerebellum (Dart, 1923, fig. 8) above the cerebral surface and the almost vertical position of the paraflocculus. Although the anterior portion of this cast is missing, the relative proportions of the cerebrum and cerebellum are apparent. Nothing is known in regard to the trigeminal specialization and the proportions of the olfactory peduncles are likewise unknown.

Each cerebral hemisphere is bounded medially on the dorsal aspect (Dart, 1923, fig. 9) by the sagittal sinus, posteriorly by the cerebellum, and laterally by the Gasserian ganglion. The hinder end of the Sylvian depression, which marks the boundary between the cerebral hemisphere and the Gasserian ganglion, is filled with the cast of the middle cerebral vessels. Behind the sagittal sinus is a rather large median tentorial depression from which rather broad tentorial sulci run transversely on each side, separating the cerebrum and the cerebellum. The Gasserian ganglia were obviously well developed and participated in the modeling of the lateral walls of the cranial cavity.

The cerebellum is relatively immense and is sharply elevated above the cerebrum. It rises to a height of 20 to 35 mm. above the cerebrum along the tentorial sulcus. On the lateral aspect the enlarged paraflocculus presumably did not project outward beyond the level of the Gasserian ganglion. The elevated lobus medius cerebelli is markedly asymmetrical. Extending obliquely across the posterior aspect of the cerebellum on each side is a
huge jugular leash which emerges from the cranial cavity through the foramen lacerum posteriorius. Coursing across the posterior aspect of the cerebellum below the lobus medius cerebelli and above the medulla oblongata is a fairly wide furrow which seemingly marks the position of a secondary tentorial bony projection on the internal surface of the supraoccipital.

The ventral aspect of this cast (Dart, 1923, fig. 11) reveals structures entirely comparable to those found on the endocranial cast of Dorudon sensitivus. At the anterior end of this cast is a broad swelling which may represent the tubercula olfactoria and at the hinder end of the latter is a short intertemporal sulcus. The optic chiasma should lie immediately behind this. Dart (1923, p. 640) points out that the well-marked contraction of the area between the olfactory peduncles and the tuber cinereum demonstrates the relative atrophy of the optic chiasmic region. A small area behind the latter corresponds in position to the tuber cinereum. Posteriorly (Dart, 1923, fig. 10) the base of the brain passes into the rather broad medulla oblongata. Below the paraflocculus on the left side is a remnant of the acoustic nerve (VIII). The cubic capacity of this incomplete cast is 790 cc. and when complete it must have been in excess of 800 cc. For the dimensions of this endocranial cast see table 55 (p. 200).

HYOID BONES

Two of the elements in the hyoid apparatus are associated with the Stuttgart skull (No. 11787). If one may assume that Prozeuglodon isis has a hyoid apparatus somewhat similar to that of Basilosaurus cetoïdes, then the rounded rod-like element, measuring 110 mm. in length and 12 mm. in diameter, is possibly the epihyal. The anterior end of this bone is somewhat thicker than the posterior end. As regards Basilosaurus cetoïdes, however, the epihyal is fused with the stylohyal. The hinder element, measuring 80 mm. in length, is incomplete at both ends. The shaft of this bone is somewhat thicker than that of the preceding and may possibly represent a portion of the thyrohyal.

VERTEBRÆ

Assuming that the vertebral column consisted of 7 cervical, 15 dorsal, 13 lumbar, 2 sacral, and 21 caudal vertebre, and computing the lengths of the centre of the missing vertebrae from the relative lengths of those that have been found, the total length of the skeleton (No. 11787, Stuttgart), including the skull, approximated 42 feet or 12.7 meters. On the basis of the same computations, the skull constituted 9.6 per cent, the neck 2.4 per cent, the dorsal series 23 per cent, the lumbar-sacral series 37.5 per cent, and the caudal series 28.5 per cent of the total length of the skeleton. The centre of the hinder dorsals and of all of the lumbars are noticeably elongated, and the post- and pre-zygapophyses of successive vertebrae do not articulate.

CERVICAL VERTEBRÆ

A complete series of cervical vertebrae belonging to this species has as yet not been described. If one can rely on the general uniformity of structure in corresponding cervical vertebrae of Basilosaurus cetoïdes, Dorudon stromeri, and Dorudon zittelii., then the neck of Prozeuglodon isis consists of seven vertebrae. Of these the fourth and the seventh are not represented among the cervical vertebrae now deposited in European museums. According to Stromer's computation (1908b, p. 132) the cervical series of Prozeuglodon isis, without the meniscus, may have measured 300 mm. in length, which is hardly one-fourth of the maximum length of the skull.

Atlas—The atlas associated with the Stuttgart skull (No. 11787; Stromer, 1908b, pl. 6, fig. 13) is somewhat crushed and is distinctly smaller than the Munich atlas (No. 1904. XII. 135). The concave articular facets for the occipital condyles are not continuous ventrally. The neural spine is vestigial. The heavy transverse processes are projected
outward and very slightly backward, and are truncated distally. Each transverse process is very slightly concave in front, but convex behind. The ventral hypapophysis is bifurcated. The hinder facets for the axis are more pyriform than oval in outline, and each of the transverse canals is greatly reduced in size.

The measurements of the Stuttgart (No. 11787) and the Munich (No. 1904. XII. 135) atlases are respectively as follows: Greatest breadth across transverse processes, 270 and 305 mm.; greatest distance between outside margins of anterior articular facets, 132 and 152.5 mm.; antero-posterior diameter of lower arch, 38 and 50 mm.; and thickness of lower arch, 20 and 39 mm. The vertical diameter of the Munich atlas is 155 mm.

The atlas (No. 9329, Cairo Mus.) referred to Prozeuglodon atrox by Andrews (1906, fig. 83A) has the usual elongated concave articular surfaces for the occipital condyles which are separated ventrally by a short interval, and are projected dorsally above the level of the large adjacent foramen for the first spinal nerve. The comparatively narrow neural arch has a low median ridge. The transverse processes are short and massive, and the ventral hypapophysis curves backward. The articular surfaces for the axis are wider dorsally than ventrally, and pass imperceptibly into the fossa for the reception of the odontoid process of the axis.

Axis—Similar in conformation to that of Basilosaurus cetoides. A portion of the transverse process is preserved on the incomplete axis (No. M. 17, Berlin) figured and described by Dames (1894, p. 197, pl. 31), while the centrum alone remains of the Stuttgart atlas (No. 11413). The axis of this species has a blunt, rounded odontoid process, nearly oval anterior articular facets, and a broad concave posterior face. The anterior articular facets of the Stuttgart axis slope obliquely in contrast to the more nearly vertical surfaces of the Berlin axis. The transverse processes are perforated at the base by a small vertebrarterial canal. The axis of this species seems to differ from that of Basilosaurus cetoides in having a smaller centrum and smaller vertebrarterial canals. The measurements of the axis (No. 11413, Stuttgart) are as follows: Transverse diameter of hinder face of centrum, 82 mm., and vertical diameter of the same, 65 mm.; and transverse diameter of neural canal, anteriorly, 52 mm.

The axis (No. 9330, Cairo Mus.) referred to Prozeuglodon atrox by Andrews (1906, fig. 83B) has a short, blunt, and rounded odontoid process, rather flat articular surfaces for the atlas, a high and massive neural spine which is directed obliquely upward and backward, and well-developed postzygapophyses. The ends of the transverse processes are divided by a notch into upper and lower portions, and they are perforated at the base by a vertebrarterial canal. The posterior epiphysis is not completely ankylosed to the centrum; this surface is much broader than high.

Third Cervical—The incomplete third cervical vertebra, which is described and figured by Stromer (No. 1904. XII. 135, Munich; Stromer, 1908b, p. 132, pl. 6, fig. 12), possesses the left transverse process, but the opposite process and the neural arch are missing. This cervical has relatively short and broad transverse processes. The large vertebrarterial canal, which pierces the base of the transverse process, is much nearer the upper than the lower edge of the latter. The centrum is compressed antero-posteriorly and a weak longitudinal ridge is present on its ventral face. When contrasted with the corresponding cervical of Basilosaurus cetoides, the third cervical of Prozeuglodon ipsis is seen to differ in having the anterior projection, which arises from the ventral edge of the transverse process, placed much nearer to the lower outer angle. The measurements of this third cervical vertebra are as follows: Antero-posterior diameter of centrum, 35 mm.; transverse diameter of anterior face of centrum, 79 mm., and vertical diameter of the same, 69 mm.

The centrum of the third cervical vertebra (No. 9332, Cairo Mus.) referred to Prozeuglodon atrox by Andrews (1906, fig. 83C) is strongly compressed antero-posteriorly;
there is a pair of blunt ridges on the ventral surface and the epiphyses are still separate. This cervical has a high neural arch, a short and stout neural spine, well-developed pre- and post-zygapophyses, and wide transverse processes, which are perforated at the base by an elongated vertebrarterial canal.

Fifth Cervical—This incomplete cervical vertebra (No. 11787, Stuttgart) has an antero-posteriorly compressed centrum, with anterior and posterior surfaces concave, a slender neural spine, and a neural canal broader than high, measuring 50 mm. transversely and 43 mm. vertically. The ventral edge of the forward and outward projecting transverse process is thickened and rounded. On the corresponding cervical of Basilosaurus cetoides, however, the curved portion of this transverse process is rather thin.

Sixth Cervical—This cervical vertebra (No. 1904. XII. 135e; Stromer, 1908b, pl. 6, fig. 1) has a small forward curved upper transverse process which is continuous above with the lateral oblique buttress supporting the prezygapophysis and is perforated at the base by a large vertebrarterial canal. The lower transverse process is very long, with antero-posteriorly expanded distal end, and is directed more downward than outward. The transverse distance between the extremities of the opposite transverse processes is 229 mm. It differs from the corresponding cervical vertebra of Basilosaurus cetoides in having the distal end of the lower transverse process more strongly expanded, the outer surface of this process lacks the oblique crest of the American species, the vertebrarterial canal is placed higher, and the neural spine apparently is weaker. The lower outer angle of the upper transverse process is nearly on a level with the lower rim of the vertebrarterial canal, while in Basilosaurus cetoides it is distinctly below the latter, the lateral oblique buttress is not so well developed as in the latter, and the neural arch is lower.

Dorsal Vertebrae

As regards the number of vertebrae in the dorsal series of Prozeuglodon isis, Stromer (1908b, p. 132) reckoned that possibly ten anterior dorsals were present. This assumption was based in part on his interpretation of the incomplete dorsal series of Dorudon zitteli in the Stuttgart collection (No. 11235). In addition to the transitional dorsal, Stromer tentatively reckoned that there were seven hinder dorsal vertebrae. Thirteen dorsal vertebrae belonging to one individual (No. 11787 Stuttgart) and consisting of seven anterior (V. th.v.), one intermediate (V.th.i.), and five hinder dorsals (V.th.1.) reveal the essential features of this portion of the vertebral column. Additional structural details were derived from an examination of a series of six anterior and five consecutive hinder dorsal vertebrae in the Munich collection (No. 1904. XII. 135). The antero-posterior diameters of the centra of five of these anterior dorsals are respectively, 79, 85, 86.5, 86, and 103 mm.

In both Basilosaurus cetoides and Zygotorhiza kochii, the dorsal series consists of 15 vertebrae, and it is quite likely that Prozeuglodon isis has the same number. Although the intermediate dorsal (V.th.i.) is considered by Stromer to be the eleventh in the series, it is now quite certain that it is actually the ninth. Consequently Stromer's view (1908b, p. 132) that Prozeuglodon isis has a greater number of hinder dorsal vertebrae than either Dorudon stromeri or Dorudon zitteli is probably incorrect.

The anterior dorsal vertebrae have a transverse oval neural canal, and their neural spines are slenderer and higher than those on the hinder dorsals. The antero-superior facets on the lateral surface of the centrum for the capitula of the corresponding ribs are present only on the eight anterior dorsal vertebrae, and the postero-superior facets are progressively reduced from the first to the seventh in the series. The articular facets on the prezygapophyses look somewhat toward the inside on the second dorsal. These processes are obviously weak on the hinder anterior dorsals. The articular surfaces on the
postzygapophyses are always quite weak, narrow, and the interval between them is rapidly reduced toward the hinder end of the dorsal series.

On the fourth dorsal vertebra (No. 11787, Stuttgart; Stromer, 1908b, pl. 6, fig. 6), for instance, the antero-posterior diameter of the pedicle of the neural arch is about equivalent to half the length of the centrum, but it is not set back at base as far from anterior end of centrum as from posterior end; the diapophysis projects outward and forward beyond level of anterior end of centrum, and is furnished with a distinct elongated lateral facet for the tuberculum of the fourth rib; a vestigial backward projecting anapophysis arises from the base of the diapophysis; the neural spine is quite high, slightly bent backward, and relatively slender, and has an expanded distal end; the prezygapophyseal facets are slightly concave; the hinder ends of the postzygapophyses do not extend backward to level of posterior end of centrum; a large deep antero-superior facet is present on lateral surface of centrum for the capitulum of the fourth rib and also a shallower postero-superior facet for the capitulum of the fifth rib.

On the hindermost of the anterior dorsals the postzygapophyses hardly extend backward to level of the posterior end of the centrum and, with the slight increase in the length of the centrum of the hinder anterior dorsals, their backward projection is correspondingly reduced. The metapophyses are large, placed near the base of the diapophyses on some of the anterior dorsals, but, gradually rising on the neural arch toward the hinder end of the dorsal series, on the ninth dorsal are transferred to the sides of the anterior edge of the neural arch, from which they project forward and upward. In *Basilosaurus cetoides*, however, these metapophyses are not differentiated from the diapophyses on the anterior dorsals. The end surfaces of the centra of the anterior dorsals are slightly concave laterally and ventrally, while the end surfaces of the hinder dorsals are convex transversely.

The ninth or intermediate dorsal (No. 11787, Stuttgart; Stromer, 1908b, pl. 6, fig. 5) has the pedicles of the neural arch abnormally widened antero-posteriorly in proportion to the length of the centrum, and they are set back at base about as far from anterior as from posterior end of centrum; the metapophysis, which projects forward and strongly upward, is not greatly enlarged, and is not extended forward beyond anterior end of centrum; the diapophysis is reduced to a rounded tuberosity on the lateral surface of the neural arch, and the parapophysis to a nearly horizontal articular facet on the upper lateral surface of the centrum; these two facets being separated by a short interval; the neural spine is very little bent backward, rather short, quite wide antero-posteriorly at base, and distinctly expanded distally; the prezygapophyses, if present, are destroyed; the hinder ends of the postzygapophyseal facets project backward to level of posterior end of centrum; no antero-superior facet for rib is present on lateral surface of centrum; the centrum is longer than broad, measuring 140 ± mm. in length, 125 mm. in breadth anteriorly, and 95 mm. in height anteriorly.

It is certain that there were at least five vertebrae in the dorsal series behind the intermediate dorsal. Two series of five hinder dorsal vertebrae are represented, respectively, in the Stuttgart (No. 11787) and in the Munich (No. 1904. XII. 135) collections. The centrum (with epiphyses) of the anteriormost one of the five consecutive hinder dorsals at Munich measures 220 mm. in length, and the hindermost one 280 mm. The hindermost dorsal of this series has a centrum four times as long, about one and a half times as broad, and twice as high as one of the anterior dorsals. On the hindermost dorsal the neural canal is 105 mm. broad and 38 mm. high. The abnormal increase in the lengths of the centra of the hinder dorsals can only be compared with similar conditions in the dorsal series of *Basilosaurus cetoides*.

The twelfth dorsal (No. 11787, Stuttgart; Stromer, 1908b, pl. 6, figs. 7, 14) has the pedicles of the neural arch widened antero-posteriorly, being about equivalent to half the
length of the centrum and placed slightly nearer the anterior than the posterior end of the centrum; the neural canal is very low and broad; the large metapophyses, which project forward and upward, are not extended forward beyond the level of the anterior end of the centrum; the neural spine is very wide antero-posteriorly, nearly vertical, and also expanded and obliquely truncated distally; the postzygapophyses are conspicuously projected backward from base of neural spine, but their hinder ends do not approach the level of the posterior end of the centrum; the transverse process (parapophysis) projects distinctly beyond lateral surface of centrum and is furnished with a distal concavity for the head of the twelfth rib. The measurements of this vertebra are as follows: Length of centrum, 260 mm.; breadth of centrum, anteriorly, 160 mm.; height of centrum, anteriorly, 130 mm.; breadth of neural canal, anteriorly, 90 ± mm.; and height of neural canal, anteriorly, 35 mm.

On the hindernost dorsal of the Stuttgart series (No. 11787) the antero-posterior diameter of the pedicle of the neural arch is 120 mm., while it measures 100 mm. on the corresponding dorsal of the Munich series (No. 1904. XII. 135). The antero-posterior diameter of the pedicles of the neural arches of the hinder dorsals does not increase in proportion to the length of the centrum, and the pedicles are placed near the middle of the centrum. The neural spines of the hinder dorsals are rather broad antero-posteriorly and low. The neural spine of the thirteenth dorsal (No. 11787, Stuttgart) measures 130 mm. in height, while an anterior dorsal has a neural spine which is 210 mm. high. The hinder dorsals, also, have the distal end of the neural spine expanded and bent forward. On the two hinder dorsal vertebrae (No. 1904. XII. 135, Munich) a longitudinal ridge is present on the ventral face of the centrum, but tubercula psoatici, which usually mark the origin of the psoas magnus muscles, are lacking.

On the intermediate dorsal vertebra and also the first two of the hinder dorsal vertebrae (tenth and eleventh) a remnant of the diapophysis exists on the outer surface of the neural arch, but on the remaining hinder dorsals the parapophyses constitute the transverse processes. The length of the transverse process of the hindernost dorsal vertebra (No. 1904. XII. 135, Munich) is 60 mm. and the antero-posterior diameter at the base, 125 mm.; it is flattened dorso-ventrally and distinguished from those on succeeding lumbar vertebrae by its shortness and by the presence of a distal facet for the head of the corresponding rib.

The centra of the hinder dorsal vertebrae are pierced dorso-ventrally by two vertical vascular canals. The metapophyses are quite strong and project forward and slightly outward, but are not extended forward beyond the level of the anterior end of the centrum on the last two in the Stuttgart series (No. 11787) or on any of the five in the Munich series (No. 1904. XII. 135).

**Lumbar Vertebrae**

Judging from the dimensions of the eight lumbar vertebrae (No. 11787) associated with the skull in the Stuttgart collection, it would appear that the anteriormost lumbar is larger than the hindernost dorsal vertebra. The hinder one in this series may possibly be a sacral vertebra. The elongation of the centra progressively increases to behind the middle of the series, and then the length of the centrum decreases faster than the breadth and the height of the same. The elongated centra distinguish these lumbar vertebrae from those of all other Fayum archaeocetes. The centrum of the third lumbar, which is the longest in this series, is about one and one half times as long as broad; it is almost five times as long, and about twice as broad and high as that of an anterior dorsal vertebra. The measurements of the third lumbar are as follows: Length of centrum, 310 mm.; antero-posterior diameter of neural spine at base, 180 mm.; height of neural spine anteriorly, 160 mm.; breadth of neural canal anteriorly, 75 mm.; and height of neural canal anteriorly, 25 mm.
The neural arches, which are proportionately smaller than on corresponding lumbar vertebrae of *Dorudon stromeri*, are placed in the middle of the centrum on the anterior lumbar. The anterior lumbars have the pedicles of the neural arches widened antero-posteriorly. The ends of the metapophyses do not project forward to the level of the anterior end of the centrum. These metapophyses are strong and project forward and upward. The neural spines of the anterior lumbars are as high as those of the posterior dorsal vertebrae, but rapidly diminish in height behind the middle of the series. The sharp-edged neural spine tends to bend slightly forward and on one anterior lumbar is 120 mm. high; on the hindermost lumbar in the Stuttgart series it is about 70 mm. high. On two isolated lumbar vertebrae (No. 1904. X. 1356, Munich) the neural spines are remarkably high, namely 190 mm., the height being approximately equivalent to the antero-posterior diameter at the base. The antero-posterior diameters of the centra of these lumbars are, respectively, 282 mm. and 283.5 mm.; the vertical diameter, from the ventral face of the centrum to the distal end of the neural spine, of the first mentioned of these lumbars is 311 mm.

The neural canals of the anterior lumbar vertebrae are slightly lower than on the hindermost dorsals. At the anterior end of the lumbar series, the neural canal is much broader than high, but becomes somewhat narrowed toward the hinder end of the series. The transverse processes of the lumbar vertebrae arise rather low on the lateral surface of the centrum. At the base the antero-posterior diameters of the transverse processes of the lumbar vertebrae range from 100 to 120 mm. These processes are restricted to the middle of the centrum. The transverse processes are sharp edged and usually not bowed; their broadened extremities are truncated and have a pointed anterior angle; and their length ranges from 70 to 90 mm. Ventrally the lumbar vertebrae are very little curved, especially in the middle between the transverse processes, where the two vascular foramina are located. The somewhat oval end surfaces of the centra are either flat or flat concave.

The eleventh or twelfth lumbar vertebra (No. 11787, Stuttgart), which has been figured by Stromer (1908b, pl. 7, fig. 10), is characterized by the relatively short pedicles of the neural arch, their antero-posterior diameters being equivalent to about one-third of the length of the centrum; these pedicles are placed nearer the anterior than the posterior end of the centrum; the large metapophyses project upward and forward, but do not extend forward to level of anterior end of centrum; the neural spine is rather short, obliquely truncated distally, and its antero-posterior diameter at the base is markedly increased; the hinder ends of the postzygapophyseal projections are farther removed from the posterior end of the centrum than the extremities of the metapophyses are from the anterior end of the centrum; the transverse process (parapophysis) is relatively short, directed obliquely downward and slightly forward, and flattened dorso-ventrally. The measurements of this lumbar vertebrae are, respectively, as follows: Length of centrum, 305 mm.; breadth of centrum anteriorly, 175 mm.; height of centrum anteriorly, 165 mm.; and height of neural spine anteriorly, 120 mm.

On the hindermost one of the eight lumbar vertebrae in the Stuttgart collection, the distal end of the transverse process is curved somewhat dorsally and it is about 25 mm. thick. Stromer (1908b, p. 134) has pointed out that this peculiarity may indicate the presence of a pelvic element, and at the same time called attention to the fact that the sacral vertebra of *Protocetus atavus* has a relatively broader and more ventrally curved transverse process. The transverse processes of this lumbar, however, do not bear a very close resemblance to those on either of the two sacral vertebrae of *Basilosaurus cetoides*. The length of the centrum of this vertebra is 300 ± mm.

**Caudal Vertebrae**

The number of vertebrae comprising the caudal series is uncertain. Only a few isolated caudal vertebrae are known and they can be distinguished readily from those of
*Basilosaurus cetoides.* In contrast to those of *B. cetoides*, the centra of the anterior caudal vertebrae of *Prozeuglodon isis* seem to be shorter in proportion to their breadth and height. Aside from their larger dimensions, the middle and hinder caudal vertebrae of *Prozeuglodon isis* likewise differ from those of *Dorudon serratus* in having longer centra and metaphyses of quite different proportions. For *Basilosaurus cetoides* a consecutive series of twenty-one caudal vertebrae (No. 12261, U. S. N. M.) are known, and for *Dorudon serratus* (Gibbes, 1847, pl. 2, fig. 8) a consecutive series of twelve hinder caudal vertebrae. The following caudal vertebrae, belonging to three different individuals of *Prozeuglodon isis*, were examined: 1 anterior and 2 small terminal caudals (No. 11787, Stuttgart); 4 hinder caudals (No. 1904. XII. 135, Munich); and 2 hinder caudal vertebrae (No. 1904. XII. 135e, Munich).

On the anterior caudals the neural arch, which occupies at most about half of the total length of the centrum, is situated toward the anterior end. The neural canal is low and broad and its floor is concave both from side to side and from end to end; a large vascular foramen is located on the floor of the neural canal. Large metaphyses arise from the anterior end of the neural arch, but no prezygapophyses are present. The hinder end of the roof of the neural arch is extended backward in the middle line, forming a blunt projection that overhangs the neural canal posteriorly. The dorso-ventrally flattened transverse processes project forward and downward. The ventral surface of the centrum is convex from side to side, particularly near the posterior end; in the middle of the ventral surface is a depression in which a pair of vascular foramina are located.

An anterior caudal vertebra in the Stuttgart collection (No. 11787), which has been figured by Stromer (1908b, pl. 7, figs. 9, 11), is quite similar in general configuration to a vertebra figured by Andrews (1906, fig. 79). It corresponds to the fourth or fifth vertebra in the caudal series of *Basilosaurus cetoides*. This caudal is characterized by a relatively short and broad centrum, relatively short pedicles on the neural arch, a rather low and broad neural canal, and a vestigial neural spine; the metaphyses project obliquely outward and forward, but do not extend forward to level of anterior end of centrum; the transverse processes are directed obliquely downward and forward; these processes are about 70 mm. long and their antero-posterior diameter at the base is 90 mm. The measurements of this caudal are as follows: Length of centrum, 240 mm.; breadth of centrum anteriorly, 150 mm.; height of centrum anteriorly, 140 mm.; breadth of neural canal, 30 mm.; and height of neural canal, 14 mm.

Near the middle of the caudal series, the metaphyses are markedly reduced in size, the neural arches are shortened, the neural canal is greatly narrowed, and the transverse processes are perforated at the base by a foramen. The neural arches are progressively reduced on the hinder caudals and are entirely absent on the terminal caudals. No transverse processes are developed on these terminal caudals. At the hinder end of the ventral surface of the anterior caudals, there is a pair of prominences for articulation with the chevron bones.

A hinder caudal vertebra in the Munich collection (No. 1904. XII. 135), which has been figured by Stromer (1908b, pl. 7, fig. 6), exhibits a very close resemblance to the eleventh in the caudal series of *Basilosaurus cetoides*. This caudal has an elongated centrum, a low and narrow neural canal, but no vestige of a neural spine; the short metaphyses project obliquely outward and upward, but terminate behind level of anterior end of centrum; the backward projecting process from roof of neural arch is short and greatly reduced; below this process each pedicle of the neural arch is perforated by a small foramen which leads from the neural canal and opens into a broad groove that extends downward across the lateral face of the centrum; this groove is bounded anteriorly by the notch at the base of the posterior edge of the transverse process; the transverse processes, which are placed
higher on the side of the centrum than on the anterior dorsal vertebrae, are very short and relatively broad. The measurements of this vertebra are as follows: Length of centrum, 200 mm.; breadth of centrum anteriorly, 130 mm.; and height of centrum anteriorly, 120 mm. A smaller hinder caudal in the Munich collection (No. 1904. XII. 135) measures 130 mm. in length, 100 mm. in breadth anteriorly, and 95 mm. in height anteriorly; the neural canal of this caudal is hardly 20 mm. broad and is less than 5 mm. high. The metapophyses persist as distinct projections on this caudal, but the hinder median projection from the roof of the neural arch is reduced to a vestige.

Two small hinder caudal vertebrae (No. 11787, Stuttgart), which are ankylosed together, are devoid of any vestiges of the neural arch, but possess paired lateral knob-like protuberances. The centra of these caudals (Stromer, 1908b, pl. 7, fig. 2) are flattened antero-posteriorly and measure, respectively, 19 mm. and 15 mm. in length; the breadth and the height of these centra are both approximately 40 mm.

FORELIMB

The forelimbs have been extensively modified for balancing and steering functions, but have retained a hinged type of elbow joint. Strong leverage for the deltoid muscle is provided by the long deltoid crest on the humerus. In so far as our present knowledge goes, the forelimb of Prozeuglodon isis differs from that of Basilosaurus cetoides in the following particulars: The scapula is less modified, the head of the humerus is relatively smaller and the deltoid crest reaches farther distally, the radius is less strongly bent forward, and the shaft of the ulna is wider in proportion to the width of the olecranon process. In Prozeuglodon isis the vertical diameter of the scapula is slightly less than the length of the humerus, while in Basilosaurus cetoides the vertical diameter of the scapula is approximately three-fourths of the length of the humerus.

SCAPULA

A left scapula in the Stuttgart collection (No. 11787) has been figured by Stromer (1908b, pl. 7, fig. 13). This scapula differs from that of Basilosaurus cetoides (No. 4675, U. S. N. M.) in being much narrower, the greatest vertical diameter being approximately equal to the greatest antero-posterior diameter, and in having the posterior angle less conspicuously prolonged backward. Aside from the characters which distinguish it from Basilosaurus cetoides, the scapula of Prozeuglodon isis may be recognized by the presence of a regularly curved vertebral edge, a concave posterior edge, and a strongly convex anterior edge. The prescapular portion of the blade is conspicuously extended forward beyond the level of anterior face of the neck. A prominent but somewhat sinuous crest, which extends upward from the base of the acromion to the vertebral edge, separates the narrow prescapular or supraspinous fossa from the large flattened postscapular or infraspinous fossa. The neck of the scapula is rather long. The large glenoid cavity has a strongly convex outer edge and a slightly convex inner edge. The acromion is thin, flat, and quite long, and projects downward and forward. The slender coracoid is destroyed. The measurements of this scapula are as follows: Greatest vertical diameter, articular head to vertebral margin, 380 mm.; greatest antero-posterior diameter, posterior angle damaged, 375 + mm.; length of acromion, superior margin at base to damaged distal end, 165 + mm.; antero-posterior diameter of articular head, 89 mm.; and transverse diameter of articular head, 74.8 mm.

HUMERUS

As compared with the humerus of Basilosaurus cetoides (No. 4674, U. S. N. M.), the left humerus in the Stuttgart collection (No. 11787) is approximately four-fifths as long, although the antero-posterior diameter of the shaft above the level of the distal rounded
angle of the deltoid crest is approximately the same. In addition, the humerus of *Prozeuglodon isis* has a smaller outer condyle. The elongation of the shaft, in addition to its larger size, at once distinguishes the humerus of *Prozeuglodon isis* from those tentatively referred to *Dorudon sitteli* and *D. stromeri*, as well as from that of *Zygorhiza kochii*. The length of this humerus (Stromer, 1908b, pl. 7, fig. 7) slightly exceeds the vertical diameter of the scapula. The lesser tuberosity is not set off sharply from the head and is distinctly convex. Between the lesser and the greater tuberosity is a hollow, which is deeper in the hinder part and is sharp-angled in front. The bicipital fossa is weak. The inner side of the upper half of the shaft is much more distinctly curved than the outer. The distal rounded angle of the deltoid crest is 115 mm. and the hinder backward swelling of the shaft perhaps 90 mm. above the distal end. The outer condyle projects distally beyond the level of the inner condyle. The measurements of this humerus are as follows: Greatest length, 408 mm.; antero-posterior diameter of proximal end, including greater tuberosity, 130 mm.; antero-posterior diameter of shaft through lower portion of deltoid crest, 118.5 mm.; antero-posterior diameter of outer condyle, 51.7 mm.; and maximum transverse diameter of distal end, 66 mm.

**Radius**

Judging from the proportions of the ulna and radius, there is reason to believe that the radius is approximately half as long as the humerus, paralleling conditions in *Basilosaururus cetoides*. In case of *Zygorhiza kochii*, however, the length of the radius apparently is equivalent to about two-thirds that of the humerus. The proximal half of the right radius (No. 1904. XII. 135e, Munich) figured by Stromer (1908b, pl. 7, figs. 3, 4, 5) is tentatively referred to this species. The concave facet for articulation with the troclear surface of the humerus occupies most of the proximal end. The anterior border of this facet is conspicuously elevated. The small ulnar facet is located on the hinder surface of the proximal end of the shaft. In general form, this radius resembles somewhat that of *Basilosaururus cetoides*. Below the anterior elevated border, the shaft is distinctly expanded in front, imparting a strongly convex curvature to this surface, while the corresponding portions of the radii of *Basilosaururus cetoides* and *Zygorhiza kochii* slope obliquely forward to the angle formed on the anterior face. The outer surface of the shaft is convex and the inner relatively flat. The measurements of this radius are as follows: Antero-posterior diameter of proximal articular surface, 30 ± mm.; transverse diameter of proximal articular surface, 36 mm.; antero-posterior diameter of shaft near distal end, 50 mm., and transverse diameter of shaft at same level, 26 mm.

**Ulna**

The distal end of the left ulna (Stromer, 1908b, pl. 7, figs. 12, 14) in the Stuttgart collection (No. 11787) is eroded away. The greater sigmoid cavity, for articulation with the trochlea of the humerus, is relatively slightly smaller in both *Prozeuglodon isis* and *Basilosaururus cetoides* than in *Zygorhiza kochii*. As compared with the ulna of *Basilosaururus cetoides* and *Zygorhiza kochii*, the olecranon is less expanded. On the anterior face, below and bordering upon the greater sigmoid cavity is the lesser sigmoid cavity which articulates with the posterior face of the head of the radius. The shaft of this ulna is laterally compressed. The measurements of this ulna are as follows: Greatest length, estimated, 270 ± mm.; greatest diameter of free end of olecranon, 100 mm.; length of anterior margin of olecranon, proximo-superior angle to greater sigmoid cavity, 85 mm.; length of greater sigmoid cavity, 40 mm.; transverse diameter of distal portion of greater sigmoid cavity, 35 mm.; and antero-posterior diameter of shaft near distal end, 80 mm.
RIBS

The rather slender shafts of the anterior ribs are antero-posteriorly flattened, strongly curved from end to end, and expanded distally into a club-like extremity. The necks of the anteriormost ribs (Stromer, 1908b, pl. 7, fig. 8) are rather short and the curved shafts are bent abruptly downward. Near the middle of the series the necks of the ribs are longer and the shafts are more strongly bowed outward. As contrasted with the anterior ribs, the upper portions of the middle (No. 11787, Stuttgart; Stromer, 1908, pl. 6, fig. 8) and hinder ribs are more nearly circular in cross-section. The distal end of a nearly complete rib in the Munich collection (No. 1904. XII. 135) 650 mm. in length measures 65 × 30 mm. in diameter. The distal end of another rib in the Stuttgart collection (No. 11787) measures 78 × 44 mm. The anterior ribs are furnished with a large tuberculum and capitulum, but the hindermost ribs are single headed.

STERNUM

The broad pre sternum (No. 11787, Stuttgart; Stromer, 1908b, pl. 6, figs. 2, 3) has a concave dorsal face, a more or less flattened ventral face, and an upturned but rounded anterior face. The measurements of this pre sternum are as follows: Antero-posterior diameter medially, 148 mm.; transverse diameter anteriorly, 127 mm.; transverse diameter posteriorly, 113 mm.; and dorso-ventral diameter posteriorly, 57 mm.

Also associated with the skeletal remains in the Stuttgart collection (No. 11787) are one large and two smaller mesosternal segments, whose diameters are, respectively, 135 × 125 mm., 130 × 120 mm., and 130 × 115 mm.; their dorso-ventral diameters are, respectively, 69, 54, and 46 mm. They are somewhat oval in outline, but angular at the ends, and have roughened lateral surfaces.

The elongated xiphisternum figured by Stromer (1908b, pl. 6, fig. 4) is somewhat convex dorsally. The hinder three-fifths of this element is abruptly narrowed behind the anterior quadrangular portion and is progressively attenuated posteriorly, measuring about 30 mm. transversely near the extremity. The hinder end is not deeply bifurcated. The measurements of this xiphisternum are as follows: Antero-posterior diameter medially, 195 mm.; transverse diameter anteriorly, 105 mm.; and dorso-ventral diameter anteriorly, 46 mm.

PLATYOSTYPHYS1 new genus

Genotype, Zeuglodon paulsonii Brandt, 1873.

Centra of lumbar vertebrae conspicuously elongated; anterior lumbar transverse diameter of transverse processes at base nearly equivalent to length of centrum; sacral vertebra has small neural canal, narrower transverse processes, and broad, strongly divergent prezygapophyses.

PLATYOSTYPHYS1 PAULSONII (Brandt)


1 *karse, broad, flat; *dse, the loin—in allusion to the unusual width of the transverse processes of the anterior lumbar vertebrae.
Type locality—In loess near Tschigirin [= Chigirin], Ukraine, U. S. S. R.

Co-type specimens—(1) Prof. A. S. Rogowitsch found one hinder dorsal vertebra and half of the neural arch of another vertebra in a crevice filled with loess in the layer of millstone grit (Mühlsandstein) on the summit of Stone Mountain, on the right bank of the Tjasma [= Tyasna] River, near Tschigirin in Ukraine, U. S. S. R. Formerly in the Anatomical Museum of the University of Kiev [= Kiev], U. S. S. R.

(2) Two additional lumbar vertebrae were found by Professor Feofilaktow in a ravine filled with loess, south of Tschigirin in Ukraine, U. S. S. R. Formerly in the Anatomical Museum of the University of Kiev [= Kiev], U. S. S. R.

Referred specimens—(1) Seven lumbar, one sacral, and two caudal vertebrae, a chevron, two rib fragments, and two small slender bones were found in a green glauconitic sand at a village called "Korobow Chutor" in the Zmijew [= Zmyev] district, 40 kilometers south of Charkow [= Kharkov], Ukraine, U. S. S. R. These specimens were deposited in the Geological Department of the University of Kharkov, Ukraine, U. S. S. R. "Charkower Stufe," lower Oligocene.

(2) Five poorly preserved vertebrae from the green glauconitic sand at the village Bugajewka in the Izjum [= Izyum] district, Ukraine, U. S. S. R. These specimens were deposited in the Geological Department of the University of Kharkov, Ukraine, U. S. S. R. "Charkower Stufe," lower Oligocene.

VEBETRAE

The ten vertebrae, which are described by Fedorovsky (1912), are numbered consecutively from one to ten. The precise positions of these vertebrae in the series will remain uncertain until a complete consecutive series is collected and described. Therefore, the identifications made by Fedorovsky may be accepted tentatively for the present. Fedorovsky also attempted to arrange the sequence of the three vertebrae described by Brandt (1873a, pp. 336–339, pl. 34) in accordance with the positions assigned to the vertebrae in his series (see table 25, p. 99).

The unusual width of the transverse processes at once distinguish the large anterior lumbers of *Platyosphys paulsonii* from those of *Prozeuglodon isis* and of *Basilosaurus cetoides*. Five of the anterior lumbar vertebrae are approximately the same size, the centrum of the largest measuring 283 mm. in length. The centra are roughly cylindrical in shape. The two posterior lumbers have somewhat shorter centra, the length of the shortest being 231 mm. The differences in the width and height of these centra as compared to those of the anterior lumbers are rather slight. The transverse processes are broad, flattened, and project obliquely outward and downward; the distal ends of these processes are destroyed on all of these vertebrae. On the five anterior lumbers, the antero-posterior diameter of the transverse process at the base is nearly equivalent to the length of the centrum. These transverse processes arise near the base of the centrum on the anterior lumbers, but are placed somewhat higher on the posterior ones. The transverse processes of the posterior lumbers (Fedorovsky, 1912, pl. 2, figs. 9, 10) are somewhat narrower and thinner, however, and the hinder edge is much closer to the posterior epiphysis than the fore edge is to the anterior epiphysis. Each of these lumbers has a pair of closely approximated elongate foramina on the ventral surface, and in some instances one or more pairs of considerably smaller foramina. The neural arches are placed nearly in the middle of the length of the dorsal surface of the centrum. The large wing-like metapophyses slope obliquely downward from the upper to the lower edge. The nipple-like postzygapophyses are much smaller and slenderer than the metapophyses. On the anterior lumbers, the transverse diameter of the neural canal is 128 mm., while it is narrowed to about 56 mm. on the posterior ones. The peculiarities of the neural spines of these lumbers are unknown.
The proportions of the vertebra identified as the sacral by Fedorovsky (1912, pl. 3, figs. 11–14) correspond rather closely with those of the posterior lumbar; the neural canal is narrow, and the position and width of the transverse process is similar, but the metaphyses, though shorter, are much broader and thicker. The postzygapophyses are more closely approximated and the combined width of the two is less. The usual pair of foramina are present on the ventral surface of the centrum.

The two vertebrae identified as caudals by Fedorovsky are imperfectly preserved. The larger of the two (No. 10, Fedorovsky, 1912, pl. 3, figs. 17, 18) is possibly either a posterior lumbar or an anterior caudal. The smaller one (No. 9, Fedorovsky, 1912, pl. 3, figs. 15–16) seems to have been correctly identified as an anterior caudal. The transverse processes of these two vertebrae are relatively narrower than those of the posterior lumbar and are moved backward much closer to the posterior epiphysis. These processes are not perforated at the base on either of the vertebrae, but on the larger caudal the anterior edge of these processes is indented at the base. The pedicles of the neural arch are rather thin at the base. The pair of foramina on the ventral surface are rather large and the small facets for the chevron are located near the hinder margin.

Table 24—Measurements (in millimeters) of the vertebrae

<table>
<thead>
<tr>
<th></th>
<th>L. 1</th>
<th>L. 2</th>
<th>L. 3</th>
<th>L. 4</th>
<th>L. 5</th>
<th>L. 6</th>
<th>L. 7</th>
<th>S. 8</th>
<th>C. 9</th>
<th>C. 10</th>
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<tr>
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<td>263</td>
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<td>137±</td>
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<tr>
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<td>136</td>
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</table>

1 Anterior epiphysis missing.  
2 Both epiphyses missing.

Table 25—Measurements (in millimeters) of the vertebrae

<table>
<thead>
<tr>
<th></th>
<th>D. 1</th>
<th>L. 1</th>
<th>L. 4</th>
<th>L. 5</th>
<th>L. 6</th>
<th>L. 7</th>
<th>S. 8</th>
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<tr>
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1 Hinder dorsal vertebra figured by Brandt (1873a, p. 388, pl. 34, figs. 1, 1a, 1b).
2 Lumbar vertebra figured by Brandt (1873a, p. 339, pl. 34, figs. 2, 2a, 2b).
3 Lumbar vertebra figured by Brandt (1873a, p. 339, pl. 34, figs. 3, 3a, 3b).
4 Major portion of transverse processes missing.
5 One or both transverse processes incomplete.

HÆMAPOPHYES

One of the chevrons is a Y-shaped bone, with the ends of the fork slightly expanded to form facets for articulation with the under surface of the caudal vertebra. The distance between the outer faces of the extremities of the fork is 71 mm. and the minimum inside distance is 23 mm. The handle of the fork is three sided and measures 24 mm. in thickness.
HYOID BONE

A small slender bone, which is broken off at the expanded end, resembles in some respects the thyrohyal of Basilosaurus cetoides. It is quite possible also that it may represent a fragment of the hindmost rib. The length of this bone in its present condition is 110 mm. The extremity is slightly enlarged and is covered with small pits; the diameters of this surface are 23 and 40 mm.

DORUDONTIDAE


Archaeocetes of small to medium size, attaining a maximum length of possibly 20 feet; maximum length of skull about 3 feet; parietal region of skull quite narrow; squamosal forms a large part of external wall of braincase; temporal fossae very large; premaxillaries and maxillaries elongated; a large pterygoid fossa for accessory air sinus of middle ear.

Permanent dental formula: I 1.2.3 1.2.3, C 1, 1, Pm 1.2.3.4, 1.2.3, M 1.2.3, incisors caniniform; cheek teeth without trace of inner portion of crown; Pm1 has laterally compressed crown and either one or two roots; remainder of upper cheek teeth (Pm2 to M2) have laterally compressed crowns and accessory denticles on their anterior and posterior cutting edges; Pm3 and Pm4 generally two rooted, but three rooted in Kekenodon; Dpm3 and Dpm4 have three roots in Dorudon osiris and Zygorhiza kochii; Pm1 caniniform; lower premolars (Pm2 to Pm4) have accessory denticles on anterior and posterior cutting edges of crown and two roots; lower molars (M1 to M3) have the anterior edge of crown grooved vertically, the accessory denticles limited to posterior cutting edge, and two roots.

Neck not unusually shortened in proportion to length of body, and more or less flexible; cervical vertebrae free; dorsal and lumbar vertebrae have high, broad neural spines, well developed transverse processes, and reduced postzygapophyses; trunk and tail not abnormally lengthened; and centra of lumbar vertebrae normal, not conspicuously lengthened.

ZYGORHIZA


Permanent dental formula: I 1.2.3 1.2.3, C 1, Pm 1.2.3.4, 1.2.3, M 1.2.3, deciduous dental formula: D 1.2.3, Dc 1, Dpm 1.2.3.4. 1.2.3.

Cingulum at base of crown of Pm2, Pm3 and Pm4 strongly developed and wide, but anterior and posterior halves do not meet medially; Pm2 is the largest of the upper cheek teeth and has at least 4 accessory denticles on anterior and posterior cutting edges of crown; Pm3 to M2 form a closed series; incisors and canine have a vertical carina on both anterior and posterior cutting edges of crown; upper cheek teeth (Pm2 to M2) have two rather widely separated roots, accessory denticles on anterior and posterior cutting edges of crown, and the enamel ornamented with vertical striæ which anastomose at intervals; Pm1 caniniform, with one root; remainder of lower premolars (Pm2 to Pm4) have laterally compressed crowns and accessory denticles on their anterior and posterior cutting edges; Pm4 is the largest of the lower cheek teeth; lower molars (M1 to M3) have accessory denticles restricted to posterior cutting edge of crown; Pm2 to M3 have two roots; pits for reception of mandibular teeth located on outer side of anterior one-rooted upper teeth and on inner side of two-rooted upper teeth, showing that the upper and lower tooth series cross over when the jaws are closed.

Skull elongated; rostrum attenuated; forehead flattened; intertemporal region narrow; sagittal crest high; lambdoidal crests bounding supraoccipital shield prolonged conspicuously backward; premaxillaries convex laterally; temporal fossæ large; large pterygoid
fossae for accessory air sinuses of middle ear; projecting ledge formed by forward prolongation of temporal rim of squamosal; hyoid apparatus consists of a small hexagonal basihyal, a pair of thyrohyals which are attenuated posteriorly and conspicuously expanded at anterior end, and a pair of slender elongated thyrohyals (epiphyal + stylohyal); forelimb relatively stout; scapula comparatively high; humerus relatively short; elbow hinged and non-rotary; shaft of radius has a conspicuous anterior angle-like prominence; width of shaft of ulna less than that of olecranor process; carpals retain synovial type of articulation; metacarpals and phalanges elongated, retaining ball-and-socket type of articulation; and pelvis unknown.

Vertebral column consists of 7 cervical, 15 dorsal, apparently 13 lumbar, 2 sacral, and at least 21 caudal vertebrae; cervical vertebrae have compressed centra, no ankylosis of consecutive centra, but with flexibility limited by interlocking of the lateral processes; atlas has hypoplastic joint process; axis has blunt odontoid process, short narrow transverse processes, and elongated neural spine; lower transverse processes of sixth cervical greatly elongated; centra of hinder dorsals, lumbars, sacrals, and anterior caudals not disproportionately elongated; on anterior caudal vertebrae the antero-posterior diameter near base of transverse process is conspicuously less than length of centrum.

**ZYGORHIZA KOCHII** (Reichenbach)

1847. *Basilosaurus kochii* Reichenbach in Carus, Resultate geologischer, anatomischer und zoologischer Untersuchungen über das unter den Namen Hydrachos von Dr. A. C. Koch zuerst nach Europa gebrachte und in Dresden ausgestellte grosse fossile Skelett, Dresden und Leipzig, pl. 18, pl. 2, figs. 3-4.


1849. *Zeuglodon brachypondylus* Müller, Über die fossilen Reste der Zeuglodonten von Nordamerica, Berlin, pp. 20, 28, 29, 31, 32, 33, pl. 3, figs. 1-2; pl. 4, figs. 1-2; pl. 5, fig. 1; pl. 8, figs. 3-7; pl. 13, figs. 1-2; pl. 19, figs. 1-5; pl. 21, figs. 6-8; pl. 26, figs. 1-3; pl. 27, fig. 1; Dames, 1894, Palaont. Abhandl., Jena, n. F., vol. 1, No. 5, p. 202.


**Type locality**—Near Clarksville, Clark County, Alabama. Ocala limestone, upper Eocene.

Müller (1849, pp. 3, 9) definitely states that the so-called “Gaumenknochken” of Carus (1847, pl. 2, fig. 1, IIg) found near Clarksville is the cranium which is figured in his memoir (Müller, 1849, pls. 3, 4, 5). Müller (1849, p. 20, pl. 13, figs. 1, 2) also describes an atlas from Clarksville and remarks that “der kleine Schädel” (Müller, 1849, pl. 3, 4, 5) came from the same locality.

**Type specimen**—Reichenbach (in Carus, 1847, p. 13) proposes “Basilosaurus Kochii” for “das kleinere Gaumenstück” which Carus had commented upon (1847, p. 6, 2d column, 4th paragraph) and figured (1847, pl. 2, figs. IIg, III, and IV). The fact that Carus and Reichenbach misidentified the cranium and called it a “Gaumenstück” is of no consequence in so far as zoological nomenclature is concerned. This imperfect cranium was subsequently freed from the matrix under the supervision of Müller and figured (1849, pl. 3, 4, 5). No. 15324a-b (m. 44), Geologisch-Paläontologisches Institut und Museum der Universität Berlin; collector, Albert C. Koch; March 1845.
Referred specimens—(1) Koch wrote Carus (1849, p. 388) that the fourth skull, which was almost complete, was found on land belonging to a Mr. Moor, approximately 13 English miles from Washington Old Court House [ = Southwest ¼ of Section 9, Township 8 North, Range 3 West, Washington County, Alabama] in the adjoining Choctaw County and near the main road which extended into the State of Mississippi. It would appear then that this skull was found near Isney, Choctaw County, Alabama, and this assumption has been corroborated to some extent by the assertion of Mr. Toomy, a local surveyor, that there was formerly an old Moore place about one mile southeast of Isney [Section 1, Township 9 North, Range 5 West]. Upper Jackson formation, upper Eocene.

Since it was obvious that Owen’s Zeuglodon cetoides had priority over any subsequent name applied to the large North American species, Carus (1849, p. 385) concluded that he could perpetuate Koch’s name Hydrarchus, by employing it as a specific name for this small archaeocete. This specimen is thus the type of Zeuglodon hydrarchus Carus. The skull is fairly well preserved, with the exception of the outer margin of the right supraorbital process, the edges of the lambdoidal crest, both zygomatic processes, both occipital condyles, and the posterior ends of both jugals, which are destroyed. The crowns of the teeth are either damaged or destroyed entirely, and M₂ is missing on both sides. The right and left mandibles, both without teeth, the sixth cervical vertebra, a posterior dorsal vertebra, the right tympanic bulla, and fragments of two ribs were associated with this skull. No. 8501, Teyler’s Museum, Haarlem, Holland; collector, Albert C. Koch; 1848.

(2) An occipital portion of the braincase and fragments of adjoining bones (Müller, 1849, pl. 27, fig. 1). Upper Jackson formation, upper Eocene. No. 15943 (m. 27), Geologisch-Paläontologisches Institut und Museum der Universität Berlin; collector, Albert C. Koch; 1848.

To Zeuglodon brachyspondylus minor, Müller (1851, p. 240) referred a series of imperfect lumbar vertebrae (Müller, 1849, pl. 19); the damaged braincase which constitutes the type of Reichenbach’s Basilosaurus kochii (Müller, 1849, pls. 3, 4, 5); the nearly complete skull which Carus named Zeuglodon hydrarchus (Müller, 1849, pl. 26), with which were associated both mandibles, a cervical, a dorsal, and a series of caudal vertebrae; a third unfigured damaged cranial fragment, and the occipital portion of another skull (Müller, 1849, pl. 27, fig. 1). All of these specimens are therefore co-types.

(3) An imperfect atlas (Müller, 1849, p. 20, pl. 13, figs. 1–2), with neural arches and extremities of transverse processes destroyed. Clarksville, Clark County, Alabama. Ocala limestone, upper Eocene. Geologisch-Paläontologisches Institut und Museum der Universität Berlin; collector, Albert C. Koch; March, 1845.


(5) The posterior halves of both mandibles, imperfectly preserved. Left mandible has badly weathered and fractured coronoid process, condyle, and hinder lower angle; Pm₃, Pm₄, M₁, M₂, and M₃ are in place. Right mandible has fairly complete coronoid process, but condyle is destroyed; M₃ is in place. An incomplete left scapula. Three small chevron bones. From the upper Jackson formation on the old farm of Sanford Mitchell, which is now owned by Robert Land, about 2 miles southeast of Melvin, Choctaw County, Alabama; southeast ¼ of southeast ¼ of Section 24, Township 11 North, Range 5 West, St. Stephens meridian. [Found near skeleton of Basilosaurus cetoides, No. 4675.] No. 4673, Division of Vertebrate Palaeontology, U. S. National Museum; collector, Charles Schuchert; November 19–24, 1894.

(6) Five one-rooted teeth; a Pm₁ with extremity of root bifurcated; the left M₁; an incomplete left tympanic bulla; right and left thyrohyals; fragments of both stylohyals;
fragments of an atlas and axis, and an incomplete fifth cervical vertebra; eight imperfect dorsal vertebrae; eleven imperfect lumbar vertebrae; four caudal vertebrae; and 28 ribs, more or less complete. From the Ocala limestone (upper Jackson formation) in the vicinity of "The Rocks" near Dead Level, Clark County, Alabama; Section 35, Township 9 North, Range 1 East, St. Stephens meridian. No. 4678, Division of Vertebrate Paleontology, U. S. National Museum; collector, Charles Schuchert; October 27, 1896.

(7) The major portion of the right premaxillary, including the ascending process, the cavity for the anterior end of the maxillary, I₂ and the alveolus for I₃; a short section of the intertemporal region of the braincase; the left jugal, with both extremities destroyed; the involucrum of the left tympanic bulla; the posterior processes of right and left periotic bones; the left stylohyal; the distal half of the right humerus; the right radius and the right ulna, complete; two carpal bones; three metacarpal bones; four more or less complete phalanges; an imperfect axis; the centrum of the seventh cervical and fragments of two other cervical vertebrae; fourteen dorsal vertebrae, more or less complete; five imperfect lumbar vertebrae; ten more or less complete caudal vertebrae; and 30 ribs more or less complete. From the upper Jackson formation on the old G. W. Zitterow farm, which is now owned by Robert Land, about 1 ½ miles southeast of Melvin, Choctaw County, Alabama; southwest ¼ of Section 24, Township 11 North, Range 5 West, St. Stephens meridian. No. 4679, Division of Vertebrate Paleontology, U. S. National Museum; collector, Charles Schuchert; November 5, 1894.

(8) An imperfect centrum of a third cervical vertebra; a damaged sixth cervical vertebra; an imperfect lumbar vertebra; two posterior caudal vertebrae; and a left tympanic bulla. From the upper Jackson formation on farm belonging to Jim Mason, 1 ½ miles southeast of Isney, Choctaw County, Alabama; northeast ¼ of Section 12, Township 9 North, Range 5 West, St. Stephens meridian. No. 4680, Division of Vertebrate Paleontology, U. S. National Museum; collector, Charles Schuchert; October 22, 1896.

(9) An imperfectly preserved left mandible, with upper and hinder portions of coronoid process, the condyle, and the hinder lower angle destroyed; crowns of four teeth (C, Pm₁, Pm₂, and Pm₃) in place but below alveolar level, and alveoli for succeeding teeth vacant; fragments of the right mandible, with the roots only of Dpm₁, Dpm₂, and Dpm₃ in situ, as well as the crown of the erupting Pm₄; two isolated incisors; two isolated deciduous teeth belonging to the left mandible (?Dpm₃ and ?Dpm₄); the parietal and adjoining frontal portion of intertemporal region of braincase; right and left tympanic bulla, incomplete; an incomplete left periotic, lacking posterior process; imperfect third and fourth cervical vertebrae; a mesosternal segment; and the postscapular portion of a right scapula. From the upper Jackson formation near Cocoa, Choctaw County, Alabama; Section 24, Township 11 North, Range 5 West, St. Stephens meridian. No. 4748, Division of Vertebrate Paleontology, U. S. National Museum; collector, Charles Schuchert; October 16, 1896.

(10) An incomplete left tympanic bulla. From the upper Jackson formation, about 2 miles southeast of Melvin, Choctaw County, Alabama; southeast ¼ of Section 24, Township 11 North, Range 5 West, St. Stephens meridian. [Found near fragments of Basilosaurus cetoides, No. 4677, U. S. N. M.]. No. 6124, Division of Vertebrate Paleontology, U. S. National Museum; collector, Charles Schuchert; November 27, 1894.


(12) A damaged left periotic, lacking posterior process and ventral portion of pars cochlearis; and a stapes. From the upper Jackson formation near Cocoa, Choctaw County, Alabama. No. 10857, Division of Vertebrate Paleontology, U. S. National Museum; collector, Charles Schuchert.
(13) A nearly complete and slightly crushed skull, with both periotics in place and with tooth series exceptionally well-preserved and complete, except for I₁, on left side of upper jaw; on right side of upper jaw, I₂, C, Pm₁, Pm₃, Pm₄, and M₁ are present, but the crowns of these teeth are either crushed or incomplete; distal extremity of both premaxillaries as well as both I₁ are destroyed; anterior end of right zygomatic process missing; both ends of right jugal incomplete; hinder plate-like prolongations of pterygoids, which enclose internal choanae, damaged; right pterygoid fossa displaced by lateral crushing; left pterygoid fossa destroyed; right and left tympanic bullae incomplete; right and left mandibles essentially complete, but without any teeth in situ; eight isolated teeth belonging to left mandible, including three incisors, the single rooted (?) canine or (?) Pm₁, and Pm₂, Pm₃, Pm₄, and M₁; seven isolated teeth belonging to right mandible, including an incisor, the single rooted (?) canine or (?) Pm₁, and Pm₂, Pm₃, M₁, M₂, and M₃; a nearly complete atlas; eight fairly complete dorsal vertebrae (first to eighth, inclusive); four imperfect lumbar vertebrae; three eroded centra, probably caudal vertebrae; and 24 fragments of ribs. From the upper Jackson formation on an old washed-out field belonging at one time to G. W. Zitterow, now owned by Robert Land, 1½ miles south and east of Melvin, Choctaw County, Alabama; northwest corner of northeast ¼ of southwest ¼ of Section 24, Township 11 North, Range 5 West, St. Stephens meridian. No. 11962, Division of Vertebrate Paleontology, U. S. National Museum; collectors, Norman H. Boss and Remington Kellogg; October 15, 1929.

(14) Hinder dorsal half of braincase; an imperfect left mandible, with Pm₂, Pm₃, M₁, M₂, and M₃ in place; three imperfect isolated incisor teeth; three isolated cheek teeth, including right Pm₁, right Pm₄, and right M₂; incomplete basihyal; six imperfect dorsal vertebrae; seven imperfect lumbar vertebrae; two anterior caudal vertebrae; preascapular portion of scapula; manubrium of sternum; and fragments of ribs. From the upper Jackson formation on a farm belonging to A. Luther Pippen, about 1½ miles southeast of Melvin, Choctaw County, Alabama; southwest corner of northeast ¼ of northeast ¼ of Section 24, Township 11 North, Range 5 West, St. Stephens meridian. No. 12063, Division of Vertebrate Paleontology, U. S. National Museum; collectors, Norman H. Boss and Remington Kellogg; October 17, 1929.

(15) Ten consecutive vertebrae, comprising the eight hinder lumbar or lumbar-sacral, and the two anterior caudals; the imperfectly preserved right mandible, with Pm₃, Pm₄, and M₃ in place; and the isolated Pm₂ and M₁. From the upper Jackson formation on land belonging to Robert Land, about 1 1/16 miles southwest of Melvin, Alabama; lot 13, southwest ¼ of southeast ¼ of Section 17 (200 yards north of line between sections 17 and 20), Township 1 North, Range 18 East, Choctaw meridian, Clarke County, Mississippi. No. 12335, Division of Vertebrate Paleontology, U. S. National Museum; collectors, Norman H. Boss and Remington Kellogg; October 14, 1929.

(16) An incomplete right periotic bone. From the upper Jackson formation in wash on old Sanford Mitchell field, now owned by Robert Land, about 2 miles southeast of Melvin, Choctaw County, Alabama; near center of Section 24, Township 11 North, Range 5 West, St. Stephens meridian. No. 12975, Division of Vertebrate Paleontology, U. S. National Museum; collectors, Norman H. Boss and Remington Kellogg; October 15, 1929.

(17) An incomplete skull, comprising the upper portion of the braincase, both supraorbital processes of frontals, left squamosal, both exoccipitals, right occipital condyle, basioccipital, portions of nasals, right periotic, and the hinder portion of right tympanic bulla of a quite young individual. From the upper Jackson formation, about one mile east of Melvin, Ala., in northwest ¼ of southwest ¼ of Section 17, Township 1 North, Range 18 East, Clarke County, Mississippi. No. 13773, Division of Vertebrate Paleontology, U. S. National Museum; collectors, Norman H. Boss and Remington Kellogg; October 21, 1929.
(18) The anterior end of the right mandible, measuring 168 mm. from anterior extremity to broken hinder end, with II, I2, and I3 in situ; the symphysial portion of the left mandible, measuring 493 mm. in length, with alveoli for I3, C, PmI, Pm2 and Pm4; and two isolated premolars, the left Pm1 and Pm2. From the Ocala limestone (upper Jackson formation), east bank of Flint River, less than one mile south of mouth of Cedar Creek, Crisp County, Georgia. No. 13774, Division of Vertebrate Palæontology, U. S. National Museum; collector, D. A. Harris; 1925.

(19) A nearly complete skull, but lacking one jugal, both lachrymals, the anterior ends of both maxillaries, and the tooth bearing portions of both premaxillaries; the right maxillary has alveoli for C, Pm1, and Pm4, as well as the right Dpm2 and Dpm3 and the erupting crowns of Pm2 and Pm3; the left maxillary has alveoli for Pm1 and Pm4, as well as the erupting crowns of Pm2 and Pm3; twelve detached teeth, including the left M1 and M2, as well as portions of the right Pm4, the right I3, the left M3, the right and left I3, the left Dpm3, the left DIm, the lower right D0, the left Dpm1, and the right and left Dpm3; the right pterygoid lacks the anterior process and the left pterygoid lacks the posterior process; both tympanic bullae are incomplete; the right mandible has empty alveoli for I1, I2, and I3, as well as the erupting crowns of C, Pm1, Pm2, and Pm3; and the fully erupted Pm4, M1, M2, and M3; the hinder root and corresponding portion of crown of Dpm3, and also the hinder end of the ramus, including the condyle, are destroyed; the left mandible has empty alveoli for I2, I3, Pm4, M1, M2, and M3, as well as the erupting crowns of C, Pm1, and Pm2, and the nearly erupted Pm3; but the hinder end of the ramus, including the condyle, is destroyed; six incomplete cervical vertebrae, including the atlas, axis, as well as the centro of the third, fourth, fifth and sixth cervicals; the centra of ten dorsal vertebrae, including the first, the third to the eighth inclusive, and the tenth to the twelfth inclusive; all of these dorsals, with the exception of the tenth, lack both epiphyses as well as the neural arch and its processes; and fragments of several ribs. From the upper Jackson formation, approximately 5 feet below the top of the Yazoo clay member, about 2 miles east of North State street entrance to campus of Millsaps College, Jackson, in northwest corner of southwest 1/4 of northwest 1/4 of Section 36, Township 6 North, Range 1 East, Choctaw meridian, Hinds County, Mississippi. Millsaps College Museum; collectors, J. Magruder Sullivan, Edwin Underwood and Gladden Caldwell; April 1933.

(20) A nearly complete skull of an adult individual with both pterygoids in situ; right and left tympanic bullae detached; on right side of upper jaw, I1, I3, C, Pm1, Pm2, and Pm3 were present when specimen was found, but were broken off during preparation; on left side of upper jaw, I3, C, Pm3, Pm4, and M1 were likewise present; distal end of left premaxillary eroded; zygomatic processes of both squamosals damaged; jugals and lachrymals missing on both sides; hinder plate-like prolongations of pterygoids destroyed; coronoid process of right mandible incomplete and hinder end, including condyle, missing; the alveoli for I1, I3 and C are filled with matrix, but the remaining teeth, including Pm1, Pm2, Pm3, Pm4, M1, M2 and M3 are present although more or less damaged; left mandible lacks hinder lower angle and most of condyle, and has alveoli for I1, I2, I3, C and Pm1, and has Pm2, Pm3, Pm4, M1 and M2 with more or less complete crowns; the crowns of four one-rooted teeth, including the right upper canine, the right I3 and the right I1; the crowns and portions of the roots of four detached one-rooted teeth belonging to the mandibles; four incomplete cervical vertebrae, including the 3d, 4th, 5th and 6th; the centra and detached processes of fourteen dorsal vertebrae, comprising a consecutive series from the 2d to the 15th, inclusive; three anterior lumbar vertebrae; the manubrium and one mesosternal segment; and fragments of ribs. From the upper Jackson formation in an eroded gulley on field belonging to Robert Land, 1 mile southeast of Melvin, Choctaw County, Alabama; southeast 1/4 of southeast 1/4 of Section 14, Township 11 North, Range
5 West, St. Stephens meridian. Millsaps College Museum, Jackson, Mississippi; collector, J. Magruder Sullivan; July 1926.

SKULL

General conformation of skull (pl. 10) somewhat similar to that of *Dorudon stromeri*, except that the supraoccipital shield is narrower, the nasals are relatively shorter, the outer nasal fossa is extended relatively farther forward, and the rostrum is more strongly narrowed in front of Pm2.

Parietals (fig. 29) normal in relation to adjacent bones, contributing the roof for the cranium and the major portion of the intertemporal constriction, and meeting on the midline to form a high sagittal crest that extends forward almost to level of hinder ends of frontals; dorsal profile (fig. 31) rises gradually behind level of anterior edge of orbit, but at the apex of the supraoccipital shield the lambdoidal crests are conspicuously elevated laterally above the level of the sagittal crest; each parietal contributes a portion of slightly convex lateral cranial wall and meets the squamosal in a dentate suture that runs downward and forward; squamosal rather large, its upper surface convex from before backward; ventro-anterior or temporal margin of squamosal extended forward as a thin shelf; zygomatic process slender, compressed from side to side, obliquely truncated ventrally at extremity in region of contact with hinder end of jugal, and with its crest-like upper edge continued backward and upward along outer and hinder edge of squamosal to join with lambdoidal crest, and forming with the latter the posterior boundary of the enormous temporal fossee; supraoccipital shield (fig. 32) rather broad, strongly concave transversely, with vertical medial ridge near apex, and bounded laterally by prominent lambdoidal crest, for which the anterior face is contributed by the corresponding parietal and the posterior face by the supraoccipital; exoccipital relatively wide, with rather thick and somewhat sinuous external edge; upper edge of exoccipital more or less free and not confluent with lambdoidal crest of squamosal, but slightly below the latter; foramen magnum large, its transverse diameter being greater than its vertical diameter; occipital condyles elliptical in outline, considerably broader above than below, slightly convex from side to side, and borne on short condylar processes; intertemporal region moderately long and narrow; lateral walls of intertemporal constriction are nearly vertical above sphenorbital fissure; groove for optic nerve originating at optic foramen (which in other archaeocetes is situated anterior to and above level of sphenorbital fissure) extends forward and upward on lateral surface of orbitosphenoid and then curves outward on ventral face of supraorbital process of frontal; parietals and frontals quite thick in region of sutural union; supraorbital process of frontal broadened, extended laterally beyond level of jugal, and arched at extremity; postorbital angle of supraorbital process (pl. 11, fig. 1) noticeably thicker than preorbital angle; orbit relatively large; anterior end of laterally flattened jugal mortised into outer face of maxillary as in *Dorudon osiris* and terminated not more than 20 mm. in front of preorbital angle of supraorbital process; lachrymal wedged between preorbital end of supraorbital process and the jugal, forming part of anterior wall of orbit, and mortised into hinder end of maxillary; an open groove for lachrymal duct present; lateral surface of maxillary strongly grooved below anterior extremity of jugal; nasals attenuated anteriorly, slightly convex from side to side, and attain their maximum width posteriorly at level of point of divergence; posterior extremities of nasals widely divergent, separated by broad wedge-like process of combined frontals, and not extended backward to level of hinder ends of maxillaries; anterior extremities of nasals constitute posterior border of dorsal nasal fossa, which they overhang to some extent, the posterior end of the dorsal nasal fossa being above anterior edge of crown of Pm2 and the anterior end being above the canine; the premaxillaries contribute the floor and the lateral walls of the dorsal nasal fossa;
Fig. 29—Zygorhiza kochii (Reichenbach). Skull, dorsal view, No. 11962, United States National Museum. X 10. \( \text{am.f.} \), antorbital foramen; \( \text{c.} \), occipital condyle; \( \text{fr.} \), frontal; \( \text{ju.} \), jugal; \( \text{la.} \), lacrimal; \( \text{max.} \), maxillary; \( \text{na.} \), nasal; \( \text{pa.} \), parietal; \( \text{pmx.} \), premaxillary; \( \text{s.o.c.} \), supraoccipital; \( \text{s.o.r.p.} \), supraorbital process of frontal; \( \text{sq.} \), squamosal; \( \text{zyg} \), zygomatic process of squamosal. Upper Eocene, upper Jackson formation, Alabama.

Fig. 30—Zygorhiza kochii (Reichenbach). Skull, ventral view reconstructed, No. 11962, United States National Museum. X 10. \( \text{bo.} \), basicranial; \( \text{c.} \), occipital condyle; \( \text{f.hy.} \), hypoglossal foramen; \( \text{h.pt.} \), hamular process of pterygoid; \( \text{j.n.} \), notch for jugular leash; \( \text{ju.} \), jugal; \( \text{max.} \), maxillary; \( \text{m.e.a.} \), groove for external auditory meatus; \( \text{p.} \), pars cochlearis of petrotic; \( \text{pal.} \), palatine; \( \text{pmx.} \), premaxillary; \( \text{pr.pa.} \), paroccipital process; \( \text{pr.p.p.} \), posterior process of petrotic; \( \text{pt.} \), pterygoid; \( \text{sq.} \), squamosal; \( \text{zyg} \), zygomatic process of squamosal. Upper Eocene, upper Jackson formation, Alabama.

ascending process of premaxillary lodged in a groove on upper internal border of maxillary and terminated posteriorly above Pm4; the narrow ascending process of maxillary overrides the supraorbital process of frontal and its inferior process projects backward below the latter; inferior process of maxillary attenuated, closely appressed to internal surface of anterior portion of jugal, and on it are located the two molars; the large antorbital foramen lies above interval between Pm2 and Pm3; flat oral surfaces of premaxil-
laries extended backward to level of Pm2 as a narrow wedge-like tongue, separating anterior extremities of maxillaries; major portion of palatal surface (fig. 30) contributed by more or less flattened horizontal plates of maxillaries; true molars set off from palatal surface by a deep excavation; a cavity for reception of apex of mandibular Pm2 located between Pm1 and Pm2, a larger cavity internal to interval between Pm2 and Pm3, a somewhat larger cavity internal to interval between Pm3 and Pm4, and a small cavity internal to interval between Pm4 and M1 for apices of corresponding cheek teeth of mandible; bony palate prolonged backward by elongation of palatines and adjacent thin plates of pterygoids, forming an enclosed tube for internal choanae; a V-shaped elevation is present on palatal surface of this choanal tube; anterior ends of palatines not reaching to level of anterior edge of Pm4; vertical plate of vomer does not project backward beyond level of posterior margins of palatines; suture between basioccipital and basisphenoid obliterated; median basicranial region bounded laterally in front by hamular plates of pterygoids and behind by lateral descending plate-like processes of basioccipital; large ovoidal pterygoid fossa for accessory air sinus of middle ear partially overspread below by pterygoid, the roof being contributed by the alisphenoid and the underlying thin plate of the pterygoid, the outer wall by the postero-external limb of the pterygoid and the bifid anterior end of the squamosal, and the inner wall by the hamular plate of the pterygoid; mandibular branch of trigeminal nerve passes outward from cranial cavity through open recess behind the posterior border of alisphenoid and reaches temporal fossa through foramen ovale which is formed by the divergence of the falciform process and the dorsal portion of the anterior end of the squamosal; postero-external limb of pterygoid suturedly united with bifid anterior end of squamosal; ventral surface of attenuated zygomatic process of squamosal occupied by an ovoidal concave glenoid articular surface which extends downward upon short curved postglenoid process; a well-defined channel for external auditory meatus, which originates on postero-internal margin of ventral surface of squamosal, continues its course outward behind the base of the postglenoid process of that bone; paroccipital process rather large, conspicuously prolonged downward, with ventral concavity for reception
of stylohyoid, but separated from hinder edge of lateral descending process of basioccipital by the wide notch for jugular leash; posterior process of periotic wedged between exoccipital and hinder end of squamosal; small hypoglossal foramen located on hinder margin of notch for jugular leash.

For measurements of the skulls, see table 62 (p. 246).

The skull of an adult individual belonging to Millsaps College Museum [see, (20), referred specimens] shows some structural details more clearly than any of the other skulls. The lateral post-parietal foramina are rather large. They open dorsally. The post-parietal foramen (fig. 31c) on the lateral surface of the right parietal is located about 25 mm.
above the parieto-squamosal suture and about 95 mm. anterior to the most backwardly projecting portion of the lambdoidal crest. In position, these foramina correspond rather closely with those present on the skull of Basilosaurus cetoides (see fig. 3). In the case of marsupials and some insectivores, the post-parietal foramen (Gregory, 1910, p. 248) transmits a vessel which is connected with the venous system of the transverse sinus.

The alisphenoid is a rather conspicuous element in the outer wall of this cranium in the region of the temporal fossa. It is bounded by the parietal, frontal, pterygoid and squamosal. The anterior edge of the alisphenoid forms the outer lip of the sphenoidal fissure. The measurements of the alisphenoid are as follows: antero-posterior diameter, 85 mm., and vertical diameter, 50 mm.

A fracture of the skull of the adult individual (fig. 31b) across the inter-temporal constriction of the level of the sphenoidal fissure has exposed the natural casts of some of the nerve channels. The lateral edge of the olfactory peduncle is about 22 mm. distant from the lateral surface of the corresponding parietal and its dorsal surface is located 74 mm. below the dorsal surface of the parietals (not including the sagittal crest). The transverse diameter of the olfactory peduncle is 13 mm. The casts of the slender optic nerves, which emerge at the optic foramina (55 mm. anterior to this fracture) are appressed to the lateral surfaces of the olfactory peduncle. They measure 7 x 9 mm. The casts for the opposite ophthalmic divisions of the trigeminal nerves are located at the horizontal level of the olfactory peduncle. The cast of the right ophthalmic division measures transversely and vertically, 14 x 20 mm. The cast of the right maxillary division of the trigeminal nerve at this fracture is located 1 mm. below the right ophthalmic division and measures 14 mm. in width and 13 mm. in height. On each side near the outer surface of the parietal and 12 mm. above the level of the dorsal surface of the ophthalmic division is a small vascular canal (5 mm. in diameter). This canal opens into the orbit at the top of the optic foramen and probably transmits the ophthalmic artery. The maxillary division of the trigeminal nerve leaves the cranial cavity through the sphenoidal fissure (fig. 31c), which lies between the alisphenoid and the orbitosphenoid. This fissure is located about 55 mm. anterior to the level of the anterior end of the pterygoid fossa and on the right side at least 242 mm. in front of the hinder face of the occipital condyle. The maxillary division of the trigeminal then extends forward in the groove on the lateral surface of the orbitosphenoid to the sphenopalatine foramen and then outward along the nearly transverse groove in the maxillary to the infraorbital foramen. This foramen is located above the inferior process of the maxillary on which the molars are located. It is hidden by the jugal (fig. 31a) when the skull is viewed from the side. Anteriorly, the groove for the maxillary division of the trigeminal lies below and adjacent to the channel for the optic nerve. The sphenopalatine or internal-orbital foramen is located in the palatine at the angle where the palate meets the frontal and maxillary. The hinder edge of this foramen is located 110 mm. in front of the sphenoidal fissure. This sphenopalatine foramen measures at least 30 mm. antero-posteriorly and 12 mm. vertically on both of the skulls belonging to Millsaps College Museum. On one skull belonging to Dorudon ostiris (No. 11786, Stuttgart) the sphenopalatine foramen (Stromer, 1906b, p. 119) is oval in outline. Previously, Stromer (1903c, pl. 10, fig. 2.c) had concluded that this opening was a crevice-like fissure. The foramen, if correctly identified, transmits the sphenopalatine nerve, a branch of the maxillary division of the trigeminal. The short and rather deep groove for the optic nerve originates at the optic foramen, which, on the right side, is located at least 55 mm. anterior to the hinder edge of the sphenoidal fissure and also at least 75 mm. above level of palatal surface of the skull. It extends forward and upward on lateral surface of orbitosphenoid and then curves outward on ventral face of supraorbital process of frontal. The right optic foramen is located 110 mm. in front of level of anterior end of pterygoid.
fossa and at least 297 mm. in front of hinder face of occipital condyle. By careful preparation on the left side of the intertemporal constriction, the courses of the optic nerve and of the ophthalmic division of the trigeminal nerve were exposed. The osseous septum that separates these two nerves terminates anteriorly about 27 mm. behind the level of the optic foramen. Both nerves issue through the optic foramen. A much smaller foramen is located in the frontal at the fronto-orbitosphenoid suture about 30 mm. in front of the hinder edge of the optic foramen. This foramen is identified as the ethmoid foramen, which transmits the artery and the nasal branch of the ophthalmic division of the trigeminal nerve.

An accidental vertical fracture of the interorbital region of the immature skull belonging to the Millaps College Museum revealed the unusual thickness of the parietal bones. At the level of the anterior ends of the pterygoid fossae, each of these parietal bones has a maximum vertical diameter of 78 mm. above the passages for the olfactory peduncles. The vertical diameter of the cranium at the level of this fracture, measured from basisphenoid to edge of sagittal crest, is 125 mm. The maximum transverse diameter of the left parietal bone at this fracture, 45 mm. below the dorsal edge of the sagittal crest, is 30 mm.

Figures 32 and 33—Zygophysa kochii (Reichenbach). Skull, posterior view, No. 11962, United States National Museum. X1. c., occipital condyle; ex.oc., exoccipital; j.n., notch for jugular leash; l.pr., lateral process of basisphenoid; pgl., postglenoid process of squamosal; s.oc., supraoccipital; sq., squamosal; zyg., zygomatic process of squamosal. Upper Eocene, upper Jackson formation, Alabama.

Figures 32 and 33—Zygophysa kochii (Reichenbach). Dorsal view of juvenile cranium, No. 13773, United States National Museum. X1. c., occipital condyle; ex.oc., exoccipital; fr., frontal; pa., parietal; s.oc., supraoccipital; s.or.pr., supraorbital process of frontal; sq., squamosal; zyg., zygomatic process of squamosal. Upper Eocene, upper Jackson formation, Mississippi.

Figures 32 and 33—Zygophysa kochii (Reichenbach). Dorsal view of juvenile cranium, No. 13773, United States National Museum. X1. c., occipital condyle; ex.oc., exoccipital; fr., frontal; pa., parietal; s.oc., supraoccipital; s.or.pr., supraorbital process of frontal; sq., squamosal; zyg., zygomatic process of squamosal. Upper Eocene, upper Jackson formation, Mississippi.
of the left parietal, the curvature of the lambdoidal crest was established. A definite contact was located also between the left exoccipital and the left squamosal. When these fragments were placed in what appeared to be their normal positions it was found that the ratios of the transverse diameters of the main portions of the braincase to its anteroposterior diameter were remarkably close to those of the immature skull belonging to Millsaps College museum.

It is fairly certain that the lambdoidal crest did not project far enough backward to conceal the exoccipitals, when the skull is viewed from above. That the lambdoidal crests are sharply defined is shown by the abrupt upturning of the hinder ends of both parietals where they abutt against the supraoccipital. The foramen magnum seemingly was rather large in proportion to the transverse diameter of the cranium. The articular surface of the right occipital condyle is rough and pitted. The exoccipitals are small (vertical diameter at extremity of left exoccipital not more than 41 mm.) and have the extremity turned slightly backward. The curvature of the dorsal surface of the squamosal is quite similar to that of the skull of an adult (fig. 29). The temporal rim of the squamosal is thin and compressed dorso-ventrally. Unfortunately the zygomatic process of the left squamosal is destroyed except for the basal portion. The convex swelling of the parietals in the region of the cerebral lobes is more pronounced than on the skull of an adult. The sagittal crest is low, but quite distinct. The temporal ridges on the outer margins of the intertemporal portion of the frontals are elevated and inclose a depression about 15 mm. wide, into which the slender anterior process of the combined parietals projects forward. The supraorbital process is arched at the extremity and the preorbital angle is rounded. The postorbital angle is missing on both processes. The anterior edge of the right frontal has a shallowly grooved depression (8 mm. wide) which extends backward 33 mm. behind the level of the preorbital angles of the supraorbital processes. This depression lodges the hinder end of the ascending process of the maxillary. The depression on the right frontal is complete, but the one on the left frontal has been destroyed. A gap of at least 12.5 mm. for lodging the hinder ends of the nasal bones separates the depressions on the opposite frontals.

<table>
<thead>
<tr>
<th>Table 26—Measurements (in millimeters) of the juvenile skull</th>
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<tbody>
<tr>
<td>Distance from anterior extremity of left frontal to posterior face of supraoccipital shield below apex</td>
</tr>
<tr>
<td>Distance from anterior extremity of frontal to posterior face of occipital condyle</td>
</tr>
<tr>
<td>Maximum transverse diameter across preorbital angles of supraorbital processes</td>
</tr>
<tr>
<td>Transverse diameter across supraorbital processes, near center</td>
</tr>
<tr>
<td>Distance between outer edges of exoccipitals, estimated</td>
</tr>
<tr>
<td>Distance from inner margin of right occipital condyle to outer margin of right exoccipital</td>
</tr>
<tr>
<td>Maximum oblique-vertical diameter of right occipital condyle</td>
</tr>
<tr>
<td>Maximum transverse diameter of right occipital condyle</td>
</tr>
<tr>
<td>Distance from posterior face of supraoccipital shield below apex to end of anterior process of parietal</td>
</tr>
<tr>
<td>Least intertemporal breadth of skull in parietal region</td>
</tr>
<tr>
<td>Least intertemporal breadth of skull in frontal region</td>
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</table>

**TYMPANIC BULLA**

All of the tympanic bullae in the National Museum collection are imperfectly preserved. The thin brittle outer lip, which arches over the thick rounded involucrum, is usually damaged even in the best-preserved specimens. Both of the tympanic bullae associated with the skull (No. 11962, U. S. N. M.) lack most of the thin outer lip as well as the sigmoid process. The sigmoid process is preserved, however, on one left tympanic bulla (No. 4880, U. S. N. M.). In case of four of these tympanic bullae, the maximum transverse diameter does not exceed 66 per cent of the maximum length. The same ratio of width to length is about 68.4 per cent in the case of *Dorudon intermedius*, 73.8 per cent in the case of *Dorudon osiris* and 77.3 per cent in the case of *Dorudon stromeri*. 
The thin outer lip of the bulla (fig. 34a) is curved inward and arches over the elongate cavum epitympanicum. The contour of the tympanic cavity, which is bounded by the over-arching outer lip and by the involucrum, is quite like that of *Dorudon osiris*. The aperture for the eustachian tube at the anterior end of the tympanic cavity is somewhat constricted and the anterior end of the bulla is bluntly truncated. In front of the aperture of the eustachian tube, the dorsal surface of the involucrum is distinctly flattened and in this detail this bulla resembles that of *Balaenoptera borealis*, although the outer lip is not similarly widened along the dorsal rim.

On the outer lip and near the middle of its length, the *processus sigmoideus* is located. The distal end of the sigmoid process is twisted almost at right angles to its basal portion. The transverse diameter of the *processus sigmoideus* (21.7 mm.) is unusual as it exceeds the free height of this process. Although strongly compressed in an antero-posterior direc-

![Diagram of Zygorhiza kochii](image)

**Fig. 34—Zygorhiza kochii** (Reichenbach). Tympanic bullae. *a*, ventral view of right tympanic bulla, No. 11962; *b*, posterior view of left tympanic bulla, No. 4680, United States National Museum. ×1. *cl.*, vertical cleft; *e.p.*, base of external pedicle of posterior process; *in.*, involucrum; *i.p.*, base of internal pedicle of posterior process; *pr.m.*, processus medius; *pr.p.*, processus posterius; *pr.s.*, processus sigmoideus. Upper Eocene, upper Jackson formation, Alabama.

tion, all the faces of the sigmoid process are curved. The sigmoid process is so strongly directed obliquely backward that its basal portion is appressed to the anterior face of the *processus medius*. There is no visible evidence to indicate that the close approximation of these two processes is the result of crushing, for this condition is clearly observable on two tympanic bullae in the National Museum collection and also on the right bulla figured by Müller (1849, pl. 2, figs. 3, 5). Thus in this detail, there is a close resemblance to the conditions existing in *Delphinapterus leucas* and *Monodon monoceros*.

Judging from analogous relations of the tympanic bulla and periotic in Recent Mysticeeti and Odontoceti, the *proc. sigmoideus*, *medius*, and *posterius* form the frame for the tympanic membrane. Like in Recent Cetacea there is a gap in this frame in the interval between the dorsal rim of the sigmoid process and the anterior edge of the outer pedicle of the posterior process. This gap corresponds to the *incisura Rivini*. The *annulus tendi-
neus, which encircles the tympanic membrane, seems to have been attached to the anterior edge of the thin basal pedicle of the posterior process which originates just behind the median process on the outer lip, to the groove which follows along the ventral edge of the inner face of the median process, to the inner edge of the basal portion of the sigmoid process which is appressed to the anterior face of the median process, and to a ridge on hinder concave surface of sigmoid process which is continuous below with the last-mentioned ridge and which extends obliquely upward and inward to a point above its dorso-internal angle. In so far as one can judge from the osseous structures, the attachment of the tympanic membrane was quite similar to that existing in Monodon monoceros. Like in Monodon, the narrow groove for the annulus tendineus follows the ventral edge of the inner face of the median process. This groove is quite distinct on the median process of one bulla (No. 4680, U. S. N. M.), but is very much reduced on another bulla (No. 11962, U. S. N. M.).

The so-called posterior conical apophysis or median process consists of a 9 to 12 mm. broad, low convexity on the outer lip between the sigmoid process and the outer pedicle of the posterior process. The curvature of the anterior face of the median process is much steeper than that of the posterior face. A vertical cleft, 16 to 30 mm. in depth, separates the thickened hinder edge of the outer lip from the involucrum. Through this cleft (fig. 34b), according to Pompeckj (1922, pp. 68–69), some connection existed with an air sinus located between the tympanic bulla and the proc. paroccipitalis, and this sinus may have been extended dorsally in the fissura petroso-paroccipitalis. A similar cleft, somewhat shorter and wider at the apex, is present on the bulla of Megaptera nodosa. In Tursiops truncatus as well as in some other genera of odontocetes, a small elongated aqueduct opening on the hinder face of the bulla, which is bounded on the dorsal side by the basal portion of the posterior process, communicates with the tympanic cavity.

The posterior process was broken off all the bullæ examined. From the remnants which are preserved it would appear that the attachment of the basal pedicles of the posterior process to the tympanic bulla is unusually weak. The narrow inner pedicle at the base of the horizontally enlarged posterior process was ankylosed to the postero-external angle of the involucrum at the epitympanic edge of the above-described cleft. The outer pedicle was even more fragile than the inner one and was ankylosed to the postero-internal angle of the outer lip at the epitympanic edge of this cleft. As regards the Mysticeti, the pedicle of the posterior process of the tympanic bulla is ankylosed to the involucrum in the same relative position as the inner pedicle of the bulla of Zygoryxia kochii, but is much more strongly constructed. In case of the Odontoceti, the base of the posterior process is broadly attached to the hinder ends of both the involucrum and the outer lip of the bulla.

In front of and above the base of the sigmoid process and on the inner dorsal edge of the thin outer lip, the short fissura Glaseri is located. The extremity of the slender anterior process of the malleus was either lodged in this fissure or else ankylosed with the outer lip of the bulla along the dorso-internal margin of this fissure. On the external surface of the outer lip, slightly above the fissura Glaseri, there is a shallow faintly defined groove which runs forward and slightly downward. This has been identified as the sulcus for the chorda tympani. The anterior process was not preserved on any of these bullæ.

The dorsal portion of the dense involuted portion of the tympanic bulla is constricted rather abruptly in front of the level of the fissura Glaseri. The hinder half of the involucrum is expanded transversely and is strongly convex. The dorsal surface of the anterior half of the involucrum is flattened and slopes obliquely to the inner edge. The dorsal surface of the entire involucrum is rather smooth, but is faintly and finely grooved in a dorso-ventral direction on the hinder face and also in front of the constriction. The maxi-
maximum transverse diameter of the involucrum varies from 47 to 52 per cent of the maximum antero-posterior diameter.

The ventral surface of the tympanic bulla is strongly curved from before backward and from side to side. On the hinder fourth of this surface is a broad, deep median hollow which is bounded laterally by a narrow outer and a broader inner convexity. Viewed from behind, the inner surface of the tympanic bulla is nearly straight, while the outer surface is strongly curved. The hinder edge of the ventral surface is bounded by a rather sharp-edged crest, which is coextensive with the involucrum.

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<td>Left</td>
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<td>Maximum diameter of bulla</td>
<td>85±</td>
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<td>Maximum antero-posterior diameter of bulla</td>
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<td>78</td>
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<td>Maximum transverse diameter of bulla</td>
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<td>54.6+</td>
<td>56.8</td>
<td>53</td>
<td>52.5</td>
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<tr>
<td>Vertical distance from dorsal edge of median process (conical apophysis) to ventral face of bulla</td>
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<td>47.3</td>
<td>...</td>
<td>38</td>
<td>46.5</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Maximum transverse diameter of involucrum</td>
<td>39.4</td>
<td>37.4</td>
<td>...</td>
<td>38</td>
<td>38.5</td>
<td>36.5</td>
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</table>

**PERIOTIC**

The right (pl. 15, fig. 1) and left periotic bones are attached to the nearly complete skull (No. 11962) in the National Museum collection. Four isolated periotic bones belonging to as many individuals were also utilized in determining structural details which otherwise could not have been observed without the removal of one of the periotics attached to the skull. These four periotics unquestionably belong to somewhat younger individuals than the animal to which the skull belonged. One of these periotics (No. 10855, U. S. N. M.) is exceptionally complete, and the others are very well preserved but lack the posterior process.

The periotic of this archaeocete is quite similar to that of *Dorudon asper* in many details. It is characterized in part by the dorsal prolongation of the denser outer portion to form an inwardly curved and laterally compressed superior plate-like process (fig. 35b), which is applied to the squamosal on the inner wall of the cranium, by the location of the *foramen singulare* at the base of the anterior face of the *crista transversa*, by the relatively small size of the *tractus spiralis foraminosus*, and by the deeply excavated fossa for the stapedial muscle. The elongated posterior process (pl. 15, fig. 1) is firmly wedged between the exoccipital and the squamosal, as in the Mysticeti. With reference to the antero-posterior axis of the periotic, the posterior process is slightly twisted outward. On the ventral surface of the posterior process are slight ridges and grooves. Near the middle of its length this process on the right periotic (No. 11962, U. S. N. M.) measures 15 mm. antero-posteriorly. At the proximal end of the posterior process, a short thin inwardly projecting ledge overhangs the steep inner face which forms the outer wall of the posterior excavation for the stapedial muscle.

Viewed from the ventral side, the pars cochlearis is seen to be distinctly flattened anteriorly, but the ventral surface as a whole curves from before backward. On the outer border of the pars cochlearis is a distinctly raised crest which may follow the course of the internal carotid artery. Anteriorly the pars cochlearis rises rather steeply and is set off from the anterior process by the deep narrow groove for the tensor tympani muscle. The inner or cerebral border of the ventral surface of the pars cochlearis is either rounded or obliquely truncated.
The *fenestra rotunda* is generally elliptical in outline and is situated on the hinder surface of the *pars cochlearis* somewhat above the level of the ventral surface of the posterior process. The long axis of the *fenestra rotunda* is nearly horizontal, and its transverse and vertical diameters range from a minimum of $3.8 \times 2.3$ mm. to a maximum of $5.5 \times 3.2$ mm. On one right periotic (No. 4748, U. S. N. M.) a deep furrow (fig. 36) marks the former position of an open groove which at some time during the animal's growth extended

**Fig. 35—Zygorhiza kochii** (Reichenbach). *Left periotic, immature individual, No. 10855, United States National Museum. ×1.*  
*a.* ventral view; *b.* cerebral view. *a.c.* aperture of aquaeductus cochleae; *a.i.c.F.* internal aperture of aquaeductus Fallopii; *aq.F.* epitympanic orifice of aquaeductus Fallopii; *c.f.* channel for facial nerve; *d.e.* fossa at aperture of ductus endolymphaticus; *f.b.i.* fossa incisus for processus breve of incus; *f.c.m.* fossa for head of malleus; *f.s.*, foramen singulare; *f.e.o.*, fenestra ovalis; *f.e.r.*, fenestra rotunda; *f.t.t.* channel for tensor tympani muscle; *p.c.*, pars cochlearis; *pr.a.p.*, anterior process of periotic; *pr.p.p.*, posterior process of periotic; *pr.s.p.*, superior process of periotic; *t.s.f.*, tractus spiralis foraminosus. Upper Eocene, upper Jackson formation, Alabama.

**Fig. 36—Zygorhiza kochii** (Reichenbach). *Left periotic, juvenile individual, No. 4748, United States National Museum. ×1.*  
*a.* ventral view, posterior process destroyed; *b.* cerebral view, superior process partly destroyed. *a.c.* aperture of aquaeductus cochleae; *a.i.c.F.* internal aperture of aquaeductus Fallopii; *aq.F.* epitympanic orifice of aquaeductus Fallopii; *c.f.* channel for facial nerve; *d.e.* fossa at aperture of ductus endolymphaticus; *f.c.e.* foramen centrale; *f.c.m.* fossa for head of malleus; *f.s.*, foramen singulare; *f.st.* fossa for insertion of stapedial muscle; *f.e.o.*, fenestra ovalis; *f.e.r.*, fenestra rotunda; *p.c.*, pars cochlearis; *pr.a.p.*, anterior process of periotic; *pr.p.p.*, posterior process of periotic, broken off at base; *pr.s.p.*, superior process of periotic, incomplete posteriorly; *t.s.f.*, tractus spiralis foraminosus. Upper Eocene, upper Jackson formation, Alabama.
across the posterior face of the *pars cochlearis* from the *fenestra rotunda* to the cerebral orifice of the *aquaeductus cochleae*. On the extero-lateral surface of the *pars cochlearis*, near its upper limit and behind the middle of its length, the *fenestra ovalis* is situated. The foot plate of the stapes is firmly lodged in the *fenestra ovalis* and is held in position by a very narrow ledge which is sunk 2 to 3 mm. below the level of the epitympanic rim of the fenestra. The *fenestra ovalis*, which leads into the vestibule of the osseous labyrinth, is irregularly elliptical in outline and varies in size from $4.7 \times 3.6$ mm. to $5.2 \times 3.7$ mm. The two small orifices of the semicircular canals are situated on the outer side of the roof of the vestibule, 4.8 mm. above the level of the epitympanic margin of the fenestra ovalis. The relatively large *ductus endolymphaticus* enters the vestibule at its postero-internal angle.

The epitympanic orifice of the Fallopian aqueduct (fig. 35a), which opens into a deep narrow groove, about 1.5 mm. in width anteriorly and separated internally from the *fenestra ovalis* by the narrow rim of the latter, is located on the roof of the *recessus epitympanicus* and above the level of the *fenestra ovalis*. This groove for the facial nerve is slightly wider posteriorly and terminates at about the level of the antero-internal angle of the posterior process. Behind this groove is a deep rugose fossa, which in Recent Cetacea corresponds to the area for the attachment of the stapedial muscle. The area for the stapedial muscle is extended downward behind the *fenestra ovalis* upon the outer face of the *pars cochlearis* and externally upon the nearly vertical inner face of the posterior process. The roughened surface of the fossa for the stapedial muscle is sunk below the level of the hinder end of the groove for the facial nerve, while at its posterior limit a thin transverse wall of bone rises on one right periotic (No. 12975, U. S. N. M.) to the level of the *fenestra rotunda*. This fossa constitutes the ventral boundary between the *pars cochlearis* and the posterior process.

External to the epitympanic orifice of the *aquaeductus Fallopii* is a deep, elongated and irregular cavity, which constitutes the *fossa incudis*. This small fossa for lodging the *crus breve* of the incus encroaches upon the postero-external angle of the fossa for the head of the malleus. The large fossa for the head of the malleus is situated on a protuberance in front of the epitympanic orifice of the *aquaeductus Fallopii* and is bounded anteriorly and laterally by a thick elevated crest. This fossa is concave from side to side and placed obliquely on this protuberance. A narrow fissure, which is incompletely closed on one right periotic (No. 12975, U. S. N. M.), is present between the thickened inner portion of this protuberance and the *pars cochlearis*. The deep narrow groove internal to this fissure presumably lodged the *tensor tympani* muscle, whose hinder end was inserted on the manubrium of the malleus.

On the external face of the periotic a deep dorso-ventrally curved groove seems to mark the hinder limit of the anterior process. The cavity formed by this groove has been identified as the *fovea epityubaria* and, if correctly identified, it lodges the *processus tubarius* of the tympanic bulla. The outer wall of this cavity is formed by the free edge of the squamosal behind the basal portion of the falciform process of this bone. The external face of the anterior process is strongly convex, a slight crest is developed on its ventral face, and its internal face is obliquely flattened in a ventral-dorsal direction to about the level of the entrance to the Fallopian aqueduct. Above this level the inner face of the anterior process is irregularly concave and the curvature of this surface passes imperceptibly into that of the thin superior process of the periotic.

Viewed from the internal or cerebral side, the dorsal margin of the thin, curved plate-like superior process is nearly straight and the cerebral surface is irregularly hollowed out. Below the superior process is the ventrally placed *pars cochlearis*. The large internal acoustic meatus is the most prominent structure on the cerebral face of the periotic. The
six periotics available for comparison exhibit considerable variation not only in the shape but also in the dimensions of the internal acoustic meatus, the diameters of the smallest meatus being 7.2 × 13.3 mm. (No. 4748, U. S. N. M.) and those of the largest meatus being 10.5 × 15.8 mm. (No. 10855, U. S. N. M.). The internal acoustic meatus is conspicuously smaller at its fundus than at its cerebral rim and it is sunk about 10 mm. deep into the pars cochlearis. The small tractus spiralis foraminosus is well defined, with a minute foramen centrale at its anterior end, and it is located for the most part on the ventral side of the fundus. A thin osseous partition, which does not rise to the level of the cerebral rim of the internal acoustic meatus, separates the fundus from the cerebral entrance to the aquaeductus Fallopii. The facial nerve passes through the aqueduct of Fallop-is and then emerges in the epi tympanic recess as described above. At the base of the anterior face of this thin osseous partition and adjacent to the aquaeductus Fallopii is the minute orifice of the foramen singulare, through which passes the vestibular branch of the acoustic nerve. In most of the Recent Odontoceti, the orifice of the foramen singulare is either located on the rim of this thin crista transversa or else within the fundus of the internal acoustic meatus. The small orifice of the aquaeductus cochlearis is situated outside of the internal acoustic meatus and at the postero-internal angle of the pars cochlearis. Behind the posterior rim of the internal acoustic meatus and above the orifice of the aquaeductus cochlearis is a deep, elongated cavity for the sacculus endolymphaticus, and the small cerebral orifice of the aquaeductus vestibuli for the ductus endolymphaticus is located at the bottom of this cavity.

The dorsal half of the hiatus epitympanicus is formed by the hollowed-out area on the outer border of the periotic lying between the protuberance for the fossa which lodges the head of the malleus and the base of the almost vertically rising anterior face of the posterior process, while the ventral half is limited by the sigmoid process anteriorly and by the basal portion of the posterior process of the tympanic bulla posteriorly. This hiatus epitympanicus seems to be peculiar to the Cetacea, and in Recent Odontoceti it forms the connecting passage between the cavum epitympanicum and the sinus pneumaticus squamosi.

An isolated right periotic bone (No. 12975, U. S. N. M.) was sectioned to expose the structure of the cochlea. It will be observed (fig. 37) that the turns of the cochlea are almost vertical in relation to the antero-posterior axis of the periotic, while in all Recent odontocetes the turns of the cochlea are approximately horizontal to the same axis. Furthermore, there is an obvious elongation of and an "unwinding" of the turns of the cochlea in periotics of Recent odontocetes. The cochlea has the form of a short, broad cone;
the central part of its base lies at the level of the inner rim of the *fenestra rotunda*, while its apex is directed forward and comes into close relation with the bottom (*fundus*) of the internal acoustic meatus in the region of the *tractus spiralis foraminosus*. On this periotic the cochlea measures about 8.2 mm. across the base and about 11.5 mm. from base to apex. The cochlea makes two and a half turns around a central conical pillar, the *modiolus*, and the latter has a maximum length of about 7 mm. The *lamina spiralis ossea*, a very thin ridge of bone, winds around the *modiolus* like the thread of a screw, and projecting not more than half-way into the cochlear tube, incompletely divides it into two passages, of which the hinder one is the *scala tympani* and the anterior one the *scala vestibuli*. This *lamina spiralis ossea* commences at the vestibule and ends near the apex of the spiral in a sharp-edged *hamulus*. The *scala vestibuli*, the anterior of the two passages in the coiled cochlea, begins in the vestibule, and its basal turn is slightly smaller than that of the *scala tympani*, but near the apex these two *scalae* have approximately the same diameter. The hinder one of the two passages of the cochlea, the *scala tympani*, commences at the *fenestra rotunda*. The *aqueductus cochleae*, a passage measuring about 9 mm. in length and opening on the cerebral face of the periotic, leads to the *scala tympani*.

**Table 28—Measurements (in millimeters) of periotics**

<table>
<thead>
<tr>
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</tr>
</thead>
<tbody>
<tr>
<td>Maximum transverse diameter of periotic at level of <em>fenestra ovalis</em></td>
<td>31</td>
<td>26.5</td>
<td>32.5</td>
<td>27+</td>
<td>26.8+</td>
<td>26.5+</td>
<td>26.5+</td>
<td>26.5+</td>
</tr>
<tr>
<td>Maximum length of periotic, tip of anterior process to tip of posterior process</td>
<td>64</td>
<td>75</td>
<td>78</td>
<td>40.5</td>
<td></td>
<td></td>
<td>41.5</td>
<td>41.5</td>
</tr>
<tr>
<td>Maximum dorso-ventral depth of periotic, from most inflated portion of tympanic face of <em>pars cochlearis</em> to dorsal margin of superior plate-like process</td>
<td>37.2</td>
<td>37</td>
<td>54+</td>
<td>40.5</td>
<td></td>
<td></td>
<td>41.5</td>
<td>41.5</td>
</tr>
<tr>
<td>Distance between <em>fenestra rotunda</em> and tip of anterior process</td>
<td>36.5</td>
<td>37</td>
<td>48+</td>
<td>40.5</td>
<td>46.5</td>
<td>40.5</td>
<td>40.5</td>
<td>41.5</td>
</tr>
<tr>
<td>Distance between <em>fenestra rotunda</em> and tip of posterior process</td>
<td>30.6</td>
<td>30</td>
<td>40.5</td>
<td>46.5</td>
<td>34.5</td>
<td>34.5</td>
<td>34.5</td>
<td>41.5</td>
</tr>
<tr>
<td>Distance between epitympanic orifice of <em>aqueductus Fallopian</em> and tip of anterior process</td>
<td>28</td>
<td>30.5</td>
<td>37.8</td>
<td>32.6</td>
<td>34.5</td>
<td>34.8</td>
<td>4</td>
<td>34.5</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of <em>pars cochlearis</em></td>
<td>29.7</td>
<td>29.5</td>
<td>37.5</td>
<td>30.5</td>
<td>30.5</td>
<td>32.2</td>
<td>30.8</td>
<td>30</td>
</tr>
<tr>
<td>Transverse versus vertical diameters of internal acoustic meatus</td>
<td>7.2 x 13.3</td>
<td>10.5 x 15.8</td>
<td>8 x 15</td>
<td>9 x 14.4</td>
<td></td>
<td></td>
<td>29</td>
<td>29</td>
</tr>
<tr>
<td>Extremity of anterior process to anterior edge of fossa for <em>malleus</em></td>
<td>21.7</td>
<td>22.5</td>
<td>30</td>
<td>26.5</td>
<td>27.5</td>
<td>25.5</td>
<td>25.5</td>
<td>25.5</td>
</tr>
<tr>
<td>Maximum transverse diameter of <em>pars cochlearis</em> behind level <em>fenestra ovalis</em></td>
<td>18.2</td>
<td>15.5</td>
<td>19.6</td>
<td>20.2</td>
<td>18</td>
<td>17.5</td>
<td>16.5</td>
<td>16.5</td>
</tr>
<tr>
<td>Greatest length of posterior process</td>
<td></td>
<td>27.8</td>
<td>37.5</td>
<td>42.5</td>
<td>32</td>
<td></td>
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MANDIBLE

The mandible (fig. 31) of this archaeocete is characterized by the rather slender horizontal ramus, moderately high coronoid process, and a somewhat reduced hinder lower angle. From before backward the left horizontal ramus increases in depth quite gradually up to *Pm₃*, the vertical depth at level of *I₂* being 45.5 mm., and at *Pm₃* at least 67 mm.; the depth of the left ramus at level of posterior edge of alveolus of *Pm₄* is 68 mm.; and at the posterior edge of alveolus of *M₃* it is 138 mm. The increase in the vertical depth of the mandible becomes more perceptible behind *Pm₃*, and *Pm₄* marks the transition to the somewhat steeply rising convex anterior edge of the coronoid process. The external face (pl. 14, fig. 1) of the horizontal ramus is convex, and on the internal face the flat symphysial surface (pl. 14, fig. 2) extends backward to behind the level of *Pm₂*. There
are several small mental foramina on the outer face of the horizontal ramus, those below the incisors and canines being nearer the ventral edge, while the hinder ones are located in front of and behind Pm3, but the latter are nearer the alveolar edge. The posterior edge of the thin but rather broad coronoid process is rounded and indented above the condyle. On the outer face of the mandible a prominent ridge extends forward a short distance from the condyle. The condyle is broad, somewhat curved dorso-ventrally, and scarcely curved from side to side. On the internal face of the left mandible below the coronoid process and 140 mm. anterior to the level of the hinder face of condyle is the large orifice of the alveolar or mandibular canal.

It should be noted, however, that the available material from the Ocala limestone of Georgia differs in some minor details from the corresponding skeletal parts of the typical form that occurs in the upper Jackson formation on the gulf coastal plain and in the Ocala formation in Clark County, Alabama. The slightly greater dimensions of the mandible (No. 13774, U. S. N. M.), especially the greater vertical depth of the anterior end, the shorter diastema between Pm1 and Pm2, and the lesser number of accessory denticles on the hinder cutting edge of the crown of Pm2 (see p. 123) are the chief points of difference. The anterior end of this mandible is complete. The alveolus for 11 is smaller than the others, indicating that the anteriormost incisor is somewhat smaller than the others. The diastema between the alveoli for Pm1 and Pm2 is only 19 mm. A similarly shortened diastema is found on the left mandible of an immature individual (Millsaps College Museum). On the latter the interval between the alveoli for Dp1 and Dp2 is 24.5 mm., but the vertical depth of the anterior end of the mandible approximates the normal measurements for the adult.

| Table 29—Measurements (in millimeters) of mandibles |
|---------------------------------|------|------|------|------|------|------|
|                                | No. 13774 | No. 13774 | No. 13774 | No. 13774 | No. 13774 | No. 13774 |
|                                | U. S. N. M. | U. S. N. M. | U. S. N. M. | U. S. N. M. | U. S. N. M. | U. S. N. M. |
| Length of mandible, from hinder face of condyle to extremity | 734± | 712± | 718± | 712± | 718± | 712± |
| Vertical height of mandible through coronoid process | 186 | 202 | 207 | 238± | 207 | 238± |
| Anterior-posterior diameter of symphysis | 48 | 39.5 | 35 | 40 | 295 | 317 |
| Vertical height of mandible at level of alveolus of C, anteriorly | 315± | 322± | 315± | 322± | 315± | 322± |
| Vertical height of mandible at level of alveolus of Pm2, anteriorly | 46.5 | 47 | 46.5 | 47 | 46.5 | 47 |
| Vertical height of mandible at level of alveolus of Pm3, anteriorly | 57 | 58 | 57 | 58 | 57 | 58 |
| Vertical height of mandible at level of alveolus of M3, anteriorly | 67 | 65 | 67 | 65 | 67 | 65 |
| Vertical height of mandible at level of alveolus of M3, posteriorly | 133 | 138 | 134 | 133 | 138 | 134 |
| Anterior edge of Pm2 to hinder edge of M3 | 290± | 287± | 290± | 287± | 290± | 287± |
| Anterior edge of Pm2 to hinder face of condyle | 456 | 470 | 468 | 456 | 470 | 468 |
| Anterior edge of Pm3 to hinder face of condyle | 338 | 402 | 425 | 338 | 402 | 425 |
| Posterior edge of M3 to hinder edge of coronoid process | 144 | 137 | 152 | 144 | 137 | 152 |
| Posterior edge of M3 to hinder face of condyle | 185 | 189 | 213 | 185 | 189 | 213 |
| Diastema between I2 and I3 | 24.5 | 31 | 24.5 | 31 | 24.5 | 31 |
| Diastema between I3 and C | 34 | 37 | 34 | 37 | 34 | 37 |
| Diastema between C and Pm1 | 41 | 38 | 43.5 | 38 | 43.5 | 38 |
| Diastema between Pm1 and Pm2 | 52 | 31.5 | 32.5 | 38 | 31.5 | 32.5 |
| Diastema between Pm2 and Pm3 | 26 | 24 | 26 | 24 | 26 | 24 |

PERMANENT DENTITION

The tooth formula is: 8 1.4.3 8. 1.4.3 8. 1.4.3 8. The dentition (fig. 31) of the upper and lower jaws is not only heterodont, but also anisodont. At the anterior end of the upper tooth row, the pits for the reception of the apices of the lower single-rooted teeth are located on the
outer side of the grasping teeth, while the larger cavities for the apices of the lower cheek teeth are on the inside of the two-rooted serrated cheek teeth, showing that the upper and lower tooth series cross over when the jaws are closed. The distance from the anterior edge of the alveolus of the first incisor to the anterior edge of alveolus of second premolar is certainly greater above than below, and conversely the length of the lower serrated cheek tooth series is much greater than that of the upper. The upper teeth hereinafter described, unless noted otherwise, are in situ in the nearly complete skull (No. 11962, U. S. N. M.).

Both of the first incisors and the corresponding portions of the premaxillaries are destroyed. The succeeding incisors (pl. 13) are caniform and have long slender roots but no perceptible neck. The second upper incisor has a relatively long, sharp-pointed, recurved, and laterally compressed crown, with carinate anterior and posterior cutting edges; it is directed forward, outward, and downward. The laterally compressed crown of the third upper incisor is smaller than that of I₂, and curves inward and backward. The enamel-covered crowns of the incisors as well as that of the canine are ornamented with vertical striæ which anastomose at intervals.

The high enamel-covered crown of the canine (pl. 13) is compressed from side to side, striated vertically with anastomosing ridges, furnished with carinate anterior and posterior cutting edges, and inclined outward. The preservation of the left canine is much better than the one on the right side.

The hinder root of Pm₃ and Pm₄ is almost twice as thick transversely as the anterior root, and the vertical furrow on its hinder surface gives the false impression of a bifurcated root. The accessory denticles on the anterior cutting edge of the crown on all of the premolars are smaller and farther removed from the apex of the principal cusp than those on the posterior edge. The enamel surface of the crown of the upper and lower premolars is ornamented with more or less vertical striæ which anastomose at intervals, and these striæ are coarser on the inner face than on the outer.

The antero-posterior diameter of the crown of Pm₁ (pl. 13) at the base is much greater than that of the canine, and the root below the base of the crown is pinched in at the middle on the outer and inner faces; the enamel on the crown is striated vertically with anastomosing ridges. The steep anterior carinate edge is faintly serrated and on the hinder edge below the sharp edge of the principal cusp there are three small accessory denticles. The crown of the left Pm₁ is fairly well preserved with the exception of the apex, but the crown of the right Pm₁ is badly damaged. The crown of Pm₁ is less flattened laterally than on the succeeding cheek teeth, and it marks the transition between the high slender-crowned single-rooted grasping teeth and the laterally compressed and serrated crowns of the shearing teeth. Pm₁ has two roots and its alveolus is narrower than that of the canine.

Contrasted with the other upper serrate-edged cheek teeth, the crown of Pm₂ (pl. 12) is noticeably longer than that of Pm₃ and Pm₄, and in this detail there is a close resemblance to a juvenile Prozeuglodon isis. In the mandible, Pm₂ is conspicuously smaller than either Pm₃ or Pm₄. The hinder cheek teeth, Pm₂ to M₂ inclusive, have two roots, and the hinder roots of Pm₃ and Pm₄ are enlarged on the inside.

The enamel-covered crown of Pm₂ is considerably longer than that of the corresponding lower premolar and furthermore its anterior edge slopes less steeply. The anterior half of this crown is bowed inward. Pm₂ has a high principal cusp, with four small accessory denticles on the steep anterior edge of the crown, the upper one of these being not sharply set off from the anterior serrated edge of the principal cusp; on the posterior cutting edge there are five accessory denticles, comprising a small basal one, three quite large ones, and a minute upper denticle which is not sharply differentiated from the hinder cutting edge of the principal cusp. The enamel crown of Pm₂ is ornamented with anastomos-
ing vertical strie, especially on the inner face, and these strie extend over upon the surfaces of the accessory denticles. There is a strong crenelated cingulum on the anterior and posterior portions of the inner face of the crown.

The hinder upper cheek teeth, Pm₃ to M₂, form a closed series. The apex of the crown of Pm₃ (pl. 12) does not project ventrally beyond that of Pm₂. The three accessory denticles on the anterior edge are smaller and do not extend as far toward the apex of the crown as the four on the hinder edge. The sharp cutting edges of the principal cusp are not denticulated. The enamel surface of the crown of Pm₃, especially on the inner side, is ornamented with a series of more or less fine vertical strie which anastomose at intervals; this ornamentation does not extend over upon the smooth surface of the large posterior accessory denticles. There is a distinct crenelated cingulum, which is interrupted medially, on the anterior and posterior halves of the inner face of the crown. The hinder root is somewhat larger and is distinctly wider transversely than the anterior root. The two roots do not diverge very strongly.

The crown of Pm₄ (pl. 12) is smaller and shorter than that of Pm₃. The principal cusp is about as large as that of Pm₃, but the three accessory denticles on the anterior edge of the crown are smaller and farther removed from the apex of the principal cusp than the three on the posterior edge. The crenelated cingulum on the antero-internal face of the crown is approximately the same width as that on Pm₃. The crenelated cingulum on the postero-internal face of the crown is wide. The enamel on the inner and outer faces of the crown is relatively smooth. This enamel also extends farther downward on the inner face of the crown than on the outer in both Pm₃ and Pm₄.

The crown of M₁ (pl. 12) is low and noticeably smaller than that of Pm₄. This molar has a short, broad principal cusp, and has two small accessory denticles and a minute basal one on the anterior edge of the crown, and two larger denticles and a minute basal one on the hinder edge. A narrow sharp-edged cingulum is present on the anterior and posterior portions of the inner face of the crown. The enamel on the inner and outer faces of the crown is faintly striated.

The crown of M₂ (pl. 12) is the smallest of the serrate-edged cheek teeth. It has a broad principal cusp, and the accessory denticle on the anterior edge of the crown is smaller than either of the two accessory denticles on the hinder edge. There is a short and narrow cingulum on the postero-internal portion of the crown. The enamel surface of the crown is faintly striated. The crowns of both of these molars are considerably smaller than that of Pm₄.

On the anterior half of the mandibular tooth row (pl. 10), the larger pits for the reception of the apices of the upper grasping teeth are located on the outer surface of the mandible and in the intervals between the alveoli of the anterior single-rooted teeth, while the smaller pits for the apices of the larger upper premolars, Pm₂, Pm₃ and Pm₄, are likewise located on the outside of the mandibular cheek teeth in the intervals between Pm₂, Pm₃, Pm₄, and M₁. The hinder cheek teeth, Pm₃ to M₃ inclusive, form a closed series. The antero-posterior diameters of the crowns of Pm₃ and Pm₄ are approximately the same, but the crown of Pm₄ is actually slightly larger. In case of both Dorudon ostiris and Dorudon stromeri, Pm₃ is unquestionably the largest tooth in the mandibular cheek tooth series.

The anterior ends of both mandibles associated with the skull (No. 11962, U. S. N. M.) were destroyed by weathering before they were found. None of the teeth were in situ in either of these mandibles. The isolated teeth associated with these mandibles have been identified by comparison with those in situ in other mandibles (Nos. 4673, 4748, and 12063, U. S. N. M.). These teeth are shown on the illustration of the left mandible (fig. 31) in their respective alveoli.
The mandibular incisors are incisiform and have sharp-pointed crowns, no perceptible neck, and long slender roots. These lower incisors have smaller crowns than the corresponding upper ones. The sharp-pointed and laterally compressed crowns of these incisors have carinate anterior and posterior cutting edges, and the enamel is ornamented with vertical striæ.

The crown of the mandibular canine is slightly larger than those of the incisors. The sharp-pointed enamel crown of this tooth is compressed from side to side, striated vertically with anastomosing ridges, furnished with carinate anterior and posterior cutting edges, and directed slightly outward.

The single rooted Pm1 was not represented among the isolated teeth associated with this specimen.

Both Pm2 (pl. 13) were found associated with these mandibles (No. 11962, U. S. N. M.). The crown of this tooth is curved inward from base to apex. The basal half of the anterior edge of the crown of Pm2 is strongly serrated, the principal cusp is high and sharp edged, and there are three accessory denticles on the hinder cutting edge. The enamel on the crown is striated vertically with anastomosing ridges. There is no cingulum on either the inner or the outer faces of the crown. The two backwardly directed roots are widely separated, the neck is very short, and the posterior root is much larger than the anterior one.

An isolated Pm2 found in the matrix alongside a left mandible (No. 13774, U. S. N. M.) has two fairly large accessory denticles on the lower part of the anterior cutting edge of the crown as well as a rather small denticle near the base of the anterior edge of the principal cusp. On the posterior cutting edge of the crown of this tooth is an unworn rudimentary denticle at the base of the principal cusp, below which are two fairly large accessory denticles and a minute basal denticle. The apices of these accessory denticles as well as that of the principal cusp are strongly worn. The enamel on both faces of the crown as well as on the accessory denticles on its hinder cutting edge are striated vertically with anastomosing ridges. The measurements of this Pm2 are as follows: Maximum length, from worn apex of principal cusp to extremity of anterior root, 75 mm.; antero-posterior diameter of crown at base, 41; and maximum transverse diameter of crown at base, 14.

The Pm3 (pl. 13) belonging in the left mandible (No. 11962, U. S. N. M.) has a crown which is considerably longer than that of Pm2. This premolar has a large principal cusp, four accessory denticles on anterior cutting edge of crown, and four larger ones on the hinder cutting edge. The enamel crown of Pm3 is ornamented with anastomosing vertical striæ, especially on the inner face, and these striæ extend over upon the accessory denticles. No cingulum is present on either the inner or the outer face of the crown. The roots, which are more widely separated than on Pm2, are about equal in size and connected below the crown by a thin isthmus.

The apex of the crown of Pm4 (pl. 13) projects dorsally above those of Pm3 and M1. The principal cusp is about as large as that of Pm3, but the accessory denticles on the anterior cutting edge are larger. The four accessory denticles on the anterior edge of the crown are smaller than the three on the hinder edge. The crown is curved inward from base to apex, and the enamel on its inner and outer faces is relatively smooth. The enamel surface of the crown extends farther downward on the inner face than on the outer. No cingulum is developed. As regards size, the anterior and posterior roots of this premolar are of about equal proportions. The anterior root of both of the Pm4 (No. 11962, U. S. N. M.) is nearly straight, but the distal half of the hinder root is bent backward.

Immediately behind Pm4 are three closely crowded molars (No. 12063, U. S. N. M.), which are distinguished from the premolars by the absence of accessory denticles on the anterior cutting edge of the crown. The anterior edges of the crowns of M1, M2, and M3
**Table 30—Measurements (in millimeters) of premaxillary and maxillary teeth**

<table>
<thead>
<tr>
<th></th>
<th>M2</th>
<th>M1</th>
<th>Pm4</th>
<th>Pm3</th>
<th>Pm2</th>
<th>Pm1</th>
<th>C</th>
<th>I3</th>
<th>I4</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R</td>
<td>L</td>
<td>R</td>
<td>L</td>
<td>R</td>
<td>L</td>
<td>R</td>
<td>L</td>
<td>R</td>
</tr>
<tr>
<td>Antero-posterior diameter at base of enamel crown (No. 11962, U. S. N. M.)</td>
<td>23.7</td>
<td>25.8</td>
<td>25.9</td>
<td>45</td>
<td>42.8</td>
<td>50.5</td>
<td>49</td>
<td>53.8</td>
<td>32.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>R</td>
<td>L</td>
<td></td>
</tr>
<tr>
<td>Vertical height of enamel crown, inferior margin of external surface to apex of crown (No. 11962, U. S. N. M.)</td>
<td>14.5</td>
<td>12.5</td>
<td>13.5</td>
<td>31</td>
<td>38</td>
<td>39.6</td>
<td>42</td>
<td>33.7</td>
<td>28.5</td>
</tr>
<tr>
<td>Maximum transverse diameter at base of enamel crown (No. 11962, U. S. N. M.)</td>
<td>11.8</td>
<td>11.7</td>
<td>20.7</td>
<td>20+</td>
<td>21.8</td>
<td>14.7</td>
<td>13</td>
<td>14.5</td>
<td>14.5</td>
</tr>
<tr>
<td>Maximum length of tooth, crown plus root</td>
<td>50.5</td>
<td>50.5</td>
<td>13+</td>
<td>14+</td>
<td>19.5</td>
<td>19.6</td>
<td>13</td>
<td>14</td>
<td>14</td>
</tr>
<tr>
<td>Antero-posterior diameter at base of enamel crown (M. C. M.)</td>
<td>26</td>
<td>29.8</td>
<td>47.5</td>
<td>49.5</td>
<td>45</td>
<td>35+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vertical height of enamel crown, inferior margin of external surface to apex of crown (M. C. M.)</td>
<td>11.7</td>
<td>14.7</td>
<td>19.5</td>
<td>19.6</td>
<td>13</td>
<td>14</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum transverse diameter at base of enamel crown (M. C. M.)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum length of tooth, crown plus root (M. C. M.)</td>
<td>43+</td>
<td>32.5+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Table 31—Measurements (in millimeters) of mandibular teeth**

<table>
<thead>
<tr>
<th></th>
<th>M3</th>
<th>M2</th>
<th>M1</th>
<th>Pm4</th>
<th>Pm3</th>
<th>Pm2</th>
<th>Pm1</th>
<th>C</th>
<th>I3</th>
<th>I4</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R</td>
<td>L</td>
<td>R</td>
<td>L</td>
<td>R</td>
<td>L</td>
<td>R</td>
<td>L</td>
<td>R</td>
<td>L</td>
</tr>
<tr>
<td>Antero-posterior diameter at base of enamel crown (No. 11962, U. S. N. M.)</td>
<td>36.3</td>
<td>37.3</td>
<td>37.5</td>
<td>37.5</td>
<td>36.4</td>
<td>36.7</td>
<td>36.2</td>
<td>55</td>
<td>46</td>
<td>45.2</td>
</tr>
<tr>
<td>Vertical height of enamel crown, inferior margin of external surface to apex of crown (No. 11962, U. S. N. M.)</td>
<td>31</td>
<td>30.5</td>
<td>24+</td>
<td>23</td>
<td>43+</td>
<td>47.3</td>
<td>45.2</td>
<td>44.8</td>
<td>35.6</td>
<td>35</td>
</tr>
<tr>
<td>Maximum transverse diameter at base of enamel crown (No. 11962, U. S. N. M.)</td>
<td>14.7</td>
<td>15.5</td>
<td>16+</td>
<td>15+</td>
<td>16.6</td>
<td>16.8</td>
<td>14</td>
<td>17</td>
<td>13.3</td>
<td>13.3</td>
</tr>
<tr>
<td>Maximum length of tooth, crown plus root</td>
<td>71</td>
<td>79</td>
<td>63.5+</td>
<td>55+</td>
<td>34.3</td>
<td>39.2</td>
<td>72.7</td>
<td>78</td>
<td>77</td>
<td>872.2</td>
</tr>
<tr>
<td>Antero-posterior diameter at base of enamel crown (M. C. M.)</td>
<td>36</td>
<td>32.5</td>
<td>37</td>
<td></td>
<td>54.5</td>
<td>54</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vertical height of enamel crown, inferior margin of external surface to apex of crown (M. C. M.)</td>
<td>13.5</td>
<td>14.5</td>
<td>16</td>
<td></td>
<td>15.6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum length of tooth, crown plus root</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antero-posterior diameter at base of enamel crown (No. 2063, U. S. N. M.)</td>
<td>33.3</td>
<td>35.5</td>
<td>32.3</td>
<td>35</td>
<td>53.8</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vertical height of enamel crown, inferior margin of external surface to apex of crown (No. 2063, U. S. N. M.)</td>
<td>21.5+</td>
<td>28.5</td>
<td>27.5+</td>
<td></td>
<td>42</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum transverse diameter at base of enamel crown (No. 2063, U. S. N. M.)</td>
<td></td>
<td></td>
<td>14+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum length of tooth, crown plus root</td>
<td>45.5</td>
<td>76</td>
<td>57</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
are grooved for the reception of the posterior edge of the preceding teeth. The antero-posterior diameter of the crown of M1 is generally longer than that of either M2 or M3. The enamel crowns of these molars are rather smooth and have a curved vertical ridge on the internal side of the anterior face. The sequence of the isolated molar teeth has been definitely established from those in situ in two otherwise incomplete mandibles (Nos. 12063 and 4673, U. S. N. M.). The number of accessory denticles on the crowns of these molars progressively increase from M1 to M3, the first molar having three and the hindermost five. All three lower molars have high, sharp-edged and pointed accessory denticles, which are quite large in comparison to the principal cusp. The apex of the principal cusp M1 (pl. 13) of one individual (No. 11962, U. S. N. M.) is worn off, but is preserved on the corresponding molar in mandibles belonging to other individuals (Nos. 12063 and 12335, U. S. N. M.). The broad anterior edge of the large principal cusp is nearly vertical and there are three accessory denticles on the hinder edge, and of these the upper one is the largest. The distally attenuated roots of this molar are long and slender.

The grooved anterior face of the principal cusp of M2 is curved backward and there are four rather large accessory denticles on the hinder cutting edge. No cingulum is developed. The long roots of this molar are closely approximated.

The sharp-pointed principal cusp of M3 (pl. 13) rises very slightly above the adjacent accessory denticle on the hinder cutting edge of the crown. The five accessory denticles on the hinder edge increase in size from the base to the apex of the crown. The elongated slender roots of this molar are closely approximated below the crown.

The alveoli of the anterior teeth, I1 to Pm3 inclusive, in the upper and lower jaws are separated by interspaces of varying width and the minimum interspace is between Pm3 and Pm4. The maximum interspace occurs between I3 and C in the upper jaw and between C and Pm1 in the mandible.

Although the upper premolars of Zygorhiza and Dorudon are approximately equal in size, those of the former are characterized by having a conspicuous and rather wide crenated cingulum at the base of the crown, but the two halves do not meet medially. The cheek teeth of Zygorhiza kochii differ from those of Dorudon serratus in the following particulars: Pm2 has one more accessory denticle on the anterior and two more denticles on the posterior cutting edges, and Pm4 has one less accessory denticle on the posterior cutting edge.

**SEQUENCE OF ERUPTION OF PERMANENT DENTITION**

The sequence of the eruption of the permanent teeth is tentatively given as: M1, M2, M3, Pm4, I1, Pm3, I2, Pm2, I3, Pm1, C1.

The probable normal sequence of eruption of the permanent teeth is indicated in remarkable detail by the teeth in situ or associated with the skull and mandibles (fig. 38) belonging to the Millsaps College Museum. Conclusions based on a single specimen must necessarily remain tentative until a series of successive stages representing the sequence of eruption is available for study. Nor can the comparative stability of the sequence of eruption of the permanent teeth of these archaeocetes be ascertained with any degree of certainty from only one stage in this replacement process.

In this skull the left M1 and M2 were fully erupted, but became detached when that portion of the maxillary was damaged during the excavation of the skull. The hinder end of the right maxillary is similarly damaged and both molars are now missing.

The evidence afforded by the positions of the crowns of the permanent premolars with respect to the rims of their alveoli indicates that these erupting cheek teeth follow one another in rapid succession. The crowns of the permanent premolars appear below the corresponding deciduous cheek teeth which persist in progressive stages of the tooth-
shedding process, the accessory denticles on the anterior cutting edge of the crown of the permanent premolar fitting into grooves on the hinder face of the anterior root of the deciduous premolar and those on the hinder cutting edge into grooves on the anterior face of the posterior root.

Although Pm₄ is now detached on both maxillaries, the high transverse septum dividing the alveolus into two sockets for as many roots shows conclusively that this premolar was fully excluded. No remnants of the sockets for the roots of Dpm₄ are visible.

The apex of the principal cusp of the left Pm₃ projects at least 27 mm. beyond the level of the rim of its alveolus, but the apex of the basal accessory denticle on the anterior cutting edge of the crown is fully 12 mm. below the level of the anterior rim of the alveolus. The ends of the anterior and of the postero-internal roots of Dpm₃ are still implanted in their respective sockets.

The apex of the principal cusp of the right Pm₂ projects 17 mm. above the level of the rim of its alveolus, but the apex of the basal accessory denticle on the anterior cutting edge of the crown is 18 mm. below the level of the anterior rim of the alveolus. In the right maxillary the remnant of the anterior root of Dpm₂ is implanted in its socket, but all trace of the socket for the hinder root has been obliterated.

The anterior premolar is missing in both maxillaries. The alveolus for this tooth in the right maxillary measures 31.5 × 16.2 mm.

Although the anterior ends of both maxillaries are damaged, a portion of the right alveolus for the canine is preserved.

Unfortunately, the tooth-bearing portions of both premaxillaries are destroyed and all the upper incisor teeth, with the exception of the right I₃, are missing. The basal two-thirds of the crown of the right I₃ and a portion of the root were found. This tooth seems to have been fully erupted.

In the right mandible, Pm₄, M₁, M₂, and M₃ are fully erupted and function normally. All of the molars and Pm₄ as well were erupted in the left mandible, but were dislodged prior to deposition of overlying sediments, as the alveoli were filled with matrix when found. It is quite likely that M₁ is erupted first and that the other molars appear in succession. Evidence for this assumption is found in the relative positions of the base of the crown of these three lower molars with reference to the rims of their respective alveoli. The base of the hinder edge of the crown of M₁ is fully 12 mm. above the rim of the alveolus, while the apex of the basal accessory denticle on the crown of M₃ is at least 5 mm. below the level of the rim of its alveolus.

All trace of the bone scars left by the atrophied sockets for the roots of Dpm₄ have been obliterated and Pm₄ has assumed its normal position in the right mandible.

In the right mandible, Dpm₃ has been pushed upward in the alveolus by the erupting crown of Pm₃, the extremities of its two roots being still embedded in their respective sockets which are located at the anterior and posterior ends of the crown of Pm₃. As regards the right Pm₃, the apex of the principal cusp projects 28 mm. above the center of the outer rim of its alveolus, and the remainder of the crown, although completely formed, lies within the walls of the alveolus. In the left mandible, the apex of the principal cusp of Pm₃ projects at least 35 mm. above the center of the outer rim of its alveolus, and a remnant alone of the extremity of the hinder root of Dpm₃ is visible in the alveolus.

The crown of the right Dpm₂ has been destroyed, but the ends of its two roots are implanted respectively in the alveolus in front of and behind the erupting crown of Pm₂. On both of these mandibles, the apex of the principal cusp of Pm₂ projects about 6 mm. above the level of the inner rim of its alveolus.

The apex of the crown of the erupting Pm₁ in the right and left mandibles is about 3.5 mm. below the level of the rim of its alveolus. In the left mandible a portion of the outer
wall of this alveolus is destroyed, exposing the whole crown of Pm1. This tooth has a high principal cusp and a rather large accessory denticle at the base of the hinder cutting edge of the crown.

The crown of the developing canine in the left mandible is pressed against the hinder wall of the alveolus for the deciduous canine and its apex is about 4 mm. below the level of the rim of this alveolus. It is certain that the mandibular canines do not make their appearance before all three lower molars are fully erupted, and judging from the position of the apex of the crown of the canine with respect to the rim of its alveolus and the relative positions of the four permanent premolars in their respective alveoli, it would seem that the canines do not become fully erupted before all of these cheek teeth are functioning.

The incisors are not now in situ in either of these mandibles. Two permanent incisor teeth identified as the right and left I3 belong to this specimen. Although detached, the association of a deciduous incisor and three permanent incisors with the skull and mandibles is fairly conclusive evidence that the molars and Pm4 are fully erupted before the lower incisors become functional. Some additional evidence for this assumption is found in the relative positions of the crowns of the erupting I3 and Pm4 on the skull and mandibles of Dorudon stromeri.

A left mandible belonging to another immature individual (No. 4748, U. S. N. M.) furnishes some supplementary data in regard to the replacement of the deciduous dentition. It seems to represent a slightly earlier stage in this process. The three lower molars and Pm4 are now detached from this jaw, but the alveoli show that they were fully erupted. The crown of the erupting Pm3 has been dislocated in its alveolus and rotated about 90 degrees by some fortuitous injury to the jaw prior to fossilization. This tooth has a large principal cusp, whose anterior edge measures 21 mm. and its hinder edge 30 mm. in length; the anterior edge of the principal cusp is distinctly denticulated. The crown of the erupting Pm2 barely projects above the level of the rim of its alveolus. The crown of the developing Pm1, which lies entirely below the level of the rim of its alveolus, is directed forward, not upward. The position of the canine within its alveolus is quite similar to that of Pm1.

These mandibles show that the deciduous dentition persists until the molars become functional, and that the milk teeth are then progressively replaced from the hinder end of the series toward the canine. Dp3 is not replaced by Pm3 until Pm4 is fully excluded and functionally effective. The position of the crowns of the remaining premolars in their respective alveoli indicates that this procedure is repeated until all the premolars have assumed their respective functions.

DECIDUOUS DENTITION

The deciduous dental formula is: D1 1:2:3, Dc 1, Dpm 1:2:3:4.

All of the deciduous upper incisors (fig. 38) were lost when the tooth-bearing portions of the premaxillaries were destroyed. The deciduous upper canines, as well as both Dpm1, are likewise missing.

The crown of the right Dpm2 is unusually low and the enamel is relatively smooth. There are at least three accessory denticles on the anterior and on the posterior cutting edges of the crown. The extremity of the anterior root is still firmly attached in the alveolus of the erupting Pm2 anterior to the middle accessory denticle on the anterior edge of the crown of the latter, but the end of the hinder root is free. Regressive processes associated with the development of the crown of the erupting Pm2 have resulted in the formation on the roots of Dpm2 of concavities that correspond in position to the accessory denticles on the crown of the permanent premolar. There are three deep hollows on the posterior face of the anterior root of Dpm2, including an elongate one for the apex and the anterior edge
of the principal cusp of Pm2, a much deeper one for the adjacent accessory denticle and a shorter one for the next accessory denticle on the anterior cutting edge of the crown. The elongate concavity on the anterior face of the hinder root rests on the hinder cutting edge against the accessory denticle that is adjacent to the principal cusp of Pm2, while the concavity on the free end of this root rests upon the second accessory denticle on this edge of the crown. In the left maxillary, the anterior and posterior roots of Dpm2 are solidly implanted in the alveolus in front of and behind the crown of the developing Pm2.

The crown of Dpm3 is slightly larger than that of Dpm2 and the enamel is likewise smooth. The principal cusp of this deciduous cheek tooth is slightly larger than the adjacent denticle on the hinder cutting edge. Three small accessory denticles are present on the anterior cutting edge of the crown. The distal accessory denticle of the three on the posterior cutting edge is relatively large, the middle one is approximately the same size as the distal denticle on the anterior cutting edge, and the basal denticle is quite small. A slight cinguloid ridge is present below the two hinder denticles at the base of the outer surface of the crown. Dpm3 has three roots. The milk tooth preserved in the right maxillary has a long anterior root whose extremity is implanted in the alveolus in front of the basal denticle on the anterior cutting edge of the crown of the erupting Pm3, a shorter postero-internal root whose extremity is implanted in a separate socket opposite the internal face of the hinder end of the crown of Pm3, and a very short atrophied postero-external root which rests against the outer face of the distal accessory denticle on the hinder cutting edge of the crown of Pm3 and which is connected by an osseous isthmus with the postero-internal root. A series of four step-like hollows for the principal cusp and the three accessory denticles on the anterior cutting edge of the crown of Pm3 are present on the

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**Fig. 38—Zygophiza kochii (Reichenbach).** Skull and mandible in lateral view showing position of deciduous teeth, the fourth premolar and the molars in upper and lower jaws erupted, and the three anterior premolars in both jaws in process of eruption. Pm4 is erupted but quite unworn, Pm3 is erupting, Pm2 and Pm1 are in less advanced stages of eruption, the canine has not reached the alveolar level, and I3 is partially erupted. Millisaps College Museum. × 1/4. al., alisphenoid; ant.f., anterior foramen; c., occipital condyle; cm., condyle of mandible; cor., coronoid process of mandible; ex.oc., exoccipital; fr., frontal; j., jugal; la., lacrimal; max., maxillary; pa., parietal; pal., palatine; plg., postglenoid process of squamosal; pmz., premaxillary; s.or.pr., supraorbital process of frontal; sq., squamosal; zyg., zygomatic process of squamosal. Upper Eocene, Yaxoo clay, upper Jackson formation, Mississippi.
hinder face of the anterior root; three of these hollows are present on the anterior face of the united posterior roots of Dpm3.

The detached tooth identified as the left DlI has a very slender root, its maximum diameters being 13.5 and 9.8 mm. The root is rather flat internally and convex externally. No groove is present on the hinder face of the root. The conical crown is curved backward and a fine vertical carina marks the position of its anterior and posterior cutting edges. The enamel on the external face of the crown is fairly smooth, but the rugose internal face is ornamented with anastomosing striae.

The apex of the crown of the lower right Dc is worn off. The enamel is fairly smooth on the external surface of the crown, but is ornamented with fine vertical striae on the basal half of the internal face. The anterior and posterior cutting edges of the crown are marked by fine carinæ. The postero-internal face of the distal half of the root is deeply hollowed out for the crown of the developing C, the cavity extending through the cementum and into the dentine beyond the closed pulp cavity. The cementum is destroyed on the anterior and internal faces of the root.

The apex of the crown of the left DpmI is damaged, but the root is complete. On the external face of the crown the enamel is relatively smooth, but on the posterior half of the internal face it is ornamented with fine vertical striae. A rather small denticle is present at the base of the hinder edge of the crown and the cutting edges are marked by fine vertical carinæ. Below the neck, the root is rather wide antero-posteriorly (21.5 mm.), but it is flattened transversely (13.5 mm.) and is attenuated toward the distal end. About 5 mm. below the base of the enamel crown, the internal face of the root is characterized by a narrow antero-posterior swelling. A broad elongated cavity for the crown of the developing PmI is present on the hinder three-fourths of the root.

Dpm2 is not represented among the detached teeth. In the right mandible the ends of the anterior and posterior roots of this deciduous tooth are firmly implanted in the alveolus in front of and behind the base of the crown of the erupting Pm2.

The upper portion of the anterior root and the adjoining portion of the crown are destroyed on the right Dpm3, but the posterior root is complete and implanted in the alveolus behind the middle accessory denticle on the hinder cutting edge of the crown of the erupting Pm3. The extremity of the anterior root is likewise firmly implanted in the alveolus in front of the middle accessory denticle on the anterior cutting edge of the crown of the erupting Pm3. The anterior root and a portion of the crown of the left Dpm3 was also found. This tooth has a prominent principal cusp and at least three accessory denticles on the anterior and on the posterior cutting edges of the crown. A series of four step-like hollows for the principal cusp and the accessory denticles on the anterior cutting edge of the crown of Pm3 are present on the hinder face of the anterior root; at least three of these hollows are present on the anterior face of the posterior root of Dpm3.

All of these deciduous teeth are characterized by rather thin and less conspicuously wrinkled enamel and by distinctly smaller crowns than those of their successors in the permanent dentition.

**Table 32—Measurements (in millimeters) of the deciduous teeth**

<table>
<thead>
<tr>
<th>Antero-posterior diameter of base of enamel crown</th>
<th>DlI Right</th>
<th>DlI Left</th>
<th>DpmI Right</th>
<th>DpmI Left</th>
<th>Dpm2 Right</th>
<th>Dpm2 Left</th>
<th>Dpm3 Right</th>
<th>Dpm3 Left</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transverse diameter of base of enamel crown</td>
<td>12.8</td>
<td>15.7</td>
<td>19</td>
<td>41.5</td>
<td>43.5</td>
<td>....</td>
<td>....</td>
<td>....</td>
</tr>
<tr>
<td>Vertical height of enamel crown, inferior margin of external surface to apex of crown</td>
<td>9.5</td>
<td>9.9</td>
<td>10</td>
<td>10</td>
<td>13.2</td>
<td>13</td>
<td>....</td>
<td>....</td>
</tr>
<tr>
<td>Maximum length of tooth, crown plus root</td>
<td>19.5</td>
<td>15+</td>
<td>15+</td>
<td>15+</td>
<td>15+</td>
<td>....</td>
<td>24+</td>
<td>24+</td>
</tr>
<tr>
<td>15+</td>
<td>7.5</td>
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<td>62.5</td>
<td>62.5</td>
<td>62.5</td>
<td>62.5</td>
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</tbody>
</table>

1 Specimen belonging to Millsaps College Museum.

2 Upper portion of crown incomplete.

3 Apex of principal cusp missing.
HYOID BONES

The hyoid apparatus of *Zygorhiza kochii*, so far as known, differs only in some minor details from that of *Basilosaurus cetoides*. A damaged basihyal (No. 12063, U. S. N. M.) has the dorsal and ventral surfaces strongly depressed medially, the circular concavity on the dorsal face (pl. 16, fig. 1) being much larger and deeper than that on the ventral face. The anterior and posterior borders of the dorsal surface are not depressed as in *B. cetoides* and the hinder end of this bone is rounded in a dorso-ventral direction. The entire left side of this basihyal is destroyed. On the right side the oblique surface for the attachment of the expanded end of the thyrohyal is shallowly concave. The measurements of the basihyal are as follows: Greatest length, 56 mm.; and greatest dorso-ventral diameter, 23.7 mm.

The right and left thyrohyals (pl. 16, figs. 2–3) of another individual (No. 4678, U. S. N. M.) are essentially complete with the exception of their distal extremities. These thyrohyals have a conspicuously expanded anterior end, the transverse diameter being about 65 per cent of the vertical diameter. The hinder half of the attenuated slender shaft is strongly bent inward. The anterior portion of the shaft is oval in cross-section, but the hinder end is strongly compressed from side to side, producing ridge-like dorsal and ventral edges. The measurements of the right and left thyrohyals are, respectively: Greatest length, 130 + and 131 + mm.; greatest vertical diameter of anterior end, 34.3 and 33.5 mm.; greatest transverse diameter of anterior end, 20.5 and 21.5 mm.; and greatest vertical diameter of hinder end, 11 and 11.6 mm.

Four fragments of the two stylohyals of this individual (No. 4678, U. S. N. M.), the longest 83 mm. in length, show that the shafts of these bones are more slender than the distal portions of the thyrohyals. An incomplete left stylohyal (pl. 16, fig. 4) belonging to a larger individual (No. 4679, U. S. N. M.) has a curvature somewhat similar to that of *Basilosaurus cetoides*, but the shaft is flattened only on the inner face. On the lower edge and about 25 mm. behind the anterior end is a narrow rugose ridge about 20 mm. in length for the attachment of some hyoid muscle. The laterally flattened anterior end is capped by a thin epiphysis. About 75 mm. behind the anterior end, the stylohyal is triangular in cross-section, but is ovoidal in cross-section at the broken distal end. The measurements of this left stylohyal are as follows: Greatest length, 192 + mm.; width of proximal end, 12.5 mm.; thickness of proximal end, 9 mm.; maximum width of shaft, 15.8 mm.; and maximum thickness of shaft, 12.5 mm.

VERTEBRAE

The vertebral column (pl. 1, B) as reconstructed consists of 7 cervical, 15 dorsal, 15 lumbar-sacral, and 21 caudal vertebrae. The total length of the skeleton in a straight line is approximately 16 feet 2 inches or 4.93 meters. The intervals shown between the vertebrae are assumed to represent the original amount of intervertebral substance. Taking the total length of the skeleton as 100 per cent, the skull constitutes 16.8 per cent, the neck 5.1 per cent, the dorsal series 19.6 per cent, the lumbar-sacral series 24.8 per cent, and the caudal series 33.7 per cent. As compared to *Protocetus atavus*, the articular surfaces of the pre- and post-zygapophyses are greatly reduced, and the articular connections between successive thoracic and lumbar vertebrae are consequently much weaker.

CERVICAL VERTEBRAE

A consecutive series of six cervical vertebrae belonging to one immature individual (Millsaps College Museum) are available for description, but most of them are incomplete. Hence the structural peculiarities of the vertebrae in this series have been de-
scribed in part from isolated vertebrae belonging to at least seven different individuals. The atlas and axis are curiously interlocked as in *Basilosaurus cetoides*. The atlas has a ventral hypophysis which projects backward below the centrum of the axis. The axis has a short plug-like odontoid process; the antero-basal angle of the neural spine projects forward above the atlas in front, while its distal end projects backward over and beyond the short neural spine of the third cervical. There is a progressive increase in the width of the interval separating the pre- and likewise the post-zygapophyses from the third to the sixth cervical vertebra. The atlas, axis, and third cervical have their transverse processes directed rather strongly backward. The lower transverse processes of the third, fourth, and fifth cervical vertebrae have a slender ventral projection which

Fig. 39—*Zygophiza kochii* (Reichenbach). Atlas, No. 11962, United States National Museum. a, anterior view; b, posterior view; c, ventral view; d, lateral view. × ½. hyp., hypophysis; tr., transverse process. Upper Eocene, upper Jackson formation, Alabama.

is directed downward and forward. The sixth cervical has elongated and ventrally directed lower transverse processes. The seventh cervical apparently has transverse processes similar to those of *Basilosaurus cetoides*.

*At*las—Transverse processes of atlas (Nos. 11962 and 4678, U. S. N. M.) broad, directed strongly backward, and perforated at base by a large vertebrarterial canal; upper and lower projecting angles of transverse process thickened distally, anterior surface (fig. 39a) decidedly concave but overhung by thin antero-dorsal border, and ventral border thickened and rounded; neural arch very little elevated and flattened dorsally; dorsal foramina (fig. 39d) for first cervical nerves laterally placed and larger than the vertebrarterial canals; hypophysis destroyed but obviously thickened at base and projected backward below axis; anterior articular facets for occipital condyles of skull concave, broader above than below, curving obliquely forward and upward, and sepa-
rated ventrally by a short hiatus (13 mm.); posterior facets (fig. 39b) for articulation with axis more or less flattened externally and concave internally, sub-reniform in outline, distinctly set off from posterior surface of centrum, and joined ventrally by a broad isthmus; vertical diameter of transverse processes distally (67 mm.) slightly more than one-third of greatest transverse distance between dorso-external angles of transverse processes (186.5 + mm.). Additional measurements (see table 33) for the atlas (No. 11962, U. S. N. M.) found associated with the skull and mandibles are as follows: Greatest vertical height of atlas, ventral face of centrum to dorsal surface of neural arch, 98 + mm.; maximum distance between ventro-external angles of transverse processes, 176.5 mm.; maximum distance between outer margins of anterior articular facets, 114 mm.; maximum distance between outer margins of posterior articular facets, 108.5 mm.; and vertical diameter of right posterior articular facet, 47 mm.

The atlas of the specimen belonging to the Millsaps College Museum has a short, obtusely pointed hypapophysis. Although this individual is obviously immature, the dimensions are quite similar to those of an adult, as is shown by the following measurements: Maximum distance between outer margins of anterior articular facets, 111 mm.; maximum distance between outer margins of posterior articular facets, 101 mm.; vertical diameter of right posterior articular facet, 43 mm.; and greatest vertical height of atlas, ventral face of centrum to dorsal surface of neural arch, 98 mm.

The atlas (fig. 40) of this archaeocete differs from that of *Dorudon stromeri* (No. 1904. XII. 134e, Munich) in having relatively shorter transverse processes, the roof of the neural arch much less deeply scalloped anteriorly, and a vestigial neural spine.

Axis—Transverse processes of axis (Nos. 4679 and 4678, U. S. N. M.) short, directed more backward than outward, quite thin distally, faintly bifurcated at extremity, and perforated at base by vertebrarterial canal; no longitudinal carina on ventral surface of centrum; posterior face of centrum concave; the large anterior articular facets curve forward along base and sides of the short plug-like odontoid process; the broad longitudinal ridge on dorsal face of odontoid process (fig. 41a), which is set off on each side a wide groove, is continuous posteriorly with ridge of same width on dorsal surface of centrum, but the latter is abruptly narrowed posteriorly; a deep elongated hollow is present on each side of this median ridge; neural canal viewed from in front cordiform in outline; neural spine rather broad posteriorly, with concave hinder face (fig. 41c) conspicuously thickened at base, with crest-like anterior edge, and with obliquely flattened antero-ventral angle conspicuously extended forward; postzygapophyses projected backward and inclined obliquely upward, with curved ventral postzygapophysial facets. Additional measurements (see table 33) for the best preserved of these two axes (No. 4679, U. S. N. M.) are as follows: Greatest vertical diameter of axis, ventral face of centrum to tip of neural spine, 128 + mm.; maximum distance between outer angles of transverse processes, 120 ± mm.; antero-posterior diameter of neural spine at base, 52 mm.; maximum distance between outer margins of anterior articular facets, 105 ± mm.; and vertical diameter of extremity of transverse process, 27 mm.
The axis of the immature individual belonging to the Millsaps College Museum has a less noticeably developed dorsal ridge on the odontoid process, a more slender neural spine, and more nearly vertical postzygapophyseal facets. Greatest vertical diameter of axis, ventral face of centrum to tip of neural spine, 136 mm., and antero-posterior diameter of neural spine at base, 46 mm.

The axis of this species differs from that of Dorudon stromeri (No. 1904. XII. 134e, Munich) not only in having larger vertebrarterial canals, each of which opens behind into a large deep elongate fossa which is extended dorsally upon the neural arch, but also in the greater transverse distance between the outer margins of the postzygapophyseal facets.

Third Cervical—Anterior and posterior faces of centrum deeply concave; centrum broader than high and relatively thick, its antero-posterior diameter being more than two-fifths of its greatest transverse diameter; transverse process directed obliquely outward and backward, perforated at base by a very large vertebrarterial canal, and has the lower and presumably the upper outer angles rounded; lower bar of transverse process rather large, its vertical diameter being slightly more than half of its horizontal diameter, and from near the base of its ventral edge a narrow projection arises which slopes obliquely forward and downward; upper bar very narrow and thin, and dorsally forms a buttress at the base of the outer face of the pedicle of the neural arch; the deep concavity on lateral face of centrum forms inner wall of vertebrarterial canal; contour of ventral face of centrum modified by presence of broad protuberance; neural arch, with exception of basal portions of its pedicles, and likewise the pre- and post-zygapophyses destroyed; pedicles of neural arch compressed antero-posteriorly and set back at base from anterior and posterior ends of centrum. This diagnosis is based on incomplete cervical vertebrae belonging to two adult individuals (Nos. 4680 and 4748, U. S. N. M.) and to one immature individual (Millsaps College Museum). The conformation and structural peculiarities of the transverse processes of this vertebra are quite similar to those of the third cervical of Basilosaurus cetoides.

Fourth Cervical—Centrum approximately as broad as high; transverse process perforated at base by a large vertebrarterial canal; lower bar of transverse process quite thick at base and directed obliquely outward and forward; upper bar narrow and quite thin, forming outer boundary of vertebrarterial canal, and continuous above with oblique external buttress on pedicle of neural arch; lateral surface of centrum in region of verte-
brarterial canal shallowly concave; ventral surface of centrum with low median protuberance; pedicle of neural arch compressed antero-posteriorly, its transverse diameter being twice its antero-posterior diameter, its hinder edge being nearly vertical, and its external buttress, which supports the prezygapophysis, sloping obliquely forward and upward; pedicles of neural arch arise from dorso-lateral angles of centrum and are set back at base from anterior and posterior ends of centrum; prezygapophysial facet large, elongated, and situated for the most part on the oblique inner face of the prezygapophysis; flattened postzygapophysial facet directed obliquely upward and outward, and situated on under surface of postzygapophyses. This fourth cervical vertebra (No. 4748, U. S. N. M.) lacks both epiphyses, both transverse processes are incompletely preserved, and the roof of the neural arch as well as the pre- and post-zygapophyses on the left side are missing. The fourth cervical of the immature individual belonging to the Millsaps College Museum has both epiphyses attached to the centrum. The breadth of the centrum is, however, distinctly greater than the transverse diameter.

Fifth Cervical—Centrum approximately as broad as high and quite thick, its antero-posterior diameter being slightly less than half of its greatest transverse diameter; lateral surface of centrum rather deeply excavated between base of pedicle of neural arch and point of origin of lower transverse process; lower transverse process dorso-ventrally flattened at base and directed forward, downward, and outward; base of transverse process slopes obliquely downward from its posterior to its antero-ventral margin; small vascular foramina are located on ventral surface of centrum between the lateral longitudinal ridge and the median elevation; pedicle of neural arch, which arises from the dorso-lateral angle of centrum, wider antero-posteriorly than transversely, its oblique external buttress sloping forward and upward, and not set back at base as far from posterior as from anterior end of centrum. This description is based largely on a vertebra (No. 4678, U. S. N. M.) that has most of the processes broken off near their bases. The fifth cervical vertebra of the immature individual belonging to the Millsaps College Museum has a much thinner centrum than that described above and the lower transverse processes are flattened antero-posteriorly at their bases.

Sixth Cervical—Anterior and posterior surfaces of centrum deeply concave; centrum wider than high and quite thick, its antero-posterior diameter being less than three-fifths of its greatest transverse diameter; upper transverse process short and rounded distally, continuous above with the oblique external buttress that supports the prezygapophysis and below with the lower transverse process, and incloses the large vertebrarterial canal at its base; lower transverse process very long, robust, with slightly expanded distal ends and directed more downward than outward; a vascular foramen on each side of median longitudinal ridge on ventral surface of centrum; pedicle of neural arch, which arises from dorso-lateral angle of centrum, much wider transversely than antero-posteriorly, not set back at base as far from posterior as from anterior end of centrum, and strengthened by an oblique external buttress that slopes forward and upward; neural canal broader than high; neural spine short and thin; prezygapophyses widely separated; prezygapophysial facets flattened and nearly horizontal.

This diagnosis is based in part on the essentially complete sixth cervical vertebra (Müller, 1849, p. 33, pl. 26, fig. 2) associated with the skull in Teyler's Museum, Haarlem, in part on an incomplete vertebra in the U. S. National Museum (No. 4680) and in part on the damaged cervical of the immature individual belonging to the Millsaps College Museum. According to Müller (1849, p. 33), the transverse diameter of the centrum of the sixth cervical vertebra in Teyler's Museum is 63.5 mm., and the transverse diameter of the neural canal is 34.5 mm. The sixth cervical of this archaeocete differs from that of Dorudon stromeri in having much longer lower transverse processes,
wider neural canal, larger vertebral arterial canals, wider centrum, and more widely separated prezygapophyses.

Seventh Cervical—Centrum quite thick, its antero-posterior diameter being approximately half of its greatest transverse diameter; posterior end of centrum more deeply concave than anterior end; when viewed from in front the contour of anterior end of centrum is almost pentagonal; transverse process projects outward and forward from near middle of lateral surface of centrum and its base slopes obliquely forward from posterior to anterior edge; pedicle of neural arch compressed antero-posteriorly and set back at base farther from posterior than from anterior end of centrum; neural canal relatively narrow at base; a very large reniform postero-superior facet for articulation with capitulum of first rib. The position of its processes as well as the conformation of the damaged centrum (No. 4679, U. S. N. M.) of the seventh cervical indicate that this vertebra must have been somewhat similar to that of Basilosaurus cetoides.

Table 33—Measurements (in millimeters) of cervical vertebra

<table>
<thead>
<tr>
<th></th>
<th>Atlas</th>
<th>Axis</th>
<th>C. 3</th>
<th>C. 4</th>
<th>C. 5</th>
<th>C. 6</th>
<th>C. 7</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>No. 11962</td>
<td>U.  S.  N.  M.</td>
<td>M.    C.  M.</td>
<td>No. 4679</td>
<td>U.  S.  N.  M.</td>
<td>M.    C.  M.</td>
<td>No. 4678</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of centrum</td>
<td>73</td>
<td>66</td>
<td>64.5</td>
<td>55.0</td>
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<td>22.5</td>
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<td>Vertical diameter of centrum anteriorly</td>
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<td>43.0</td>
<td>56.7</td>
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<td>46</td>
<td>43</td>
<td>51.8</td>
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<tr>
<td>Transverse diameter of centrum anteriorly</td>
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<td>53.5</td>
<td>49</td>
<td>53</td>
<td>53.8</td>
</tr>
<tr>
<td>Greatest height of neural canal anteriorly</td>
<td>54</td>
<td>50</td>
<td>39.5</td>
<td>37</td>
<td>36.3</td>
<td>38.0</td>
<td>39.3</td>
</tr>
<tr>
<td>Greatest transverse diameter of neural canal anteriorly</td>
<td>49</td>
<td>52</td>
<td>39.6</td>
<td>37</td>
<td>36.3</td>
<td>38.0</td>
<td>39.3</td>
</tr>
<tr>
<td>Least antero-posterior diameter of right pedicle of neural arch</td>
<td>20.6</td>
<td>15.8</td>
<td>9.3</td>
<td>10</td>
<td>11.5</td>
<td>9.8</td>
<td>17</td>
</tr>
</tbody>
</table>

1 Centrum + odontoid process.  
2 Posteriorly.  
* Both epiphyses missing.

Dorsal Vertebrae

It can be stated with considerable certainty that the dorsal series of this archaeocete consists of at least fifteen vertebrae. A consecutive series of 8 anterior dorsals of one individual (No. 11962, U. S. N. M.) and 14 consecutive dorsals of another (No. 4679, U. S. N. M.) established the sequence of these vertebrae. These two series of dorsal vertebrae show that the first to eighth dorsals, inclusive, are represented in the shorter series and the second to fifteenth, inclusive, are represented in the longer series. It is likewise certain that the ninth in the series, counting backward from the anteriormost one, is the intermediate or transitional dorsal. In addition to the above, there are 4 anterior and 2 hinder dorsal vertebrae of another individual (No. 12063, U. S. N. M.), and 8 imperfect dorsal vertebrae of another (No. 4678, U. S. N. M.).

Although the centra (pl. 1) progressively increase in length, breadth, and height toward the hinder end of the series, the centra of the hinder dorsals are not disproportionately elongated. The seven anterior dorsals have anterior and posterior facets on the lateral surface of the centrum for capitula of corresponding ribs, the anterior facet articulating with a portion of the capitulum of its own rib and the hinder one with a portion of the capitulum of the succeeding rib, while the eighth dorsal has only the anterior facet. The five anterior dorsals have relatively slender neural spines, those of the first and second being narrower antero-posteriorly than those of the succeeding dorsals. The neural
spines of the nine anterior dorsals rake strongly backward, while the hinder dorsals have neural spines that are much wider antero-posteriorly and also more nearly vertical. The laterally projecting diapophyses of the anterior dorsals arise rather high on the side of the neural arch and their lateral articular facets gradually change in outline and in position from the first to the eighth dorsal, being replaced behind the latter by the metapophyses. Beginning with the ninth dorsal, the metapophyses arise from the sides of the anterior borders of the neural arch and from the basal portion of the neural spine, from which they project forward and upward. All of these dorsal vertebrae have articulating pre- and post-zygapophyses which shows that the vertebrae in this series were rather firmly interlocked. The dorsal vertebrae available for this study show that considerable variation may be expected in the shape and position of the lateral facets on the diapophyses. The transverse processes of the tenth dorsal are rudimentary, while those of the five hinder dorsals progressively increase in length.


First Dorsal—This vertebra (No. 11962, U. S. N. M.) resembles the corresponding dorsal of Dorudon zittelii (No. 11235, Stuttgart) in having a slender neural spine, which rakes backward. The prezygapophyses are dorso-ventrally flattened plates which extend forward slightly beyond the level of the anterior ends of the diapophyses. Centrum wider than long; antero-superior and postero-superior facets (fig. 42) on lateral surface of centrum for articulation with capitula of the corresponding ribs rather closely approximated; postero-superior facet almost twice as large as antero-superior facet; pedicle of neural arch rather low, somewhat compressed antero-posteriorly and possessing an antero-external sharp-edged vertical crest; articular facet for tuberculum of first rib on laterally projecting diapophysis large, elongated, concave, and slopes upward and forward; neck of diapophysis flattened dorso-ventrally between lateral facet and neural arch: prezygapophysial facets widely separated and almost horizontal in position; post-
zygapophysial facets rather narrow (15 mm.), elongate, separated by an interval of 29 mm. and nearly horizontal in position; and vertical diameter (42.5 mm.) of neural canal anteriorly greater than the transverse diameter (39.5 mm.).

Second Dorsal—Compared with the first dorsal, the slender neural spine of this vertebra (No. 4679, U. S. N. M.) takes more strongly backward, the centrum is slightly longer, and the articular facet for the tuberculum of the second rib is somewhat larger. Although the right half of the centrum is missing, this vertebra is essentially complete on the left side. Neural spine (fig. 43) rather high; an antero-superior facet of medium size and subcirculariform in outline on lateral surface of centrum for capitulum of second rib, and an elongated postero-superior facet for capitulum of third rib, these facets being separated by a much wider interval (18.5 mm.) than on first dorsal; proportions of pedicle of neural arch approximately the same as that on first dorsal and likewise inclined forward; neural canal wider than high; laterally projecting diapophysis expanded antero-posteriorly at extremity, furnished with a very large convex articular surface and projected forward beyond level of anterior end of centrum; neck of diapophysis flattened dorso-ventrally between facet and neural arch; prezygapophyses plate-like and extended forward slightly beyond level of extremities of diapophyses; prezygapophysial facets flattened, sloping obliquely forward and inward, subcircular in outline and widely separated; postzygapophysial facets longer (19 mm.) than wide (16 mm.), separated by a wide interval (25 mm.), sloping upward and backward, and their hinder extremities project backward slightly beyond level of posterior end of centrum; and maximum distance between outer margins of postzygapophysial facets, 56 ± mm.

The neural arch and neural spine of another second dorsal (No. 11962, U. S. N. M.) have been distorted by crushing.

Third Dorsal—This vertebra (No. 4679, U. S. N. M.), with the exception of the distal end of the neural spine, the hinder end of the postzygapophysis and the anterior end of the prezygapophysis, is essentially complete on the right side. Centrum larger than that of second dorsal and strongly concave laterally; basal portion of neural spine (fig. 44) somewhat wider antero-posteriorly (42 mm.) than on preceding vertebra; neural spine takes backward; pedicle of neural arch narrow antero-posteriorly (23.8 mm.), inclined forward, rather high, and slightly set back at base from anterior end of centrum; neural canal wider than high; antero-superior facet on lateral surface of centrum ovoidal in outline; postero-superior facet subpyriform in outline; neck of laterally projecting diapophysis somewhat thicker and facet for tuberculum of third rib more convex and slightly shorter than that of preceding vertebra; flattened plate-like prezygapophysial facets project forward distinctly beyond level of extremities of diapophyses; and prezygapophysial facets less widely separated (23 mm.) than on preceding dorsals; postzygapophysial facets damaged.

Another third dorsal (No. 11962, U. S. N. M.) has elongated postzygapophysial facets which are placed on under surface of hinder portion of neural arch and their hinder extremities project backward beyond level of posterior end of centrum.

Fourth Dorsal—The neural spine, the postzygapophyses, the roof of the neural arch, the laterally projecting diapophyses, and the left half of the centrum of this vertebra (No. 4679, U. S. N. M.) are destroyed. Pedicle of neural arch (fig. 45) wider antero-posteriorly (26 mm.) than on third dorsal, more nearly vertical, and its anterior edge curved upward and forward; antero-superior facet on lateral surface of centrum elongated and placed almost wholly behind level of anterior edge of pedicle of neural arch; postero-superior facet more ovoidal in outline and placed higher on lateral surface of centrum; prezygapophyses thickened dorso-ventrally, and projected forward conspicuously beyond level of anterior end of centrum; and prezygapophysial facets flattened.
The other fourth dorsal (No. 11962, U. S. N. M.) is complete except for distal portion of the neural spine. The postzygapophyseal facets of this dorsal are placed wholly on the under surface of the hinder portion of the neural arch and slope upward and backward. The neural spine is wider antero-posteriorly at the base than on the third dorsal, the neural canal is wider (50.5 mm.) than high (39 mm.), and the centrum is wider than long.

Fifth Dorsal—In general appearance this vertebra (No. 4679, U. S. N. M.) is very similar to the fourth dorsal. The centrum is likewise considerably broader than long and the anterior face is more strongly convex transversely. The anterior ends of the prezygapophyses are missing, but the proximal portions of the prezygapophyseal facets are rather widely separated (21 ± mm.). Although the postzygapophyseal facets are incompletely preserved, the curvature of the hinder edge of the neural spine at the base indicates that they extended backward beyond the level of posterior end of centrum. Neural spine (fig. 46) tapers toward extremity and rakes backward; pedicle of neural arch noticeably wider antero-posteriorly (30.8 mm.) than on preceding dorsal, its fore and hinder margins being about equally distant from corresponding ends of centrum; neural canal wider (46 mm.) than high (40.5 mm.); antero-superior facet on lateral surface of centrum oval in outline and placed almost wholly behind level of anterior margin of pedicle of neural arch; postero-superior facet gouttate in outline; neck of laterally projecting diapophysis short and broad antero-posteriorly; main axis of large lateral facet for tuberculum of fifth rib almost horizontal; and a low broad median longitudinal carina present on ventral surface of centrum.

On another fifth dorsal (No. 11962, U. S. N. M.) the subcircular prezygapophyseal facets slope obliquely downward from internal to external margins.

Sixth Dorsal—The neural spine as well as the pre- and post-zygapophyses of this vertebra (No. 4679, U. S. N. M.) are missing. The pedicle of the neural arch (fig. 47) is approximately as wide antero-posteriorly (30.5 mm.) as that of the preceding dorsal vertebra. Neural canal wider (48 mm.) than high (39 mm.); centrum broader than long; antero-superior facet placed obliquely on lateral surface of centrum and situated almost wholly behind level of anterior edge of neural arch; postero-superior facet elongated and situated on hinder border; neck of laterally projecting diapophysis short; lateral facet on diapophysis incomplete anteriorly, but otherwise larger than that of fifth dorsal; anterior ends of prezygapophyses missing; prezygapophyseal facets sloping obliquely from internal to external margins; and a low median longitudinal carina present on ventral surface of centrum.

On another sixth dorsal (No. 11962, U. S. N. M.) the main axis of the unusually large subpyriform lateral facet on the diapophysis is nearly vertical in contrast to the nearly horizontal position of the same on the previously described dorsal. The postzygapophyseal facets are located wholly on the under surface of the postero-external angles of the roof of the neural arch and their hinder extremities project posteriorly beyond the level of the posterior end of the centrum. The neural spine is similar in shape and in inclination to that of the fifth dorsal.

Seventh Dorsal—Since the neural arch is incomplete, and the diapophyses and the prezygapophyses are missing on No. 4679, U. S. National Museum, the description is based largely on No. 11962, U. S. National Museum, which, with the exception of the distal end of the neural spine, is essentially complete. Neural spine (fig. 48) relatively broad antero-posteriorly and rakes slightly backward; proportions and position of pedicles of neural arch correspond quite closely to sixth dorsal; neural canal wider (50.5 mm.) than high (38 mm.); centrum broader than long; antero-superior facet on lateral surface of centrum rather large and placed mainly behind level of anterior edge of pedicle of neural arch; postero-superior facet placed mainly on hinder face of centrum; neck of
laterally projecting diapophysis very short, its lateral articular facet for tuberculum of seventh rib being subpyriform in outline and having a distinct anterior concavity; prezygapophyses thickened, projecting forward beyond level of anterior end of centrum; prezygapophysial facets closely approximated (interval, 13 mm.); and postzygapophysial facets elongated, closely approximated (interval, 12.5 mm.), sloping upward and backward, and extended posteriorly beyond level of hinder end of centrum.

A low median longitudinal carina is present on the ventral surface of the centrum of the larger individual (No. 4679, U. S. N. M.) and the postero-superior facet on postero-external angle of centrum is relatively larger.

Eighth Dorsal—This vertebra is essentially complete in both series of dorsal vertebrae (Nos. 4679 and 11962, U. S. N. M.), although the upper half of the neural spine is missing on the latter. The basal one-third of the rather broad neural spine (fig. 49) is directed nearly vertically, while the distal two-thirds rakes strongly backward. Pedicle of neural arch rather broad antero-posteriorly (34.2 mm.), its anterior edge being nearer to anterior end of centrum than posterior edge is to hinder end; neural canal much wider (47 mm.) than high (37.5 mm.); centrum much broader than long; antero-superior facet on lateral surface of centrum very large and subpyriform in outline; no postero-superior facet present; diapophysis projects laterally from neural arch at a slightly lower level than on seventh dorsal; shape of lateral articular facet for tuberculum of eighth rib quite characteristic, being concave and broad ventrally and having an attenuated upper extension which curves forward; distance across vertebra between outer ends of diapophyses, 117 mm.; prezygapophyses greatly thickened and projected forward beyond level of anterior end of centrum; prezygapophysial facets rather widely separated (23.5 mm.) and sub-circular in outline; maximum distance between outer margins of these facets, 59.8 mm.;
postzygapophyseal facets elongated, separated medially by an interval of at least 18 mm., sloping upward and backward and extended backward slightly beyond level of hinder end of centrum; distance between outer margins of postzygapophyseal facets, 42 ± mm.; and a low median longitudinal carina present on ventral surface of centrum.

The diaphysis of the corresponding dorsal of *Dorudon zittelii* (No. 11235, Stuttgart) is quite similar in general shape to that of this archaeocete, while that of *Dorudon stromeri* (No. 1904. XII. 134e, Munich) has the main axis of the anteriorly attenuated extension of the diapophysis more nearly horizontal and the pedicles of its neural arch are more strongly inclined forward.

*Ninth Dorsal*—The roof of the neural arch, the entire neural spine, the prezygapophyses, the postzygapophyses, and the metapophyses are missing on this dorsal (No. 4679, U. S. N. M.). The relative proportions and position of the pedicles of the neural arch (fig. 50) at the base are similar to those of the eighth dorsal. Neural canal approximately as wide at the base as on eighth dorsal; centrum broader than long; diapophysis reduced to a short process projecting laterally from base of pedicle of neural arch and bearing distally an oval articular facet for articulation with tuberculum of ninth rib; elliptical facet for capitulum of ninth rib located on lateral face of centrum below and separated from the preceding facet by a deep groove; dorso-ventral axes of both facets oblique to vertical axis of centrum; distance across vertebra between outer ends of diapophyses, 116.7 mm.; and a low median longitudinal carina present on ventral surface of centrum. This vertebra thus corresponds to the transitional or intermediate dorsal.

The ninth dorsal of *Dorudon zittelii* (No. 11235, Stuttgart), however, has a remarkably slender neural spine and the diapophysis is borne on a slightly longer neck.

*Tenth Dorsal*—The hinder end of the centrum, the distal portion of the neural spine, the postzygapophyses, and the anterior ends of the metapophyses are destroyed on this
vertebra (No. 4679, U. S. N. M.). The large medially constricted facet (fig. 51) for articulation with the head of the tenth rib is borne on a very short and stout transverse process, which projects from lateral surface of centrum. The metaphyses were obviously large and projected forward beyond the level of the anterior end of the centrum. Basal portion of rather broad neural spine directed almost vertically; pedicle of neural arch relatively broad antero-posteriorly (40 mm.), its anterior edge being much nearer to anterior end of centrum than the posterior edge is to hinder end; neural canal wider (45 mm.) than high (39.5 mm.); prezygapophyseal facets rather closely approximated 21 mm.) and sloping very obliquely from external to internal margins; and a low broad median longitudinal carina present on ventral surface of centrum.

The tenth dorsal of *Dorudon zitteli* (No. 11235, Stuttgart) has a rather narrow transverse process which is directed obliquely downward, slender metaphyses which are directed forward and upward, and a neural spine which is noticeably wider antero-posteriorly than that of the ninth dorsal.

Eleventh Dorsal—The neural arch, with the exception of the basal portions of its pedicles, the entire neural spine, and the metaphyses, and the anterior epiphysis are destroyed on this vertebra (No. 4679, U. S. N. M.). The relatively short but massive transverse process (fig. 52) has a large concave distal facet for articulation with head of the eleventh rib. A prominent median longitudinal carina is present on the ventral surface of the centrum.

The eleventh dorsal of *Dorudon zitteli* has slender metaphyses which are directed forward and upward.

Twelfth Dorsal—The anterior epiphysis of the centrum, the neural arch with the exception of the basal portions of its pedicles, the entire neural spine, and the metaphyses are destroyed on this vertebra (No. 4679, U. S. N. M.). The neural canal is approximately as wide (39.5 mm.) at the base as on the eleventh dorsal. The transverse processes (fig. 53) are slightly longer than those on the eleventh dorsal and project from the middle of the centrum, but the distal facet for articulation with the head of the twelfth rib is somewhat smaller. A prominent median longitudinal carina separating elongate depressions is present on the ventral surface of the centrum.

Thirteenth Dorsal—This vertebra (No. 4679, U. S. N. M.) is essentially complete on the right side, with the exception of the anterior end of the metapophysis. Neural spine rather broad antero-posteriorly and directed nearly vertically; neural canal slightly wider (42 mm.) than high (40 mm.); pedicle of neural arch (fig. 54) broad antero-posteriorly (40 mm.), its anterior edge being nearer to anterior end of centrum than the posterior edge is to hinder end; transverse process longer than that of twelfth dorsal and directed outward and obliquely downward; distal facet on transverse process for articulation with head of thirteenth rib rather large; metaphyses large, projecting upward, outward, and slightly forward, but extending forward conspicuously beyond level of anterior end of centrum; prezygapophyseal facets reduced in size and more closely approximated; postzygapophyseal facets small, separated medially by an interval of 22.5 mm., and their hinder ends project backward to level of hinder end of centrum; maximum distance between outer margins of postzygapophyseal facets, 42.2 mm.; and a prominent median longitudinal carina separating elongate depressions present on ventral surface of centrum.

Fourteenth Dorsal—The distal end and a portion of the anterior border of the neural spine, in addition to the metaphyses, are missing on this vertebra (No. 4679, U. S. N. M.). The antero-posterior diameter of the neural spine (fig. 55) at the base is approximately the same as that of the thirteenth dorsal, but the neural spine seems to rake more strongly backward. Vertical diameter (45 mm.) of neural canal greater than transverse
diameter (42.8 mm.); pedicle of neural arch slightly wider antero-posteriorly (40 ± mm.) than that of thirteenth dorsal; anterior edge of pedicle of neural arch nearer to anterior end of centrum than the posterior edge is to hinder end; transverse processes somewhat longer than those of thirteenth dorsal and directed outward, obliquely downward, and slightly forward; distal facet on transverse process for articulation with head of fourteenth rib smaller than that on thirteenth dorsal; postzygapophyseal facets small, separated medially by an interval of at least 13 mm. and their hinder ends are extended backward slightly beyond level of posterior end of centrum; and a prominent median longitudinal carina separating elongate depressions present on ventral surface of centrum.

Fifteenth Dorsal—The distal end as well as the fore and hinder borders of the neural spine are incomplete, and the anterior ends of the metapophyses are missing on this ver-


tebra (No. 4679, U. S. N. M.). The neural spine (fig. 56) is narrower antero-posteriorly at the base than on the fourteenth dorsal and rakes backward. The metapophyses were obviously narrow processes that project upward, outward, and forward. Neural canal higher (43.5 mm.) than wide (39 mm.); pedicle of neural arch wider antero-posteriorly (42 ± mm.) than on fourteenth dorsal, but with more nearly vertical hinder edge; transverse processes rather long and directed outward, obliquely downward, and slightly forward; distal facet on transverse process for articulation with head of fifteenth rib placed obliquely, so that it looks slightly backward; prezygapophyseal facets narrow and curved from end to end; postzygapophyseal facets small, placed for the most part on postero-external angles of base of neural spine, and their hinder ends do not extend backward beyond level of posterior end of centrum; and a prominent median longitudinal carina separating elongate depressions present on ventral surface of centrum.
ZYGORHIZA

Table 34—Measurements (in millimeters) of the dorsal vertebrae (Cat. No. 4679, U. S. N. M.)

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<thead>
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<td>78.5</td>
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<td>40.5</td>
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<td>39.5</td>
<td>39.5</td>
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<td>101.5</td>
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<tr>
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<td></td>
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<td>196.5</td>
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1 Posterior face.

Table 35—Measurements (in millimeters) of the dorsal vertebrae (Cat. No. 11962, U. S. N. M.)

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<td>71.5</td>
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<td>Vertical diameter of posterior face of centrum</td>
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<tr>
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<tr>
<td>Distance across vertebra between outer ends of diapophyses</td>
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<td>Distance between tip of prezygapophysis and tip of postzygapophysis</td>
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<td>Greatest vertical height of vertebra, ventral face of centrum to tip of neural spine</td>
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<td>Maximum distance between outer margins of prezygapophyseal facets</td>
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<td>43.5</td>
<td>43</td>
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LUMBAR AND SACRAL VERTEBRAE

The lumbar region as shown in the tentative reconstruction of the skeleton of this archaeocete (pl. 1) is based on vertebrae belonging to seven individuals. Most of these vertebrae are imperfectly preserved. The structural peculiarities and proportions of these vertebrae lend support to the contention that the lumbar region, when complete, consisted of thirteen lumbar and two sacral vertebrae, although the latter differ very slightly from the former. Eight hinder lumbar vertebrae (No. 12335, U. S. N. M.), which were found lying in their normal sequence, have been utilized as a basis for the allocation of the isolated vertebrae of the other six individuals. The material available comprises eleven imperfect lumbar vertebrae of one individual (No. 4678, U. S. N. M.), seven of another (No. 12063, U. S. N. M.), five of another (No. 4679, U. S. N. M.), four of another (No. 11962, U. S. N. M.), the centra of three anterior lumbar vertebrae (No. 1599, U. S. N. M.), and an imperfect anterior lumbar vertebra (No. 4680, U. S. N. M.).
The measurements of these vertebrae show that two of these individuals (Nos. 4679 and 12335, U. S. N. M.) were somewhat larger than the others.

The centra of all these lumbar vertebrae progressively increase in length from the anterior one backward. A short median ventral carina is present on the centra of the anterior lumbar vertebrae. The transverse processes increase in length toward the hinder end of the lumbar series. On the hinder lumbars the extremities of these processes are distinctly expanded in a fore-and-aft direction. The pedicles of the neural arches are relatively wide antero-posteriorly in proportion to length of centrum. On the anterior lumbars, the anterior edge of the pedicle of the neural arch is much nearer to the anterior end of the centrum than the posterior edge is to the hinder end. At the hinder end of the lumbar series, the hinder edges of the pedicles of the neural arch are set back farther from the posterior end of the centrum. On the anterior lumbars, the neural canals are rather high and broad, but become progressively lower and narrower toward the hinder end of the series. The neural canals of the two hinder vertebrae in this series are conspicuously narrower than those of the preceding lumbers. The slender lamina-like metapophyses are directed obliquely upward and forward, and project considerably beyond the level of the anterior end of the centrum. Distinct postzygapophyseal facets are present on all of the lumbar vertebrae and the interval between these articular surfaces decreases progressively from the anterior to the hinder end of the lumbar series. The neural spines are nearly vertical, broader antero-posteriorly at the base than the pedicles of the neural arches, and their anterior and posterior borders are relatively thin.

An incomplete lumbar vertebra found in the Ocala limestone on land belonging to the Pennsylvania-Dixie Cement Corporation at Clinchfield, Houston County, Georgia, was submitted for examination during June 1935, by E. Holtzclaw. The centrum is slightly larger than any of those hereinafter described, the maximum antero-posterior diameter being 86.5 mm., the vertical diameter of the posterior face, 90 mm., and the transverse diameter of the posterior face, 100 mm.

First Lumbar—The first vertebra in the lumbar series is represented by a centrum with incomplete transverse processes (No. 4678, U. S. N. M.). It differs from the hindermost dorsal vertebra in having the transverse processes distinctly flattened dorso-ventrally and slightly widened antero-posteriorly. Although the extremities of both transverse processes are destroyed, they are probably longer than those on the last dorsal vertebra. The ventral profile of the centrum as viewed from the side is nearly straight, and a prominent longitudinal carina separates the ventral orifices of the two dorso-ventral vascular canals.

Second Lumbar—This vertebra (No. 12063, U. S. N. M.) has a nearly vertical neural spine which is rather broad antero-posteriorly, but it is not expanded transversely to form a prominent lateral vertical swelling. The antero-posterior diameter of the neural spine at its base is 56 mm. Prezygapophyseal facets are concave from before backward and separated proximally by an interval of about 15 mm.; postzygapophyseal facets placed obliquely on postero-lateral angles of roof of neural arch; pedicle of neural arch very slightly inclined forward, its anterior edge at the base rather close to anterior end of centrum, and its minimum antero-posterior diameter is 38 mm.; neural canal wider (44 ± mm.) than high (39 mm.); left transverse process essentially complete (length 84 mm.), directed outward and downward, curved somewhat backward on its distal half, and attenuated toward its distal end; orifices of the two dorso-ventral vascular canals open into elongate depressions and are separated by a bony partition which forms a short ventral carina; and lateral surfaces of centrum slightly concave from end to end above transverse processes.
Another smaller second lumbar (No. 4678, U. S. N. M.) has a neural canal of similar proportions, its transverse diameter anteriorly being 36.2 mm., and its vertical diameter 33 mm. The postzygapophyseal facets are rather large, separated by an interval of 13 mm., and slope obliquely from dorsal to ventral margins. The metapophyses arise from the sides and roof of the neural arch and project upward and forward.

Third Lumbar—The centrum of this lumbar vertebra (No. 12063, U. S. N. M.) is wider than long, the neural spine is fairly thick transversely at the base, and the transverse processes are relatively long (95.5 mm.). The postzygapophyses, metapophyses, and all of the neural spine, with the exception of its basal portion, are destroyed. Prezygapophyseal facets rather narrow, concave from before backward, but not extended upward on rising dorsal surfaces of metapophyses; pedicle of neural arch nearly vertical, its minimum antero-posterior diameter being 38 mm.; neural canal rather broad, its transverse diameter (45 mm.) being greater than its vertical diameter (38 mm.); left transverse process complete, directed outward and downward, the anterior border being quite thin and the hinder border thick and rounded; distal half of anterior margin of transverse process obliquely truncated; and ventral orifices of the two dorso-ventral vascular canals open into elongate depressions and are separated by a thin bony partition which forms a short ventral carina.

A third lumbar belonging to another individual (No. 4678, U. S. N. M.) lacks the neural spine and all of the neural arch, with the exception of the basal portions of its pedicles, and the extremities of the transverse processes are destroyed. The minimum antero-posterior diameter of the pedicle of the neural arch (39.5 mm.) is equivalent to four-sevenths of the length of the centrum (70 mm.). The anterior and posterior faces of the centrum are slightly concave.

Fourth Lumbar—This vertebra (No. 12063, U. S. N. M.) has a complete neural arch and neural spine, and fairly well-preserved metapophyses, but the postzygapophyseal facets are for the most part destroyed. The anterior end of the centrum is damaged, the left transverse process is missing, and the right transverse process has an incomplete anterior border. Neural spine (fig. 57) rather broad antero-posteriorly, the corresponding diameter at its base being 59 mm., somewhat thickened transversely especially on basal half, but without forming a prominent lateral vertical ridge, and having anterior and posterior borders quite thin; prezygapophyseal facets narrow and concave from end to end; postzygapophyseal facets narrow, separated posteriorly by an interval of 11 mm., and projected backward beyond level of hinder end of centrum; pedicles of neural arch set back at base farther from anterior end of centrum than on second lumbar; neural canal broader (45 mm.) than high (38.5 mm.); metapophyses compressed from side to side, their dorsal and ventral surfaces sloping from external to internal margins and directed obliquely forward, upward, and outward; transverse process directed outward, downward, and slightly forward, and has a quite thin anterior border and a thickened hinder border; ventral orifices of the two dorso-ventral vascular canals open into a rather deep median concavity; and greatest vertical height of vertebra from ventral face of centrum to tip of neural spine, 228 mm.
The centrum of another fourth lumbar vertebra (No. 4678, U. S. N. M.) has a strong ventral carina which separates the ventral orifices of the two vertebral arterial canals. The transverse processes of this vertebra are directed downward and slightly forward.

Fifth Lumbar—The distal three-fourths of the neural spine, the extremities of the metapophyses, and the postzygapophyseal facets are destroyed on this lumbar (No. 4678, U. S. N. M.). The basal portions of the transverse processes indicate that they were less noticeably attenuated distally than those of the fourth lumbar. Neural spine rather broad, its antero-posterior diameter at the base being 63.5 mm.; metapophyses arise rather high up on sides of neural arch and project forward and upward; prezygapophyseal facets narrow and slightly concave from end to end; pedicles of neural arch nearly vertical, quite broad, their minimum antero-posterior diameter (40.2 mm.) being equivalent to approximately four-sevenths of length of centrum (71.2 mm.) and their anterior edges are much nearer to anterior end of centrum than their hinder edges are to posterior end; neural canal rather broad and quite high, its transverse diameter anteriorly being 34.2 mm. and its vertical diameter 30 mm.; ventral profile of centrum, viewed from side, slightly concave; and a prominent ventral carina separates ventral orifices of the two dorso-ventral vascular canals.

Sixth Lumbar—The anterior ends of the metapophyses, the distal half of the neural spine, and the distal ends of the transverse processes of this vertebra (No. 12063, U. S. N. M.) are destroyed. Centrum wider than long; neural spine slightly narrower antero-posteriorly than on fourth lumbar, its antero-posterior diameter at base being 51 mm.; prezygapophyseal facets reduced to short curved surfaces on anterior border of neural arch; postzygapophyseal facets separated by a rather wide interval and projected backward beyond level of hinder end of centrum; metapophyses elongated; compressed from side to side and curved forward, outward, and upward; neural canal slightly wider (41 mm.) than high (38 mm.); no perceptible change in antero-posterior diameter of pedicle of neural arch, its minimum antero-posterior diameter (38 mm.) being more than half the length of centrum (67.5 mm.); anterior edge of pedicle of neural arch much nearer to anterior end of centrum than posterior edge is to hinder end; transverse process directed outward and strongly downward; distal third of anterior border of transverse process obliquely truncated; and ventral orifices of the two dorso-ventral vascular canals slightly depressed below level of ventral face of centrum and separated by a bony partition which forms a short ventral carina.

An imperfect sixth lumbar belonging to a smaller individual (No. 4678, U. S. N. M.) has the pedicles set back at base farther from anterior end of centrum than on any of the preceding lumbar vertebrae. The transverse processes are directed downward and slightly forward.

Another sixth lumbar (No. 4679, U. S. N. M.) has the transverse processes directed obliquely downward and outward. The minimum antero-posterior diameter of the left transverse process is 28 mm. All three of these vertebrae are characterized by the horizontal and vertical enlargement of both ends of the centra.

Seventh Lumbar—This vertebra (No. 4678, U. S. N. M.) lacks the neural spine, the postzygapophyses, and most of both metapophyses. Centrum somewhat wider than long; neural canal slightly lower and narrower than on preceding lumbar; metapophyses arise at a lower level from sides and roof of neural arch; transverse processes directed obliquely downward and slightly forward; extremities of transverse processes obliquely truncated; ventral orifices of the two dorso-ventral vascular canals separated by short median longitudinal carina.

Eighth Lumbar—Eight consecutive vertebrae (No. 12335, U. S. N. M.), which were found lying in a nearly straight line and articulating with one another, have furnished
incontestible data on the structural peculiarities of each vertebra in the hinder half of this series. These vertebrae were found very close to the surface in a cultivated field and were thoroughly saturated with water at the time of discovery. Their structural peculiarities and dimensions were determined while the vertebrae were still saturated with water. During and subsequent to the evaporation of the water content, these vertebrae have undergone considerable disintegration. In addition to the eighth lumbar in this series, there is available the corresponding lumbar of a smaller individual (No. 4678, U. S. N. M.), which lacks the neural spine, the metapophyses, and the neural arch with the exception of the basal portions of its pedicles. The extremities of the transverse processes are likewise destroyed. Neural spine large, the anterior and posterior edges quite thin, and a pronounced side-to-side thickening behind middle of its antero-posterior diameter, forming a broad lateral vertical ridge; antero-posterior diameter of neural spine at base (62 mm.) equivalent to four-fifths of length of centrum (76 mm.); metapophyses elongated, curved upward and forward, extended forward conspicuously beyond level of anterior end of centrum and compressed dorso-ventrally, the dorsal surface being slightly convex and the ventral surface nearly flat; distance from tip of right metapophysis to antero-ventral angle of neural spine, 32 mm.; neural canal wider than high, the transverse diameter anteriorly being 39 mm.; minimum antero-posterior diameter of left pedicle of neural arch, 37.7 mm.; transverse processes rather broad, directed outward and downward; lateral surface of centrum above transverse process concave from end to end; ventral surface of centrum rather broad and concave; and ventral orifices of the two dorso-ventral vascular canals rather large and separated by a thin bony partition which forms a short ventral carina.

Ninth Lumbar—In addition to the ninth lumbar in the consecutive series (No. 12335, U. S. N. M.), an incomplete lumbar of a smaller individual (No. 4678, U. S. N. M.) has been used in formulating the following diagnosis. The neural spine, metapophyses, and pedicles of the neural arch are quite similar to those of the eighth lumbar, but the centrum is slightly longer, its antero-posterior diameter being 77.5 mm. Neural canal slightly narrower than that of eighth lumbar, its transverse diameter anteriorly being 38 mm.; transverse processes rather broad, thickened dorso-ventrally at base, and directed outward and downward; and position and size of ventral orifices of the two dorso-ventral vascular canals and also curvature of ventral surface of centrum essentially the same as on eighth lumbar.

Tenth Lumbar—This imperfect vertebra (No. 12335, U. S. N. M.) furnishes most of the structural details of the tenth in the lumbar series. The rather broad neural spine rakes slightly backward and its antero-posterior diameter at base is slightly greater than that of the ninth lumbar. The neural spine is less noticeably expanded from side to side behind the middle of its antero-posterior diameter, its maximum transverse diameter near the base being 14.5 mm. The metapophyses differ very slightly from those of the preceding lumbar. Neural canal somewhat narrower and not quite so high as that of ninth lumbar, its transverse diameter anteriorly being 30.5 mm.; pedicles of neural arch relatively wide, the minimum antero-posterior diameter of left pedicle being 45 mm.; length of centrum 78 mm.; transverse processes directed outward, downward, and slightly forward, and somewhat constricted antero-posteriorly near the middle, but strongly expanded distally; and ventral orifices of the two dorso-ventral vascular canals rather large and separated by a thin bony partition which forms a short ventral carina.

The right transverse process and the posterior half of the centrum of another individual (No. 4679, U. S. N. M.) furnish some additional details. The elongated transverse process of this vertebra (length 112 mm.) has a thin anterior edge and a rounded hinder edge. It is directed outward and obliquely downward, expanded antero-posteriorly at the extremity, and obliquely truncated distally from anterior to posterior angle.
The ventral orifices of the two dorso-ventral vascular canals are separated by a short median longitudinal carina.

Eleventh Lumbar—The centrum of this vertebra (No. 12335, U. S. N. M.) is slightly larger, the antero-posterior diameter of the pedicle of the neural arch is a little longer, the neural canal is slightly lower, the metapophyses arise at a lower level on the sides of the neural arch, and the neural spine is a little wider antero-posteriorly at the base than on the preceding lumbar. The maximum transverse diameter of the neural spine near the base is 13.3 mm. The transverse processes are moved backward on the lateral surface of the centrum and slope obliquely downward and outward.

On the corresponding lumbar of another individual (No. 4679, U. S. N. M.), the right transverse process and the centrum are complete, but the distal portion of the neural spine (fig. 58) is missing and both metapophyses are destroyed. The following additional structural details are furnished by this vertebra: Anterior edge of neural spine thin and terminating in basal triangular depression as on preceding lumbers; antero-posterior diameter of pedicle of neural arch (39 mm.) less than half length of centrum (82 mm.); lateral surfaces of centrum above transverse processes concave from end to end; transverse process (fig. 59) elongated (length 114 mm.), directed outward and obliquely downward,
conspicuously expanded distally (antero-posterior diameter, 52.8 mm.), and obliquely truncated at distal end, but has a rounded and thickened postero-external angle; ventral surface of centrum rather strongly concave; ventral orifices of the two dorso-ventral vascular canals open into a concavity and are separated by a low short longitudinal median ridge.

Twelfth Lumbar—The neural spine of this vertebra (No. 12335, U. S. N. M.) is rather broad antero-posteriorly at base (67.5 mm.) and is strongly compressed from side to side, its maximum transverse diameter at the base being 11.6 mm. The pedicle of the neural arch is relatively wide antero-posteriorly in proportion to the length of the centrum (80 mm.) and the transverse diameter of the neural canal anteriorly is 30.5 mm. The ventral surface of the centrum is concave from end to end and also from side to side. The large ventral orifices of the dorso-ventral vascular canals are separated by a bony partition which forms a short ventral carina.

The corresponding lumbar of another individual (No. 4679, U. S. N. M.) is imperfectly preserved. The neural canal is wider than high, its transverse diameter anteriorly being 35.3 mm. and its vertical diameter 30 mm. The minimum antero-posterior diameter of the pedicle of the neural arch (41.5 mm.) is equivalent to half the length of the centrum (83 mm.). The ventral orifices of the two dorso-ventral vascular canals are separated by a short median longitudinal carina.

Thirteenth Lumbar—The transverse diameter of the posterior face (85 mm.) is greater than the length of the centrum (81.5 mm.) of this vertebra (No. 12335, U. S. N. M.). The neural canal is not as high as that of the twelfth lumbar and its transverse diameter anteriorly is 30.5 mm. The metapophyses are elongated and extended forward beyond the level of the anterior end of the centrum. In direction and size, the transverse processes are similar to those on the twelfth lumbar. The hinder edge of the transverse process is much nearer to the posterior end of the centrum than its anterior edge is to the anterior end.

An incomplete vertebra of another individual (No. 4679, U. S. N. M.) has the ventral orifices of the two dorso-ventral vascular canals separated by a short low ventral carina. The neural canal is slightly narrower anteriorly than on the twelfth lumbar. The transverse diameter of the posterior face of this centrum (89.5 mm.) is likewise greater than its antero-posterior diameter (84 mm.).

A nearly complete vertebra belonging to a smaller individual (No. 12063, U. S. N. M.) is likewise tentatively identified as the thirteenth in the lumbar series. The centrum of this vertebra is wider (87.5 mm.) than long (75 mm.), the metapophyses are extended forward conspicuously beyond the level of the anterior end of the centrum, the neural canal is relatively small, the transverse processes are bowed downward, and the ventral profile of the centrum viewed from the side is strongly concave from end to end. Neural spine not noticeably thickened transversely at base, its anterior and posterior edges being quite thin; metapophyses strongly compressed from side to side, and directed strongly upward, outward, and forward; prezygapophysial facets destroyed; postzygapophysial facets closely approximated, located on ventral surfaces of postero-lateral angles of roof of neural arch, but do not project backward within 13 mm. of level of hinder end of centrum; neural canal about as high (27 mm.) as wide (27.5 mm.); pedicle of neural arch rather wide antero-posteriorly (38 mm.) and equivalent to about half the length of centrum (75 mm.); transverse processes relatively broad in proportion to their length, and directed outward, strongly downward, and slightly forward; ventral orifices of the two dorso-ventral vascular canals separated by a short bony partition; no ventral carina is present; ventral surface of centrum concave from side to side and from end to end; and lateral surface of centrum above transverse process concave from end to end.

Fourteenth Lumbar or First Sacral—The centrum of this vertebra (No. 12335, U. S. N. M.) is wider than long, its transverse diameter posteriorly being 86 mm. and its
length 83 mm. Neural canal somewhat narrower (26.5 mm.) than that of preceding lumbar; neural spine broad and rather strongly compressed from side to side, its maximum transverse diameter near base being 10 mm.; anterior edge of pedicle of neural arch rather close to anterior face of centrum, the distance from base of pedicle to anterior end of centrum being 11.5 mm.; ventral surface of centrum strongly curved from end to end, its ventro-lateral surfaces being strongly hollowed out; orifices of the two dorso-ventral

| Table 36—Measurements (in millimeters) of the lumbar vertebra (No. 4678, U. S. N. M.) |
|-----------------------------------------------|---|---|---|---|---|---|---|---|---|---|---|---|
| Maximum antero-posterior diameter of centrum | 65.5 | 66 | 70 | 70.5 | 71.2 | 73 | 74.8 | 76 | 75.6 | 76 | 73.5 | 77.5 |
| Transverse diameter of anterior face of centrum | 73 | 73 | 78 | 79.5 | 79.8 | 79.2 | 79.7 | 79.5 | 78.6 | 71.5 | 77.5 |
| Vertical diameter of anterior face of centrum | 61.5 | 64 | 64 | 64 | 70 | 70 | 72.2 | 74.6 | 76 | 71.5 | 73.5 |
| Transverse diameter of posterior face of centrum | 77.5 | 75 | 75 | 80.5 | 81.5 | 80.5 | 83 | 81 | 71.5 | 73.5 |
| Vertical diameter of posterior face of centrum | 64 | 66 | 63 | 71.5 | 75 | 76 | 75 | 75 | 75 | 75 | 75 |
| Greatest vertical diameter of neural canal anteriorly | 33 | 30 | 30 | 30 | 30 | 30 | 30 | 30 | 30 | 30 | 30 |
| Greatest transverse diameter of neural canal anteriorly | 36.2 | 36.5 | 36.5 | 34.2 | 33.2 | 33.2 | 33.2 | 33.2 | 33.2 | 33.2 | 33.2 |
| Least antero-posterior diameter of pedicle of neural arch | 41.6 | 39.5 | 41.5 | 41.5 | 41.5 | 41.5 | 41.5 | 41.5 | 41.5 | 41.5 | 41.5 |

| Table 37—Measurements (in millimeters) of the lumbar vertebra (No. 4679, U. S. N. M.) |
|-----------------------------------------------|---|---|---|---|---|---|---|---|---|---|---|---|
| Maximum antero-posterior diameter of centrum | 75.6 | 82 | 83 | 84 | 84 | 84 | 84 | 84 | 84 | 84 | 84 | 84 |
| Transverse diameter of anterior face of centrum | 72.3 | 78.8 | 79.5 | 79.5 | 79.5 | 79.5 | 79.5 | 79.5 | 79.5 | 79.5 | 79.5 | 79.5 |
| Vertical diameter of posterior face of centrum | 86.5 | 89.4 | 89.5 | 89.5 | 89.5 | 89.5 | 89.5 | 89.5 | 89.5 | 89.5 | 89.5 | 89.5 |
| Vertical diameter of posterior face of centrum | 75 | 77.7 | 77.5 | 77.5 | 77.5 | 77.5 | 77.5 | 77.5 | 77.5 | 77.5 | 77.5 | 77.5 |
| Greatest vertical diameter of neural canal anteriorly | 37 | 35 | 36 | 35.3 | 35 | 35 | 35 | 35 | 35 | 35 | 35 | 35 |
| Greatest transverse diameter of neural canal anteriorly | 39 | 41.5 | 41.5 | 41.5 | 41.5 | 41.5 | 41.5 | 41.5 | 41.5 | 41.5 | 41.5 | 41.5 |

| Table 38—Measurements (in millimeters) of the lumbar vertebra (No. 12063, U. S. N. M.) |
|-----------------------------------------------|---|---|---|---|---|---|---|---|---|---|---|---|
| Maximum antero-posterior diameter of centrum | 64 | 65.6 | 69 | 67.5 | 75 | 77.5 | 77.5 | 77.5 | 77.5 | 77.5 | 77.5 | 77.5 |
| Transverse diameter of anterior face of centrum | 76.9 | 78 | 74 | 74 | 74 | 74 | 74 | 74 | 74 | 74 | 74 | 74 |
| Vertical diameter of anterior face of centrum | 69 | 73 | 73 | 73 | 73 | 73 | 73 | 73 | 73 | 73 | 73 | 73 |
| Vertical diameter of posterior face of centrum | 69 | 83.5 ± | 85 | 85 | 85 | 85 | 85 | 85 | 85 | 85 | 85 | 85 |
| Vertical diameter of posterior face of centrum | 71 | 71.5 | 73 | 73 | 73 | 73 | 73 | 73 | 73 | 73 | 73 | 73 |
| Greatest vertical diameter of neural canal anteriorly | 39 | 38 | 38.5 | 38 | 38 | 38 | 38 | 38 | 38 | 38 | 38 | 38 |
| Greatest transverse diameter of neural canal anteriorly | 44 | 45 | 45 | 41 | 41 | 41 | 41 | 41 | 41 | 41 | 41 | 41 |
| Greatest transverse diameter of neural canal posteriorly | 46 | 46 | 43.5 | 43.5 | 43.5 | 43.5 | 43.5 | 43.5 | 43.5 | 43.5 | 43.5 | 43.5 |
| Least antero-posterior diameter of pedicle of neural arch | 38 | 38 | 38.8 | 38 | 38 | 38 | 38 | 38 | 38 | 38 | 38 | 38 |
| Distance across vertebra between outer ends of transverse processes | 233± | 225± | 248± | 228± | 228± | 228± | 228± | 228± | 228± | 228± | 228± | 228± |
| Maximum length of transverse process | 84 | 95.5 | 90 | 86 | 86 | 86 | 86 | 86 | 86 | 86 | 86 | 86 |

1 Estimated.

vascular canals open into a depression on mid-line of ventral surface; and no ventral carina is present.

The corresponding vertebra of a smaller individual (No. 4678, U. S. N. M.) lacks most of its processes. The neural canal is quite narrow, its transverse diameter anteriorly being 22 mm.

Fifteenth Lumbar or Second Sacral—The hindermost vertebra in this series (No. 12063, U. S. N. M.) has a larger centrum than any of the preceding vertebra, the transverse
processes are somewhat wider antero-posteriorly than those of the thirteenth lumbar, the elongated metapophyses are not so strongly compressed from side to side, the neural canal is smaller, but the pedicle of the neural arch is approximately as wide antero-posteriorly (38.8 mm.). It is characterized as follows: Antero-posterior diameter of neural spine at base shorter than that of preceding vertebra; prezygapophysial facets destroyed; postzygapophysial facets rather closely approximated and located on ventral face of posterior angle of roof of neural arch; metapophyses elongated, directed upward, outward, and forward; transverse processes rather broad (antero-posterior diameter at base, 55 mm.) and bowed downward, but directed slightly forward; posterior border of transverse process obliquely truncated distally; lateral surface of centrum above transverse process concave from end to end; ventral orifices of the two dorso-ventral vascular canals separated by a median bony partition; and no ventral carina present.

The hindermost vertebra in the consecutive series (No. 12335, U. S. N. M.), with the exception of its slightly larger dimensions, does not differ in any essential detail from the above described vertebra. An imperfectly preserved vertebra belonging to a smaller individual (No. 4678, U. S. N. M.) likewise has a relatively narrow neural canal, its transverse diameter anteriorly being 18 mm.

The extremities of the transverse processes of the two hinder vertebrae in the lumbar or lumbar-sacral series are not modified for the attachment of a pelvic element. This does not necessarily indicate that the pelvic elements have been entirely lost.

Caudal Vertebrae

The assumption that the caudal series (pl. 1, B) of Zygorhiza kochii consisted of at least 21 vertebrae is based in part on the presence of 21 vertebrae in the caudal series of Basilosaurus cetoides (No. 12261, U. S. N. M.), in part on the characters of 12 consecutive hinder caudal vertebrae of Dorudon serratus (Gibbes, 1847, pl. 2, fig. 7), and in part on the relative dimensions and the structural peculiarities of ten isolated caudal vertebrae belonging to one individual (No. 4679, U. S. N. M.), two terminal caudals (No. 4680, U. S. N. M.), four middle caudals (No. 4678, U. S. N. M.), two anterior caudals (No. 12063, U. S. N. M.), and the first and second caudals of another individual (No. 12335, U. S. N. M.).

The fifth in the series (No. 4679, U. S. N. M.) is the largest of the anterior caudals and measures 90.5 mm. in length and 102.5 mm. in breadth posteriorly, while the corresponding measurements of the penultimate caudal (No. 4679, U. S. N. M.) are, respectively, 38.5 mm. and 77.6 mm. The neural spine rapidly decreases in height from the first to the fifth in the caudal series and apparently disappears entirely on either the sixth or the seventh caudal vertebra. On the anterior caudals, the neural canal is about as high as wide anteriorly. Between the first and the fifteenth in the caudal series, there is a pronounced decrease in the height of the neural canal, but its width is less noticeably diminished. The neural canal is not roofed over on the sixteenth caudal. The metapophyses of the anterior caudals progressively decrease in size from the first to the fourteenth and become vestigial on the fifteenth caudal. In correlation with the progressive lowering of the roof of the neural arch toward the hinder end of the caudal series, the metapophyses drop to a lower level on each succeeding vertebra, those on the first projecting 52 mm. or more above the top of the centrum, while those on the fourteenth do not project upward more than 33.5 mm. above the top of the centrum.

The transverse processes of the anterior caudals are relatively long and progressively decrease in length from the first to the fourteenth. The seven anterior caudals do not have their transverse processes pierced at the base by a vascular foramen. The transverse processes of the eighth to eleventh caudals, inclusive, are perforated at the base, but on the twelfth the vascular canal is open distally and is bounded in front and behind by short
portions of the transverse process. The twelfth to eighteenth caudals, inclusive, retain portions of the transverse processes, but these processes are entirely wanting on the three hinder caudals. The centra of all the caudal vertebrae are more or less contracted from side to side in the middle of their length. The centra of the five hinder caudal vertebrae are noticeably compressed antero-posteriorly, and their lateral surfaces are deeply grooved vertically. The total length of this series of 21 caudal vertebrae is estimated to be approximately 1660 mm. (5 ft. 5 in.).

First Caudal—Two anterior caudal vertebrae are available for comparison, one of which (No. 12335, U. S. N. M.) belongs in a consecutive series consisting of the eight hinder lumbar-sacral and the two anterior caudals, and the other an isolated caudal (No. 12063, U. S. N. M.). The first caudal has a short neural spine, which is relatively broad antero-posteriorly and rakes slightly backward, and elongated transverse processes which are truncated obliquely at postero-distal angle. Centrum slightly broader than long, and

approximately equal in length to hindermost lumbar-sacral vertebra; pedicle of neural arch nearly vertical, relatively low, its anterior edge much nearer to anterior end of centrum than its posterior edge is to hinder end, and its minimum antero-posterior diameter (37.5 mm.) is less than half the length of the centrum (78 mm.); transverse diameter of neural canal at base anteriorly approximately the same as its vertical diameter; neural canal posteriorly higher than wide; metapophyses elongated and extended forward conspicuously beyond anterior end of centrum; hemapophysial facets located on relatively small pro-tuberances at hinder end of centrum; and orifices of the two dorso-ventral vascular canals on ventral face of centrum separated by a bony partition and open into a longitudinal depression.

Second Caudal—The second caudal (Nos. 12063 and 12335, U. S. N. M.) has slightly narrower and shorter transverse processes, shorter metapophyses, and a shorter neural spine than the first caudal. The neural canal is not as high, but its width is approximately the same as that of the first caudal. Vertical diameter of neural canal anteriorly not more than 26 mm.; relative proportions and position of pedicles of neural arch at base similar to
those of first caudal; ventral orifices of the two dorso-ventral vascular canals open into a longitudinal depression; and hæmapophysial facets at postero-ventral end of centrum separated by a relatively wide interval.

Third Caudal—Not represented in the collection.

Fourth Caudal—This large caudal (No. 4679, U. S. N. M.) is imperfectly preserved and lacks the anterior end of the centrum, the left transverse process, all of the neural arch, the neural spine, and the metapophyses. Transverse process rather long and broad, directed obliquely downward, outward, and slightly backward, and truncated obliquely at postero-distal angle; hinder edge of transverse process much nearer to posterior end of centrum than anterior edge is to anterior end; and ventral surface of centrum shallowly depressed longitudinally between posterior protuberances for hæmapophysial facets.

Fifth Caudal—The fifth in the caudal series (No. 4679, U. S. N. M.) is essentially complete, but lacks the ventral portion of anterior face of centrum and the rudimentary neural spine. This caudal (fig. 60a) has unusually large metapophyses which project forward beyond anterior end of centrum, a rudimentary neural spine, a very low and broad neural canal (fig. 60b), and a short process projecting backward from roof of neural arch. Transverse processes rather long, projected outward and obliquely downward, and moved backward on lateral surface of centrum; hinder edge of pedicle of neural arch nearer to posterior end of centrum than on caudals behind middle of series; minimum antero-posterior diameter of pedicle of neural arch (43 mm.) about half maximum length of centrum (88.5 mm.); metapophyses project upward 60 mm. above top of centrum; and hæmapophysial facets separated by a longitudinal depression. The broken edge that remains conclusively shows that the rudimentary neural spine extended across the full length of the roof of the neural arch.

Sixth Caudal—Not represented in the collection.

Seventh Caudal—Not represented in the collection.

Eighth Caudal—The anterior half of the centrum (fig. 61) and the corresponding portions of the transverse processes and of the pedicles of the neural arch of this caudal (No. 4679, U. S. N. M.) are missing. Transverse processes short and almost horizontal and perforated at base by a large vascular canal; metapophyses short, blunt edged, and project upward at least 51 mm. above top of centrum; neural canal low and broad; no neural spine; a long process projects backward from roof of neural arch; hæmapophysial facets placed on small conical protuberances and separated by an interval of 28 mm.; and longitudinal depression between hæmapophysial facets deeper than on fifth caudal.

An eighth caudal belonging to a smaller individual (No. 4678, U. S. N. M.) has the anterior and posterior ends of the centrum eroded ventrally, the transverse processes are destroyed, as are also the neural arch and the neural spine.

Ninth Caudal—Not represented in the collection.

Tenth Caudal—The hinder half of the centrum (fig. 62a) and the corresponding portions of the transverse processes of this caudal (No. 4679, U. S. N. M.) are destroyed. It has a low broad neural canal (fig. 62b), rather large metapophyses which project upward at least 46.5 mm. above the top of the centrum, and a long distally attenuated process which projects backward from the roof of the neural arch. Horizontal transverse processes rather short and perforated at base by a vascular canal; pedicles of neural arch relatively
wide antero-posteriorly in comparison to length of centrum; and height of neural canal anteriorly (9.5 mm.) equivalent to about one-third of its transverse diameter (29.5 mm).

A tenth caudal belonging to a smaller individual (No. 4678, U. S. N. M.) lacks the extremity of the right transverse process, the right metapophysis, and a portion of the right pedicle of the neural arch.

**Fig. 62**—Zygophiza kochii (Reichenbach). 10th caudal vertebra, No. 4679, United States National Museum. $\times \frac{1}{4}$. a, lateral view; b, anterior view. mp., metapophysis; tr., transverse process. Upper Eocene, upper Jackson formation, Alabama.

**Fig. 63**—Zygophiza kochii (Reichenbach). 12th caudal vertebra, No. 4679, United States National Museum. $\times \frac{1}{4}$. a, lateral view; b, anterior view. mp., metapophysis; tr., transverse process. Upper Eocene, upper Jackson formation, Alabama.

**Eleventh Caudal**—The hinder end of the centrum of this caudal (No. 4678, U. S. N. M.) is eroded ventrally and the ends of the transverse processes are destroyed. This caudal vertebra has short transverse processes, which are pierced at the base by vascular foramina, and a robust process projecting backward from the roof of the neural arch. Metapophyses low, rounded, and projected upward at least 28 mm. above top of centrum; transverse
diameter (23.5 mm.) of neural canal anteriorly equivalent to more than three times its vertical diameter (7.5 mm.); lateral surfaces of centrum above transverse processes concave from end to end; dorso-ventral vascular canals, which pass through middle of centrum, open ventrally into a longitudinal groove; and posterior hæmapophysial facets destroyed.

Twelfth Caudal—An intermediate stage in the reduction of the transverse process, which results from the incomplete closure of the vascular foramen, is exhibited by this caudal (No. 4679, U. S. N. M.); the anterior portion of the transverse process is at least four times as wide antero-posteriorly as the hinder portion. It (fig. 63a) is further characterized by the reduction of the metapophyses, by a very low and broad neural canal (fig. 63b), and by a long attenuated process projecting backward and obliquely upward from the roof of the neural arch. Centrum strongly concave from end to end above and below transverse processes; neural arches quite thick; vertical diameter (8 mm.) of neural canal anteriorly one-third of its transverse diameter (24 mm.); and centrum pierced by a pair of dorso-ventral vascular canals which open ventrally into a narrow median longitudinal depression. This caudal lacks most of the right side of the centrum, including the right transverse process, and both hæmapophysial facets are destroyed.

The twelfth caudal of a smaller individual (No. 4678, U. S. N. M.) has the anterior end of the centrum eroded, the anterior remnant of the transverse process is destroyed on both sides, and both metapophyses are damaged.

Thirteenth Caudal—Not represented in the collection.
Fourteenth Caudal—Viewed from in front this caudal (No. 4679, U. S. N. M.) has a distinctly hexagonal outline. It (fig. 64a) is characterized by the reduction of the metapophyses, by a small low neural canal (fig. 64b), by a vestigial process projecting backward from the roof of the neural arch, and by a further reduction of the transverse process; the anterior portion of this process is approximately the same size as that on the thirteenth caudal, but the hinder portion is reduced to a mere vestige. Metapophyses thickened from side to side, rather squarely truncated distally, and project upward at least 33.5 mm. above top of centrum; centrum rather strongly contracted near middle; hemapophysial facets located on rather large protuberances and separated by an interval of at least 15 mm.; and the single ventral orifice of the two dorso-ventral vascular canals is rather small and is located medially in the ventral concavity. The right hemapophysial facet and the ventral portion of the anterior end of the centrum of this caudal are destroyed.

Fifteenth Caudal—Although the entire neural arch is destroyed on this caudal (No. 4679, U. S. N. M.), it is obvious that its reduction was nearly accomplished. The anterior portion of the transverse process (fig. 65a) is present though somewhat reduced, but the hinder portion has disappeared. Behind the anterior portion of the transverse process there is a broad vertical groove which reaches the ventral face through the depression between the anterior and posterior prominences for the chevron bones. Centrum strongly contracted medially and pierced by a pair of dorso-ventral vascular canals which open ventrally into a single orifice in median longitudinal depression; and hinder hemapophysial facets small and more closely approximated than on fourteenth caudal.

Sixteenth Caudal—The centrum of this caudal (No. 4679, U. S. N. M.) is slightly compressed antero-posteriorly and it is strongly contracted laterally, forming a broad vertical groove for a vascular vessel. This caudal (fig. 66a) retains thickened remnants of the pedicles of the neural arch, a neural groove 20.5 mm. in width, the anterior portion of the transverse process, and in addition a very small process projecting backward from near the base of the right pedicle of the neural arch is developed. Near the middle and inside of the low ridges which represent remnants of the neural arch, there are a pair of orifices for the dorso-ventral vascular canals. On the ventral surface of the centrum there is a single median orifice for these canals which opens into a longitudinal depression. The contour of the anterior face of the centrum is distinctly hexagonal. Two small hinder hemapophysial facets are present.

Seventeenth Caudal—Not represented in the collection.
Eighteenth Caudal—As compared with the sixteenth caudal, the eighteenth (No. 4679, U. S. N. M.) is somewhat shorter, more rounded, and retains a vestige of the anterior portion of the transverse process. Centrum (fig. 67a) strongly compressed antero-posteriorly, its maximum transverse diameter (83.5 mm.) being less than twice its antero-posterior diameter (49.5 mm.); centrum strongly contracted at middle and encircled by a fairly wide groove; no remnants of the neural arch persist; paired dorsal orifices of vascular canals, which pierce the centrum in a dorso-ventral direction, much larger than the minute single ventral orifice; and posterior face of centrum convex, and anterior face concave.

Nineteenth Caudal—The caudal (No. 4680, U. S. N. M.), which is identified as the nineteenth in the series, is eroded ventrally. Centrum strongly compressed antero-posteriorly and flattened dorso-ventrally; maximum transverse diameter of centrum 86 mm. and maximum antero-posterior diameter, 46.5 mm.; dorsal and ventral orifices of dorso-ventral vascular canals small and open into narrow groove which encircles centrum; and no portions of transverse processes persist.

**Table 39—Measurements (in millimeters) of caudal vertebra**

<table>
<thead>
<tr>
<th>Cat. No. 12069</th>
<th>Cat. No. 4679, U. S. N. M.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>C. 1</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of centrum</td>
<td>78.576</td>
</tr>
<tr>
<td>Transverse diameter of anterior face of centrum</td>
<td>54.5</td>
</tr>
<tr>
<td>Vertical diameter of anterior face of centrum</td>
<td>83.5</td>
</tr>
<tr>
<td>Transverse diameter of posterior face of centrum</td>
<td>86.5</td>
</tr>
<tr>
<td>Vertical diameter of posterior face of centrum</td>
<td>83.5</td>
</tr>
<tr>
<td>Greatest transverse diameter of neural canal anterior</td>
<td>26.5</td>
</tr>
<tr>
<td>Least antero-posterior diameter of pedicle of neural arch</td>
<td>38</td>
</tr>
<tr>
<td>Maximum distance between antero-external angles of metapophyses</td>
<td>81.6</td>
</tr>
<tr>
<td>Distance across vertebra between outer ends of transverse processes</td>
<td>207.5</td>
</tr>
<tr>
<td>Maximum length of transverse process</td>
<td>95r</td>
</tr>
<tr>
<td>Greatest vertical height of vertebra, ventral surface of centrum to dorsal margin of metapophysis</td>
<td>143</td>
</tr>
</tbody>
</table>

r, right process; l, left process.

Twentieth Caudal—The antero-posterior compression of the centrum of the penultimate caudal (No. 4679, U. S. N. M.) is more pronounced than on the eighteenth caudal. The lateral vertical groove (fig. 68a) which encircles the centrum is also narrower and deeper. The dorsal and ventral orifices of the dorso-ventral vascular canals are located in this groove. The posterior and anterior faces of the centrum are convex. A penultimate caudal of another individual (No. 4680, U. S. N. M.) is somewhat eroded, but otherwise resembles very closely the above mentioned vertebra.

Twenty-first Caudal—Not represented in the collection.
Hæmapophyses

Three small chevron bones, which unfortunately were not associated with the corresponding caudal vertebrae, were found in close proximity to portions of the right and left mandibles and a fragment of a scapula of *Zygorhiza kochii* (No. 4673, U. S. N. M.), and nearby were twenty-four consecutive vertebrae belonging to a skeleton of *Basilosaurus cetoides* (No. 4675, U. S. N. M.).

All of the caudal vertebrae of *Zygorhiza kochii*, with the exception of those at the hinder end of the tail, articulate with chevron bones. At the anterior end of the caudal series, the facets for articulation with the chevron bones are more widely separated than near the hinder end of the series. All three of these chevron bones are Y-shaped and the proximal ends of each arm are expanded, thus increasing the area for the facets which articulate with a pair of prominences (hypapophyses) on the hinder end of the ventral surface of the centrum.

In terrestrial mammals and Recent cetaceans, these chevrons serve to provide a larger surface for attachment of the inferior muscles of the tail and also to protect the caudal blood-vessels, which run within the canal formed by this series of bony arches. In the odontocetes, these chevrons reach their highest development near the anterior end of the series, but are never present beneath the hinder rudimentary caudal vertebrae. At the anterior end of the series, there is a marked tendency toward the lengthening of the arms of each chevron, and a reduction of the hæmal spine. In many Recent odontocetes, the sixth or seventh chevron, counting backward from the anterior end of the series, has the longest hæmal spine. With the progressive narrowing of the caudal vertebrae toward the hinder end of the series and the correlated approximation of the right and left facets for articulation with the chevron bones, the two arms of each chevron approach each other more closely at their upper ends and the hæmal spines are more noticeably broadened antero-posteriorly. Behind the middle of the series, there is a gradual reduction in the size of the chevrons, although the hæmal spines usually remain relatively broad.

The chevron (fig. 69) which is identified as the second or third in the series has elongated slender arms inclosing a high hæmal canal, and the slightly developed hæmal spine ends in a transverse keel. The hæmal spine measures 30 mm. transversely. The upper
ends of the arms are more noticeably expanded transversely than antero-posteriorly and the slightly convex articular facets slope obliquely from the external to the internal margins.

The two remaining chevrons have short laterally compressed hemal spines and somewhat shorter arms. The larger (fig. 70) of these two chevrons probably belongs behind the middle of the series. The two arms are slightly wider antero-posteriorly than the above described chevron, but are shorter and inclose a broad V-shaped hemal spine, and below their union is a thick elongated hemal spine which is bluntly truncated ventrally. The upper end of each arm is conspicuously expanded transversely, particularly on the anterior half. The articular surface is convex antero-posteriorly and slopes obliquely from external to internal margin.

The smaller chevron probably belongs near the hinder end of the series, since it has short and unusually broad arms inclosing a broad V-shaped hemal canal, and a short, broad, and robust hemal spine. The ventral edge of this hemal spine is eroded. The articular facet on the proximal end of each arm is elongated antero-posteriorly and slopes obliquely downward from external to internal margin.

<table>
<thead>
<tr>
<th>Table 40—Measurements (in millimeters) of the hemapophyses</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Maximum vertical diameter</strong></td>
</tr>
<tr>
<td>Minimum antero-posterior diameter of left arm</td>
</tr>
<tr>
<td>Minimum antero-posterior diameter of right arm</td>
</tr>
<tr>
<td>Distance between outside margins of upper articular facets</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of upper articular facet</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of hemal spine</td>
</tr>
</tbody>
</table>

1 Estimated.

FORELIMB

The general build of the forelimbs is rather stout. The joints distad of the ball-and-socket shoulder joint have not lost their synovial character and become wholly fibrous. Thus, unlike in Recent cetaceans, there is no evidence to indicate that the part of the forelimb that projects beyond the contour of the thorax is appreciably stiffened by fibrous interosseous tissue. The scapula is comparatively high, its vertical diameter being noticeably greater than the length of the humerus. In proportion to the length of the forelimb, the humerus of Zygorhiza kochii is much shorter and more robust than that of Basilosaurus cetoides. Granting that the reconstruction of the manus (pl. 1, B) is approximately correct, the humerus comprised about one-fourth of the functional length of the arm, that is the distance from tip of longest digit to proximal end of radius, plus length of humerus from trochlea to head. Both bones in the forearm are laterally flattened. When placed in their natural positions in relation to the trochlea of the humerus, a hinged and non-rotary type of elbow joint is formed. The carpal bones, judging from the two that are known, are completely ossified, somewhat compressed in a dorso-plantar direction, and possess distinct articular surfaces for articulation with the adjacent carpals. This indicates that the synovial type of articulation had not as yet been entirely lost by the carpals and that the movements of the individual bones had not been greatly restricted by connecting fibrous elastic tissue. The slender metacarpals and phalanges are rather long. The articulation of the ends of the bones in the digits is of the ball-and-socket type.

SCAPULA

Portions of two scapula show the essential characters of this bone. One of these (No. 4673, U.S. N.M.), though fractured, consists of the major portion of the anterior
half of the blade, and the other (No. 4748, U. S. N. M.) a few isolated fragments, one of which comprises the hinder border of the blade.

The scapula of *Zygorhiza kochi* seems to be much narrower, proportionately, than that of *Basilosaurus cetoides*. In general configuration, it resembles somewhat the scapula of *Dorudon stromeri* (Stromer, 1908b, pl. 5, fig. 4). The prescapular portion of the blade (fig. 71) is rather large, the anterior edge is slightly curved, and the anterior angle is abruptly truncated. A prominent crest, which extends upward from the base of the acromion to the vertebral edge, separates the prescapular fossa from the larger post-scapular fossa. The elongated acromion is thin, flat, and curved upward and forward. The coracoid process is destroyed. The shallowly concave glenoid cavity has a flattened outer border and a convex inner border. The hinder angle of the blade (fig. 71) is prolonged backward, and the hinder edge of the blade is slightly curved.

![Fig. 71—Zygorhiza kochi (Reichenbach). Left scapula partially restored, No. 4673, United States National Museum. X 4. ac., acromion; c.pr., coracoid process. Upper Eocene, upper Jackson formation, Alabama.](image)

The measurements of the left scapula (No. 4673, U. S. N. M.) are as follows: Greatest vertical diameter, articular head to vertebral margin, 238 + mm. (when complete, estimated, 252 ± mm.); length of acromion, superior margin at base to distal end, 96 mm.; greatest diameter of acromion near distal end, 37 mm.; greatest antero-posterior diameter of articular head, 60 mm.; and greatest transverse diameter of articular head, 50.5 mm.

**Humerus**

With the exception of the proximal end, which is missing, the general form of the right humerus (No. 4679, U. S. N. M.) is somewhat similar to the humeri referred to *Dorudon sitteli* (Nos. 11951a, 11417b, Stuttgart), but differs in that the backward swelling of the distal portion of the shaft is less pronounced. Viewed from behind, the upper three-fourths of the shaft is seen to be strongly bent inward. Viewed from the side (fig.
72), the backward expansion of the posterior face begins immediately above the distal one-fourth of the shaft and the deltoid crest rises abruptly at its distal end. The distal rounded angle of the deltoid crest is about 98 mm. distant from the center of the distal face of the trochlear surface, while the posterior face of the shaft begins to swell out 74 mm. above the same point. At the distal end of the anterior face of the shaft (fig. 73a) and external to the low distal continuation of the deltoid crest is the shallow coronoid fossa. Anteriorly the trochlear surface extends upward to the edge of the epiphysis. The outer condyle projects distally beyond the level of the inner condyle. The capitulum is not differentiated from the trochlea, the combined surfaces being shallowly con-

cave transversely and describe a semicircle anteroposteriorly. The outer portion of this trochlear surface, which corresponds to the capitulum, is extended upward posteriorly (fig. 73c) as a narrow flattened tongue whose maximum width does not exceed 13 mm., while the inner posterior trochlear surface, although depressed along the median vertical line below the tongue-like upward extension of the capitulum, slopes obliquely backward and inward. This structural peculiarity of the trochlea, resting as it does on the inner border of the greater sigmoid cavity of the ulna, seems to constitute a mechanical safeguard against the elbow joint being dislocated. The small olecranon fossa at the distal end of the posterior face of the shaft is shallow and terminates in a small pit above the tongue-like upward extension of the capitulum.
The measurements of this humerus are as follows: Greatest length, estimated, 230 ± mm.; antero-posterior diameter of shaft through distal portion of deltoid crest, 74 mm.; transverse diameter of shaft at same level, 33 mm.; least antero-posterior diameter of distal end of shaft, internal side, 40.5 mm.; maximum transverse diameter of distal end of shaft, 46.5 mm.; antero-posterior diameter of outer condyle, 41.5 mm.; antero-posterior diameter of inner condyle, 44.5 mm.; and maximum transverse diameter of combined trochea and capitulum, 33 mm.

Lydekker (1893, p. 559) states that the humerus in Teyler’s Museum, Haarlem, measures 8.6 inches (= 218.5 mm.).

**Radius**

The radius (No. 4679, U. S. N. M.) comprises less than one-fifth of the arm length, thus agreeing in this detail with the proportions of this element in the arm of the seal, *Zalophus*. The most significant feature of this bone (fig. 72) is the pronounced antero-posterior expansion of the shaft at the level of the distal end of the proximal one-third of its length. An elliptical rugose area, presumably for the insertion of the pronator teres, covers the anterior surface of the angle thus formed. The broad shallow groove, which crosses obliquely the anterior and internal surfaces of the proximal end of the radius, may have marked the course of some tendon. A small tuberosity is developed on the antero-internal angle of the shaft near the proximal end. The shaft of the radius is flattened laterally, although the external and internal surfaces are somewhat convex and its anterior and posterior margins are fairly sharp. The posterior portion of the distal end of the shaft is twisted outward. On the external surface of the distal end of the shaft is a broad shallow oblique groove, which may mark the position of the flexor muscles.
of the digits. The distal end of the shaft is occupied by a triangular anterior facet for the scaphoid and a much larger quadrangular posterior facet for the lunar, the two facets being separated by a pronounced sharp-edged transverse crest.

The proximal end of this radius is occupied by a large articular surface which is considerably wider transversely than antero-posteriorly. It is strongly concave antero-posteriorly and slightly convex transversely. The outer area for articulation with the capitulum of the humerus is not sharply differentiated from the inner surface for the trochlea. The last-mentioned facet does not extend over upon the internal surface of the proximal epiphysis as in Zalaphus and hence the elbow joint was not so well-perfected mechanically. The entire circumference of the proximal epiphysis is rugose, which in turn suggests the presence of a capsular cartilage enveloping the elbow joint.

This radius differs from the one tentatively referred to Dorudon stromeri (No. 11239, Stuttgart; Stromer, 1908b, pl. 5, figs. 10, 11) in the greater expansion of the shaft at the level of the anterior angle, the wider grooved surface for a tendon, and the absence of hollowed-out surfaces on the posterior face of the proximal end for articulation with the ulna.

The measurements of this radius are as follows: Greatest length, 157.5 mm.; antero-posterior diameter of proximal facet, 24.5 mm.; transverse diameter of proximal facet, 34 mm.; transverse diameter of proximal end of shaft, 31.5 mm.; greatest antero-posterior diameter of shaft at angle, 44.5 mm.; least antero-posterior diameter of shaft below angle, 32 mm.; antero-posterior diameter of distal epiphysis, 38.5 mm.; and transverse diameter of distal epiphysis, 20.6 mm.

**Ulna**

The shaft of the ulna (No. 4679, U. S. N. M.) is laterally flattened and is faintly bowed outward from end to end. The anterior and posterior edges of the shaft are fairly sharp. The olecranon (fig. 72) is rather broad and relatively short; its upper border is quite rugose. The transverse diameter of the greater sigmoid cavity is greater distally than proximally. The external margin of this cavity curves from end to end, but the internal margin is deeply notched; the short narrow groove, which leads inward, stops short of the rather deep pit which is located medially on the anterior face. This pit in conjunction with the above-mentioned notch divides the greater sigmoid cavity into an upper and a lower articular surface. The radial facet is limited to a rather rough concavity on the anterior face immediately below the distal edge of the greater sigmoid cavity. The distal surface of the lower epiphysis is largely occupied by an elongated concave facet for the ulnare. An oblique facet for articulation with the end of the radius is present on the anterior face of this epiphysis. The presence of a small facet on the posterior face of this epiphysis indicates that a pisiforme was present in the corpus.

This ulna differs from the one tentatively referred to Dorudon stromeri (No. 11239, Stuttgart; Stromer, 1908b, pl. 5, figs. 14, 26) in having an olecranon with a more upturned anterior margin and a slightly slenderer shaft.

The measurements of this ulna are as follows: Greatest length, 197.5 mm.; antero-posterior diameter of proximal end of olecranon, 60 ± mm.; length of anterior margin of olecranon, proximo-anterior angle to edge of greater sigmoid cavity, 37.5 mm.; length of greater sigmoid cavity, 33.8 mm.; transverse diameter of distal portion of greater sigmoid cavity, 30 mm.; length of anterior face of shaft below greater sigmoid cavity, 141 mm.; least antero-posterior diameter of shaft below greater sigmoid cavity, 33.5 mm.; greatest antero-posterior diameter of shaft at distal end, 42.3 mm.; greatest transverse diameter of shaft at distal end, 18.2 mm.; and antero-posterior diameter of facet for ulnare, 25 mm.
CARPUS

Although most of the elements are missing, there is no reason to assume that the carpus (fig. 74) is characterized by any unusual structural peculiarities. On the contrary, it would appear that the carpus conformed to the basic ground-plan of that of living odontocetes. The distal articular surface of the radius is divided into two distinct facets by a nearly median transverse crest. This in turn confirms the presence of an internal scaphoid and an external lunar. The direction and position of the facets on the distal end of the radius for these two carpals indicates that these two bones were separate and not ankylosed. The existence of a free centrale is of course conjectural. On the distal end of the ulna, there is a large internal facet for the cuneiform (ulnare) and a smaller oblique outer facet which no doubt articulated with the pisiform. Two carpal bones, which unquestionably belong in the distal row, and three metacarpals were associated with this right forelimb (No. 4679, U. S. N. M.). In reconstructing the carpus of this archaeocete the radius and ulna, two of the carpal bones, and three of the metacarpals were compared with those of fossil insectivores and carnivores and with Recent pinnipeds and odontocetes. The structural possibilities of the archaeocete carpus seem to be rather limited in view of the peculiarities presented by the elements which have been preserved.

The larger of the two carpal elements associated with this specimen is considered to be the unciniform, since its two distal facets articulate in a normal manner with corresponding facets on the proximal ends of the fourth and fifth metacarpals. This allocation must of course be considered as tentative until a complete carpus is found. Viewed from in front this carpal is pentagonal in outline. The slightly concave facet for articulation with the cuneiform is almost twice as large as any one of the other facets and occupies the entire proximal surface. The outer face is flattened and sub-quadrangular in outline. The internal facet for articulation with the magnum is the smallest articular surface and slopes obliquely downward and forward. The two distal facets are subequal in size and separated by a transverse crest. The internal of these two facets is strongly oblique, while the external one is almost horizontal. The dorsal and plantar faces are pitted and somewhat rugose. The measurements of the unciniform are as follows: Maximum transverse diameter, 22.6 mm.; maximum vertical diameter, 16.2 mm.; and maximum dorso-plantar diameter, 15.2 mm.

The second carpal element is either the magnum or the trapezoid. The position of the facets agrees with the assumed relation of the elements articulating with the magnum and it is therefore tentatively identified as such. Viewed from in front, this carpal is hexagonal in outline. Of the two distal facets, the outer one is the smaller. This outer facet slopes obliquely upward and articulates with the corresponding portion of the head of the fourth metacarpal. The internal of the two distal facets is almost horizontal and articulates with the head of the third metacarpal. There is a smaller rounded outer facet for articulation with the unciform. The two proximal facets slope obliquely upward to the strong transverse crest which separates them. The outer of these two facets is the larger and articulated presumably with the lunar, while the internal...
of these facets is more concave and articulated presumably with the centrale. The internal facet for articulation with the trapezoid is nearly square and is flattened. The measurements of the magnum are as follows: Maximum transverse diameter, 19.6 mm.; maximum vertical diameter, 15.4 mm.; and maximum dorso-plantar diameter, 14.8 mm. Thus it is quite probable that the trapezoid and the trapezium each articulated with a single metacarpal, the second and the first.

The carpus as reconstructed (pl. 1, B) has the usual creodont characters of separate scaphoid, lunar, and centrale, large cuneiform (ulnare), small magnum, large unciform, and the normal discrepancy in size of the trapezoid and trapezium.

**Digts**

The relative lengths of the metacarpals and the proximal phalanges (fig. 74) indicate that the digits were relatively longer than those of the Recent sea-lion (*Eumetopias stelleri*). The extent and convexity of the articular surfaces on the distal extremities of the metacarpals lead one to conclude that the digits retained a considerable mobility as contrasted with those of Recent pinnipeds and odontocetes. The metacarpals are assumed to be five in number, which progressively decrease in length from the first to the fifth. On the basis of tentative allocations, the three metacarpals associated with the right forelimb (No. 4679, U. S. N. M.) are identified as the second, fourth, and fifth.

The shaft of the second metacarpal is distinctly constricted near the middle, flattened in a dorso-plantar direction, and somewhat bowed upward from end to end. The large proximal surface for articulation with the trapezoid is faintly convex from the plantar to the dorsal margin and concave from side to side, but does not occupy the entire head. Internally there is a fairly large facet, with maximum side to side diameter of 8.5 mm., which curves over upon the inner-lateral surface of the head. This facet presumably articulated with the trapezium. Below this facet and on the inner-lateral surface of the shaft is a subtriangular facet 7 mm. in length which must have articulated with the head of the first metacarpal. A fairly large irregular proximal facet is present on the outer-lateral surface of the shaft for articulation with the head of the third metacarpal. The distal articular surface occupies the lateral and distal surfaces of the epiphysis, the dorsal and plantar surfaces of the epiphysis being slightly roughened. The measurements of the second metacarpal are as follows: Maximum length, 63 mm.; transverse diameter of proximal end, 19.7 mm.; transverse diameter of distal end, 15.2 mm.; and least transverse diameter of shaft, 8.8 mm.

The shaft of the fourth metacarpal is less noticeably constricted near the middle than that of the second metacarpal, not very strongly bowed upward, but distinctly flattened in a dorso-plantar direction. There are two distinct facets on the proximal end of this metacarpal which are separated by an oblique crest that extends obliquely from the dorsal to the plantar margin. The internal facet is considerably smaller than the outer facet and descends obliquely to the internal margin. This facet presumably articulated with the magnum. Below this facet on the inner-lateral surface of the shaft is a large rugose area (11 × 8 mm.). The outer facet on the proximal surface is concave from side to side and articulates with the unciform. The ovoidal facet on the distal end is convex in two directions, but oblique in position with reference to the longitudinal axis of the shaft. The measurements of the fourth metacarpal are as follows: Maximum length, 53.6 mm.; transverse diameter of proximal end, 15 mm.; transverse diameter of distal end, 15 mm.; and least transverse diameter of shaft, 9.8 mm.

The fifth metacarpal is noticeably shorter than the other metacarpals and is characterized by the lateral expansion of the head. The shaft of this metacarpal is strongly flattened in a dorso-plantar direction, the nearly straight internal face is sharp-edged, and the rounded outer face is strongly curved. The internal half of the articular sur-
face on the proximal end for articulation with the unciform is concave and a relatively large oblong prominence is formed on the outer half. The distal end is strongly swollen and furnished with a large convex facet for articulation with the corresponding phalanx. The measurements of left fifth metacarpal are as follows: Maximum length, 42.2 mm.; transverse diameter of proximal end, 16.4 mm.; transverse diameter of distal end, 13.7 mm.; and least transverse diameter of shaft, 14.8 mm.

The four proximal phalanges are tentatively identified as belonging to the first, second, fourth, and fifth digits. The plantar surfaces of these phalanges are curiously ornamented with closely approximated longitudinal fine striae. The quite slender proximal phalanx of the first digit has a swollen head and a dorso-plantar flattened distal end. The shaft is gradually attenuated from the head toward the laterally expanded distal end. The plantar surface of the shaft is quite flat, but the dorsal surface is strongly convex. A large concave articular surface occupies the entire proximal end. The distal end is conspicuously flattened in a dorso-plantar direction and is furnished with a nearly flat elongated distal articular surface.

The proximal phalanx of the second digit is represented by a 23 mm. long section of the proximal end of the shaft. The anterior portion of the head is eroded, but the remainder is well preserved. The large concave articular surface occupies the entire proximal end. The shaft appears to have been attenuated toward the distal end.

The proximal phalanx of the fourth digit has a laterally expanded head, and the shaft is gradually attenuated toward the distal end. The plantar surface is quite flat and the dorsal face is strongly convex. The concave articular surface on the proximal end curves upward to an elevated protuberance on the outer border. The distal end is damaged but was obviously similar to that of the corresponding phalanx of the first digit.

The proximal phalanx of the fifth digit, if correctly allocated, is conspicuously longer than the corresponding phalanx of the Recent sea-lion (Eumetopias). It likewise has a swollen head and a shaft that is attenuated toward the distal end. The distal articular end, however, is destroyed. A large rounded concave articular surface occupies the entire proximal end of the shaft.

<table>
<thead>
<tr>
<th>Table 41—Measurements (in millimeters) of the proximal phalanges</th>
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</thead>
<tbody>
<tr>
<td>Minimum length.</td>
</tr>
<tr>
<td>Transverse diameter of proximal end.</td>
</tr>
<tr>
<td>Transverse diameter of distal end.</td>
</tr>
<tr>
<td>Least transverse diameter of shaft.</td>
</tr>
</tbody>
</table>

RIBS

For one large individual (No. 4679, U. S. N. M.), the anterior six of the fifteen consecutive ribs (pl. 17) from the left side of the thorax lack the proximal end of the shaft, extending from below the tuberculum to the capitulum, but the nine hinder ones are essentially complete. On the right side, there are preserved the distal portions of the shafts of the four anterior ribs, the proximal end of the shaft, including the tuberculum and the capitulum, of the fifth rib, the distal third of the shaft of the sixth rib, and the whole or the major portions of the nine hinder ribs.

For another smaller individual (No. 4678, U. S. N. M.) fourteen ribs, four of which are nearly complete, represent all the ribs with the exception of the seventh on the right
side of the body. On the left side the fourth rib is missing and eleven of the remaining fourteen are almost complete.

The shafts of the five anterior ribs on each side of the thorax are conspicuously expanded antero-posteriorly above the distal end, forming a club-like enlargement, and the proximal half of the shaft is strongly flattened antero-posteriorly. Occasionally, the distal end of the first rib (pl. 16, fig. 5) may be somewhat cylindrical (No. 4678, U. S. N. M.). The distal enlargement of the shafts of the anterior ribs progressively diminishes behind the second, on which this tendency is most marked, to about middle of series, behind which it is barely perceptible. As contrasted with the anterior ribs, the middle portions of shafts of the eighth pair of ribs are more nearly sub-triangular in cross-section.

Of the fifteen pairs of ribs, the first are the shortest. The ribs rapidly increase in length from the first to the sixth, which is the longest, and then decrease in length toward the hindermost pair of ribs. The distal ends of all except the hindermost pair of ribs are pitted and roughened, presumably for the attachment of cartilaginous sternal ribs.

The shafts of the ribs are curved, twisted, and bowed outward to a varying extent in conformity with their respective positions in the thoracic wall. The shafts of the eight anterior pairs of ribs are bowed strongly outward; this curvature, however, reaches its maximum development on the fourth pair of ribs. The proximal portions of the fourth to the eighth ribs are bent rather sharply downward at the level of the tuberculum. The angle formed by the downward bending of the proximal end of the shaft at the level of the angulus costae becomes less and less acute behind the eighth rib, and disappears entirely on the twelfth rib.

The first rib has the thickest neck and the largest tuberculum. The capitulum of the fifth rib is borne on a long slender neck, which presumably is the longest in the series. On both sides of the thorax each of the first eight ribs has a capitulum, which articulates in part with a definite facet on the antero-superior angle of lateral face of centrum of corresponding dorsal vertebra and in part with another facet on the poster-superior angle of the preceding centrum, as well as a tuberculum which articulates with a facet on the end of the diapophysis. The tenth rib has a closely approximated capitulum and tuberculum which articulate with paired articular facets on extremity of transverse process of tenth dorsal vertebra. The twelfth to the fifteenth ribs, inclusive, have a single articular head. The three hinder ribs on the right side are certainly longer than the corresponding ribs on the left side.

First Rib—The shaft (No. 4679, U. S. N. M.) is relatively short, flattened antero-posteriorly between the middle of its length and the capitulum, and is curved or bowed outward. The lower half of the shaft is twisted so that the edge which is ventral on the proximal third of the shaft now looks forward. The shaft is conspicuously expanded above the distal end.

In the case of a smaller individual (No. 4678, U. S. N. M.), the distal end of the shaft is oval in cross-section, the outer face is flattened, the upper two-thirds of the rather wide shaft is antero-posteriorly compressed and dorso-ventrally widened, the angle is pro-
tuberant, and the large tuberculum (33.8 X 19.5 mm.) is separated from the small capitulum (19.8 X 16.7 mm.) by an interval of 13 mm. The short neck is conspicuously widened in a dorso-ventral direction. The measurements of this right rib are as follows: Greatest length, 256.5 mm.; posterior face of tuberculum to extremity of capitulum, 62.5 mm.; greatest diameter of distal club, 28.5 mm.; greatest width of shaft at level of angle, 39 mm., and thickness at the same level, 11 mm.

Second Rib—This rib (No. 4679, U. S. N. M.) is somewhat longer, the expansion of the shaft near the distal end is more pronounced, the upper portion of the shaft is
slightly narrower, and the outward torsion of the distal end is more marked than on the first rib.

Fig. 75—_Zygophyllum kochii_ (Reichenbach). Lateral views of ribs. No. 4679, United States National Museum. X 4.

6r., 5th rib, right; 13 l., 13th rib, left; 3 l., 3d rib, left;
7 l., 7th rib, left; 8 l., 8th rib, left; 9 l., 9th rib, left.
Upper Eocene, upper Jackson formation, Alabama.

The second rib on the right side of a smaller individual (No. 4678, U. S. N. M.) is somewhat shorter and less robust; the measurements are as follows: Length, from below tuberculum to extremity, 290 mm.; greatest diameter of distal club, 32.7 mm.; greatest width of shaft between tuberculum and angle, 31.2 mm., and thickness at same level, 12 mm.

Third Rib—It (No. 4679, U. S. N. M.) is characterized by a much longer and more strongly curved shaft (fig. 75), and a longer antero-posteriorly expanded distal portion.
The hinder edge of the distal third of the shaft is twisted inward, so that the edge which is dorsal above the angle now looks backward.

The third rib of a smaller individual (No. 4678, U. S. N. M.) has the upper end of the shaft turned rather abruptly downward, forming a strong curve between the poorly defined angle and the tuberculum; the anterior face of the flattened shaft is slightly convex and the hinder face is shallowly concave. The tuberculum (27.5 × 17.2 mm.) is rather large. For this rib the measurements are: Greatest diameter of distal club, 35 mm.; greatest width of shaft between tuberculum and angle, 30 mm., and thickness at same level, 11.3 mm.

Fourth Rib—This rib (No. 4679, U. S. N. M.) has a slender and strongly curved shaft, which is less noticeably expanded antero-posteriorly near the distal end, but the backward torsion of the lower half of the shaft is approximately the same as on the third rib. Owing to the twisting of the shaft, the face which proximally looks forward becomes the outer face distally; this surface is convex. The corresponding opposite face, hinder above and inner below, is distinctly flattened. The greatest width of the shaft between the tuberculum and the angle is 28 mm., and the thickness at the same level is 15.3 mm.

The fourth rib of the smaller individual (No. 4678, U. S. N. M.) is similarly curved and the greatest diameter of its distal expansion is 34.3 mm.

Fifth Rib—The slender and strongly curved shaft, which is less noticeably expanded distally than that of the fourth rib, characterizes the fifth rib (No. 4679, U. S. N. M.). The capitulum (fig. 75) of the right rib is borne on a long neck, and the tuberculum forms a low concave protuberance. Between the tuberculum and the angle, a distance of 55 mm., the shaft is nearly straight, the neck is turned sharply downward, and the lower portion of the shaft is strongly curved. The tuberculum (26.5 × 13 mm.) is separated from the capitulum (22.5 × 22 mm.) by an interval of 28 mm. The minimum width of the neck is 21 mm. and the minimum thickness is 13 mm. The torsion or backward twisting of the distal fourth of this rib is rather slight.

In the smaller individual (No. 4678, U. S. N. M.) this rib has a narrow, elongated tuberculum (25.5 × 14 mm.), separated by an interval of 17.5 mm. from a deeply pitted capitulum (maximum diameter, 25.5 mm.). The minimum width of the neck is 23.5 mm. and the minimum thickness, 14.5 mm. Although the upper half of the shaft is strongly flattened antero-posteriorly, it becomes ovoidal in cross-section near the middle of its length.

Sixth Rib—This rib (No. 4679, U. S. N. M.) is the longest in the series, the shaft is strongly bowed outward, and it is moderately expanded near the distal end. The angle is rounded, bending over the anterior face of the shaft, and is 40 mm. distant from the tuberculum. Although the shaft exhibits a decided convex curvature from the tuberculum to the distal end, the distal half is also curved backward and inward. The minimum width of the shaft above the middle of its length is 20 mm., the greatest width between the tuberculum and the angle is 29.5 mm. and the thickness at the same level is 15.3 mm.

The sixth rib of the smaller individual (No. 4678, U. S. N. M.) has a rather acute anterior edge on the lower two-thirds of the length of the shaft, and on the middle third of its length the hinder face is rather broad and flat. The minimum width of the shaft near the middle is 18 mm., the greatest width between the tuberculum and the angle is 30 mm., and the thickness at the same level is 15.4 mm.

Seventh Rib—It (No. 4679, U. S. N. M.) is shorter than the sixth, the shaft is more strongly curved, but its distal portion is not noticeably widened antero-posteriorly. The capitulum is placed obliquely on the end of the robust neck and is subtriangular in outline. The tuberculum is reniform in outline and is located on a low protuberance, which is
more elevated posteriorly than anteriorly. The tuberculum (28 × 14.2 mm.) is separated by an interval of 18.5 mm. from the rugose capitulum (maximum diameter, 28.5 mm.). The shaft (fig. 75) as a whole is more slender than those of the preceding ribs and the transversely flattened distal end is rather thin. The torsion or backward twisting of the distal end of this rib is more pronounced than on the preceding rib. The angle bends over the anterior face of the shaft at a point 50 mm. distant from the tuberculum. The hinder face of the rib between the capitulum and a point 40 mm. beyond the tuberculum is deeply concave in dorso-ventral direction, while the corresponding portion of the anterior face is convex. At the level of the angle, however, the anterior face is grooved for a short distance.

The seventh rib of the smaller individual (No. 4678, U. S. N. M.) has the middle portion of the shaft nearly circular in cross-section and the distal fourth of the shaft is narrower than the middle portion.

**Eighth Rib**—This rib (No. 4679, U. S. N. M.) has a rather wide and short neck on which the large tuberculum (31 × 15 mm.) is separated from the capitulum (29 × 19.5 mm.) by an interval of 15 mm. The shaft (fig. 75) is slender and bowed outward, and the widening of the shaft above the thin distal end is rather slight. The angle bends over the anterior face of the shaft at a point 55 mm. distant from the tuberculum. The hinder face of the rib between the capitulum and a point 30 mm. beyond the tuberculum is deeply concave in a dorso-ventral direction, while the corresponding portion of the anterior face is convex. There is a shallow groove on the anterior face in the region of the angle. The shaft of this rib is less noticeably twisted than that of the seventh; the proximal third is compressed antero-posteriorly and the distal third transversely.

The eighth rib of the smaller individual (No. 4678, U. S. N. M.) has a more deeply pitted capitulum, a less concave hinder face in the region of the tuberculum, and a much narrower and slenderer shaft.

**Ninth Rib**—The shaft (fig. 75) is less bowed outward than that of the eighth rib. This rib (No. 4679, U. S. N. M.) has the laterally compressed tuberculum (28 × 18.5 mm.) and capitulum (26.5 × 18 mm.) separated by an interval of less than 10 mm., although there is no distinct neck. These facets articulate with two closely approximated facets on the ninth dorsal. The angle is rather weak and is located 45 mm. beyond the tuberculum. The hinder face of the rib between the capitulum and a point 38 mm. beyond the tuberculum is shallowly concave in a dorso-ventral direction, and the corresponding portion of the anterior face is convex.

The ninth rib of the smaller individual (No. 4678, U. S. N. M.) has a very light and slender shaft without any obvious distal enlargement, a rather prominent angle, a deeply pitted capitulum, and narrow oblique grooves on the anterior face of the neck. The measurements of this rib are as follows: Greatest length in a straight line, 452+ mm.; posterior face of tuberculum to extremity of capitulum, 37.5 mm.; and greatest width of shaft between tuberculum and angle is 25.5 mm.

**Tenth Rib**—This rib (No. 4679, U. S. N. M.) has no distinct neck, although the ovoidal tuberculum (27.5 × 17.5 mm.) is separated from the capitulum (22 × 19 mm.) by an interval of 7 mm. The weak angle is located 48 mm. beyond the tuberculum. The proximal third of the shaft is flattened antero-posteriorly, while the distal third is transversely flattened. The torsion or backward twisting of the distal end is more pronounced than on the preceding rib.

**Eleventh Rib**—The twisting of this rib (No. 4679, U. S. N. M.) is more pronounced on the proximal one-fourth than near the distal end. On the left rib the tuberculum (22.5 × 17 mm.) is separated from the capitulum (19.5 × 17 mm.) by an interval of 6.5 mm. On the right rib the tuberculum and capitulum form a continuous surface. The weak angle
is located 48 mm. beyond the tuberculum. The hinder face of the rib between the capitulum and the angle is shallowly concave, while the corresponding portion of the anterior face is convex. The antero-posterior width (21.5 mm.) of the shaft about 100 mm. above the distal end is almost twice that of the extremity (12.5 mm.).

The eleventh rib of the smaller individual (No. 4678, U. S. N. M.) has the proximal third of the shaft more strongly twisted forward, a relatively smaller head, a more prominent angle, and a relatively slender shaft without any perceptible distal enlargement. The measurements of this rib are as follows: Greatest length in a straight line, 406+ mm.; antero-posterior diameter of articular head, 32 mm.; and greatest width of shaft between tuberculum and angle, 26.5 mm.

Twelfth Rib—This single headed rib (No. 4679, U. S. N. M.) has a strongly twisted shaft. The upper end, beginning below the angle, is bent forward while the dorsal portion of the articular head is twisted backward. The proximal third of the shaft is antero-posteriorly flattened. Owing to the torsion of the distal half of the shaft, the edge which is dorsal on the proximal third becomes the hinder one distally, and likewise the ventral edge above becomes the anterior edge below. The shaft is more strongly bowed outward and the proximal end is less abruptly bent downward above the level of the angle than on the preceding rib. The articular head (36.8 × 20.5 mm.) of the rib on the left side is not constricted medially, but the one (37.5 × 20 mm.) on the right side is distinctly constricted near the middle of its length. The rather prominent angle is located 45 mm. beyond the tuberculum. A short longitudinal depression extends outward on the hinder face of the rib from the head to near the angle. As compared to the width of the roughened extremity (18.5 mm.), the antero-posterior widening of the shaft (21 mm.) about 100 mm. above the distal end is very slight.

The torsion of the twelfth rib of the smaller individual (No. 4678, U. S. N. M.) is quite similar to that described above, but the shaft is slenderer and it also lacks the groove on the hinder face above the level of the angle.

Thirteenth Rib—The torsion of this rib (No. 4679, U. S. N. M.) is essentially the same as that of the twelfth rib. The upper portion of the elongated articular head (right, 38 × 21.5 mm.; left, 38.2 × 20.3 mm.) is strongly twisted backward. The angle (fig. 75) is located 42 mm. beyond the head, but is not very prominent. On the right rib, the width (15.3 mm.) of the transversely flattened extremity is considerably less than the antero-posterior diameter (22 mm.) of the shaft about 80 mm. above the distal end.

The thirteenth rib of the smaller individual (No. 4678, U. S. N. M.) is more strongly curved from end to end and the entire shaft is quite slender.

Fourteenth Rib—The shaft (No. 4679, U. S. N. M.) is slightly shorter than that of the thirteenth rib and the outward bowing is approximately the same. The single articular head (right, 37 × 19; left, 36.5 × 17 mm.) is elongated antero-posteriorly and its upper end is strongly twisted backward. As compared to the preceding rib, the upper portion of the shaft is less noticeably bent forward, the middle portion of the shaft is likewise sub-triangular in cross-section, and the angle is represented solely by the scar for the ilio-costalis muscle. On the right rib, the width (15.5 mm.) of the transversely flattened extremity is considerably less than the antero-posterior diameter (20.5 mm.) of the shaft about 105 mm. above the distal end.

On the fourteenth rib of the smaller individual (No. 4678, U. S. N. M.), the maximum diameter of the shaft between the angle and the head hardly exceeds the maximum antero-posterior expansion near the distal end.

Fifteenth Rib—This rib (No. 4679, U. S. N. M.) has an elongated articular head (29 × 16.5 mm.), a twisted and slightly outward bowed shaft, and a scar for the ilio-costalis muscle located about 40 mm. below the head. The articular head is placed largely on the hinder face of the proximal end of the shaft.
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The hindermost rib (pl. 16, fig. 6) of the smaller individual (No. 4678, U. S. N. M.) has a rather peculiar curvature. Below the scar for the ilio-costalis muscle, the shaft as a whole is bowed outward, but above this scar the proximal end curves upward. The proximal end of the shaft is not bent forward; the distal third of the shaft is twisted at an angle of 45 degrees to the vertical axis of the upper end. The maximum width (19.5 mm.) above the distal end is considerably greater than the minimum dorso-ventral diameter (11.5 mm.) of the shaft between the angle and the articular head. The scar for the ilio-costalis muscle is located 75 mm. below the head and the total length of the right rib is 327 + mm.

**STERNUM**

In so far as our present knowledge goes, the sternum of *Zygorhiza kochii* seems to be similar to that of *Basilosaurus cetoides*. The material representing the sternum is very scanty and is limited to a manubrium (No. 12063, U. S. N. M.) and a first segment of the mesosternum (No. 4748, U. S. N. M.). The manubrium (pl. 14, fig. 3) is clearly pathological, as it is asymmetrical in outline, and the antero-external angles have been deformed by exostosis, forming prominent elongated processes. In contrast to that of *B. cetoides*, this manubrium is broader than long. The eroded dorsal surface seems to have been somewhat convex originally, the lateral surfaces slope obliquely from the dorsal to the ventral surface, and the much smaller ventral surface is more or less flattened. The hinder end is likewise deformed; it is convex from side to side, roughened by deep pits, and has a median ventral backward projection. The measurements of this manubrium are as follows: Antero-posterior diameter medially, 73 mm.; transverse diameter anteriorly, including lateral processes, 100 mm.; transverse diameter posteriorly, 65.8 mm.; dorso-ventral diameter medially, 51.6 mm.; and dorso-ventral diameter posteriorly, 40 mm.

After this portion of the text had gone to the printer, the manubrium and a mesosternal segment of an adult individual [see (20), referred specimens] were loaned by Professor J. M. Sullivan. This manubrium resembles the corresponding preternal segment of *Basilosaurus cetoides* (see fig. 27) very closely in general contour and proportions. Aside from its smaller dimensions, this manubrium differs mainly in having a more abruptly truncated hinder end and more rounded postero-external angles. The measurements of this manubrium are as follows: Antero-posterior diameter medially, 107.5 mm.; transverse diameter anteriorly, 91 mm.; transverse diameter posteriorly, 82 mm.; dorso-ventral diameter medially, 52 mm.; and dorso-ventral diameter posteriorly, 46.5 mm.

The sternal bone tentatively identified as the first mesosternal segment (pl. 14, fig. 4) is somewhat weathered ventrally. It is transversely widened, its ends are truncated, and its original shape viewed from above seems to have been subcordate. The dorsal surface is quite flat, the lateral surfaces slope obliquely from dorsal to ventral surfaces, and the rather narrow saddle-shaped ventral surface is concave from end to end and convex from side to side. The measurements of this mesosternal segment are as follows: Antero-posterior diameter medially, 72.5 mm.; transverse diameter posteriorly, 79 + mm.; dorso-ventral diameter medially, 41.5 mm.; and dorso-ventral diameter posteriorly, 45 mm.

The mesosternal segment of the adult individual belonging to Millsaps College Museum (20) is smaller than the preceding one (No. 4748, U.S.N.M.) and is markedly asymmetrical. The lateral, the end and the saddle-shaped ventral surfaces are rough and pitted. The dorsal surface is flattened and rather smooth. The measurements of this mesosternal segment are as follows: Antero-posterior diameter medially, 64.5 mm.; transverse diameter posteriorly, 58 mm.; dorso-ventral diameter medially, 35.6 mm.; and dorso-ventral diameter posteriorly, 43.5 mm.
A REVIEW OF THE ARCHAEOCETI

ZYGORHIZA WANKLYNI (Seeley)


Type locality—Barton clay, Barton Cliff, Hampshire, England. Bartonian stage, Upper Eocene.

Type specimen—Fragments of a skull broken during removal from collecting site. Among the pieces specifically mentioned by Seeley, there were portions of both maxillaries, the left one having two alveoli (C. and Pm1) and three serrate edged cheek teeth (Pm2, Pm3 and Pm4), the parietal region of the braincase, including the high sagittal crest, a short section of the combined frontals in the region of the intertemporal constriction, and two tympanic bullae. Collected by Dr. Arthur Wanklyn in 1872; present location unknown.


SKULL

As regards the external appearance of this skull, Seeley (1876, p. 432) states that “the parietal and frontal fragment is about the same size as in Zeuglodon brachyspondylus of Müller, which similarly has the frontal region flattened, with a sharp crest along the parietal region—which, however, does not become flattened posteriorly into a narrow table as in the species described; nor has the parietal in the foreign species the folded sutural junction with the frontal of our English specimen.” The anterior extremities of the maxillaries, which are complete, exhibit the usual rounded convexity. The left maxillary fragment measures about 8 inches (203 mm.) in length. The width of the rostrum at the level of the anterior extremities of the maxillaries is 2½ inches (57 mm.). The rostrum increases in width posteriorly and, at the level of Pm2, its transverse width equals 3½ inches (88.9 mm.). The dorsal narial fossa likewise widens posteriorly and the grooves on the maxillaries for the reception of the ascending processes of the premaxillaries in this region indicate that the latter measured about 1/6 inch (15.85 mm.) in width. The parietal region of the braincase has the usual form of archaeocetes. In the intertemporal region the lateral surfaces of the parietals are nearly vertical, the transverse diameter of the constriction being about 2 inches (50.8 mm.). Behind the deep and well-marked fronto-parietal suture, the median sagittal crest rises in a convex curvature, but increases in height and width posteriorly. A short section of the intertemporal portion of the frontals, with ventral grooves for the optic nerves, is attached to the parietal region. The supraorbital processes of the frontals and the remaining portions of the skull are not mentioned in Seeley’s description, although the existence of such fragments may be inferred from his statement that “almost the whole of the skull could be reconstructed from the materials preserved by Dr. Wanklyn.”

The type skull of Zygorhiza wanklyni seems to have been even smaller than the smallest skulls of Dorudon ostris, the distance from the anterior end of the maxillary to the postero-basal angle of crown of Pm3 being 178 + mm. according to the measurements given by Seeley, while the same measurement for the latter (No. 14382, A. M. N. H.) is 195 to 200 mm. Stromer (1908b, p. 150) points out that the posterior flattening of the sagittal crest distinguishes this species from Dorudon zitteli. The alveoli and the crowns of the premolars are somewhat similar in size in both of these archaeocetes. In Zygorhiza wanklyni, how-
ever, the interspace between C. and Pm1 is about half that in *Dorudon osiris* while the interspace between Pm1 and Pm2 is less than three-fourths of that in the latter. As compared to *Dorudon serratus*, the interspace between C. and Pm1 is less than half as long, but the interval between Pm1 and Pm2 is approximately the same; the alveoli and the crowns of the premolars are much smaller than those of the latter.

**DENTITION**

An isolated single rooted tooth measuring 2 3/4 inches (69.84 mm.) in length, though the distal end of the root is missing, agrees fairly well with canines of other archaeocetes. The maximum transverse diameter of the root of this tooth is 3/4 inch (19.05 mm.). The tapering laterally compressed crown of this tooth measures 5/8 inch (15.85 mm.) antero-posteriorly, 3/4 inch (12.7 mm.) transversely at base, and one inch (25.4 mm.) in height. The curvature of the anterior face of the crown is convex and the posterior concave; there is a vertical carina on the anterior and posterior faces. The apex of the crown is blunt and rounded. The enamel is wrinkled at the base of the crown, forming short vertical folds which anastomose at intervals.

The alveolus for the canine is oval in outline and measures 7/8 inch (22.19 mm.) in length and 5/8 inch (15.85 mm.) transversely. There is an interspace 7/8 inch (14.28 mm.) long between the canine and the first premolar. In this interspace and near the outer alveolar border is located a hollow for the reception of the apex of a mandibular tooth. The alveolus of Pm1 is more than an inch (25.4 mm.) long and less than 3/4 inch (15.85 mm.) wide. The interspace behind this tooth is about 7/8 inch (14.28 mm.) long and in it is located a similar hollow. The laterally compressed crown of Pm2 measures 1 1/8 inches (44.45 mm.) antero-posteriorly, its transverse diameter at the middle is less than 3/4 inch (12.7 mm.), and its height is less than one inch (25.4 mm.). The anterior and posterior cutting edges of this premolar are moderately serrated; on each of these surfaces there are four accessory denticles with faintly crenelated edges, of which the hinder ones are larger than those in front. A narrow cinguloid ridge, which is interrupted medially, encircles the base of the crown, and the enamel on the inner surface is ornamented with vertical striæ. The interspace between Pm2 and Pm3 is 1 1/2 inch (6.35 mm.). The crown of Pm3 is about an inch (25.4 mm.) high, 1 3/4 inches (44.45 mm.) long; it has longer and thicker accessory denticles than Pm2 and they are likewise more deeply divided from each other. The posterior accessory denticles are larger than the anterior ones and all have crenelated edges. The cingulum at the base of the crown of Pm3 is conspicuously developed, although the anterior and posterior halves do not meet medially. The hindermost premolar, Pm4, is imperfectly preserved and the crown apparently is shorter than that of the preceding tooth, but the accessory denticles are slightly better developed. The crowns of the cheek teeth in each maxillary are inclined toward those in the opposite jaw.

**CERVICAL VERTEBRA**

Our knowledge of the vertebral column of this species is limited to a posterior cervical vertebra, probably the sixth, which lacks both epiphyses; the tip of the low neural spine is missing, and the right diapophysis is damaged. The centrum is very short. The neural arch is wide and high, the neural canal being rather large. The pre- and post-zygapophyses are large and their facets are oval in outline. There is a blunt median ridge on the upper surface of the centrum, on each side of which is a vascular foramen. The diapophysis and parapophysis are united to form a broad, nearly vertical, lateral process which is inclined somewhat forward and is continuous above with the oblique buttress supporting the pedicle of the neural arch. Below the blunt diapophyseal process, this lateral plate-like process is perforated by a small vertebral arterial canal. The stout parapophyses are oval in cross-section and project considerably below the level of the ventral face of the centrum. A faint hypapophysial ridge is present on the ventral face of the centrum.
The measurements of this cervical are as follows: Transverse diameter of centrum, 55 mm.; vertical diameter of centrum, 45 mm.; antero-posterior diameter of centrum, without epiphyses, 20.5 mm.; greatest transverse distance between ends of parapophyses, 104 mm.; greatest distance from lower extremities of parapophyses to tip of neural spine, 118 mm.; greatest transverse distance between anterior extremities of prezygapophyses, 85 mm.; transverse diameter of neural canal, 33 mm.; vertical diameter of neural canal, 28 mm.; and vertical diameter of vertebrartrial canal, 8 mm.

? Zygorhiza juddi (Seeley)


Type locality—Marine sandy clays belonging to the Brockenhurst series and exposed in a brickyard at Roydon, Hampshire, England. Ludian stage, uppermost Eocene.

Type specimen—An imperfect? tenth caudal vertebra. No. M. 133, Geological Department, British Museum (Natural History); collector, John W. Judd.

Caudal Vertebra

This imperfectly preserved caudal vertebra lacks both epiphyses, the metapophyses and the hinder part of the roof of the neural arch are destroyed, and the distal extremities of the transverse processes are damaged. The maximum antero-posterior diameter of the centrum, without epiphyses, is approximately 70 mm. The anterior face of the centrum is roughly hexagonal in outline and possesses the usual radiating rugosities for the attachment of the epiphysis. The transverse diameter of the anterior face is 102 mm. and the vertical diameter is 87 mm. A short thin transverse process, which is perforated at the base behind the middle by a foramen, arises below the middle of the lateral face of the centrum. The lateral face of the centrum (fig. 76) above and below the transverse process is concavely curved from end to end. There is a median longitudinal depression on the relatively narrow ventral face of the centrum and the pair of facets for the corresponding chevron are rather small. The maximum transverse width of the posterior face of the centrum is at least 106 mm. The low neural arch is depressed and is placed far forward on the dorsal face of the centrum. The maximum transverse measurement across the neural arch anteriorly is about 50 mm. and the maximum antero-posterior diameter of the same is more than 40 mm. Viewed from in front, the transversely flattened neural canal is seen to have an ovate outline; its maximum width anteriorly is 27 mm., and the greatest vertical diameter is 14 mm. The height of this neural canal posteriorly in its present condition is about 16 mm., and the width at least 20 mm. There are several nutritive foramina on the dorsal face of the centrum.
This vertebra is tentatively identified as the tenth in the caudal series. The length of the centrum, when complete, seems to have been approximately the same as that of the corresponding caudal of the largest individuals of *Zygorhiza kochii*, and the transverse diameter of its anterior and posterior faces are only a few millimeters greater. Otherwise, the conformation of the transverse processes, the neural arches, and the dimensions of the neural canal are quite similar.

**DORUDON**


Permanent dental formula: I \( \frac{1.2.3}{1.2.3} \), C \( \frac{1}{1} \), Pm \( \frac{1.2.3.4}{1.2.3.4} \), M \( \frac{1.2}{1.2.3} \); deciduous dental formula: Di \( \frac{1.2.3}{1.2.3} \), Dc \( \frac{1}{1} \), Dpm \( \frac{1.2.3.4}{1.2.3.4} \).

No obvious cingulum at base of crown of Pm2, Pm3 and Pm4; Pm2 is the largest of the upper teeth in both *Dorudon serratus* and *D. intermedius*; Pm3 is the largest in *D. osiris*; Pm2 has not more than three accessory denticles on anterior and posterior cutting edges of crown; in the permanent dentition, Pm2 to M2 form a closed series; incisors and canine have a vertical carina on both anterior and posterior cutting edges of crown; upper cheek teeth (Pm2 to M2) have two divergent roots, accessory denticles on anterior and posterior cutting edges, and the enamel faintly striated; Pm1 usually has one root, but has two roots in both *D. serratus* and *D. zittelii*; Pm1 caniniform, with one root; remainder of lower premolars (Pm2 to Pm4) have laterally compressed crowns, accessory denticles on anterior and posterior cutting edges, and two roots; Pm3 is the largest of the lower cheek teeth; lower molars (M1 to M3) have accessory denticles restricted to posterior cutting edge of crown; pits for reception of mandibular teeth located on outer side of anterior one-rooted upper teeth and on inner side of the two-rooted upper teeth, showing that the upper and lower tooth series cross over when the jaws are closed.

Skull elongated; rostrum attenuated; forehead flattened; elongated intertemporal region narrow; sagittal crest prominent; contour of supraoccipital-shield shaped in the several species to a varying extent by the backward prolongation and ventral pinching in of the lambdoidal crests; premaxillaries convex laterally; temporal fossae large; large pterygoid fosse for accessory air sinuses of middle ear; projecting ledge formed by forward prolongation of temporal rim of squamosal; hyoid apparatus presumably similar to that of *Zygorhiza*; forelimb comparatively stout; height of scapula greater than length of humerus; elbow hinged and non-rotary; shaft of radius has a greatly reduced anterior angle-like prominence; shaft of ulna noticeably widened antero-posteriorly; carpals and digits unknown; and pelvis unknown.

Vertebral column apparently consists of 7 cervical, 15 dorsal, 13 lumbar, 2 sacral and 21 caudal vertebrae; cervical vertebrae have slightly compressed centra, no ankylosis of consecutive centra, and relatively slender lateral processes; atlas has short odontoid process and relatively small vertebral arterial canal at base of transverse process; lower transverse processes of sixth cervical vertebra noticeably expanded antero-posteriorly; anterior dorsal vertebrae have slender neural spines; centra of hinder dorsals, lumbars, sacrals and caudal vertebrae are not disproportionately elongated; the manubrium is the largest of the several segments comprising the sternum; xiphisternum consists of a short quadrangular anterior portion and a long backward projecting xiphoid process whose spatulate extremity is not deeply notched; on anterior caudal vertebrae the antero-posterior diameter near base of transverse process is slightly less than length of centrum.
DORUDON SERRATUS Gibbes


Type locality—"In a bed of green sand near the Santee Canal, in South Carolina. The locality is on the plantation of R. W. Mazyck, Esq., about three miles from the entrance of the canal from the head waters of the Cooper River," Berkeley County. Santee limestone marl, lower Jackson formation, upper Eocene.

Type specimen—Consists of a right maxillary fragment (Gibbes, 1847, pl. 4, fig. 1), with Pm2, Pm3, and Pm4 in place and in addition a portion of alveolus of M1; a left maxillary fragment (Gibbes, 1847, pl. 4, fig. 4), with Pm2 and alveolus of Pm1; a detached left I2 (Gibbes, 1847, pl. 4, fig. 3); an imperfect left mandible (Gibbes, 1847, pl. 4, fig. 1), with crowns of the teeth, and also the anterior and the posterior ends of ramus destroyed; and a fragment of the right mandible (True, 1908a, pl. 3, fig. 2). No. 8763, Museum of Comparative Zoology; collector, Robert W. Gibbes; March 1845.

Referred specimens—(1) Gibbes subsequently obtained some additional remains from the same locality when marling operations were resumed by the plantation owners, and of these the following have been described and figured by Gibbes and by True: A fragment of the left premaxillary (Gibbes, 1847, pl. 3, fig. 6), with I3 in place but with crown damaged, and the alveolus of I2 (on the hinder end of this bone is a large cavity in which the anterior end of the maxillary rests); a fragment of the right premaxillary (True, 1908a, pl. 1, fig. 1), with alveolus of I3; an incomplete zygomatic process of left squamosal (True, 1908a, pl. 2, fig. 4); a fragment of right parietal (True, 1908a, pl. 2, fig. 3); two pieces of supraorbital process of right frontal (True, 1908a, pl. 2, fig. 2); right and left nasals, incomplete (True, 1908a, pl. 2, fig. 1); a fairly complete right lower incisor, portion of crown restored with wax (True, 1908a, pl. 2, fig. 7); the roots of two left lower incisors (True, 1908a, pl. 2, figs. 8, 9); two roots of a cheek tooth, possibly the left Pm4 (True, 1908a, pl. 2, figs. 11, 12); an incomplete posterior process of a periory (True, 1908a, pl. 2, fig. 5); and the inferior portion of an atlas (True, 1908a, pl. 2, fig. 13). No. 8763, Museum of Comparative Zoology; collector, Robert W. Gibbes; fall of 1845.

The twelve caudal vertebrae figured by Gibbes (1847, pl. 2, fig. 8) can not now be located.

(2) An imperfect first lower molar from a left mandible. From the county rock quarry (Kellum, 1926, p. 9), half mile south of Castle Hayne railroad station, New Hanover County, North Carolina. Upper Castle Hayne formation. No. 2335, Division of Vertebrate Paleontology, U. S. Nat. Mus.; collector, T. Wayland Vaughan; June 7, 1902.

SKULL

The skull (fig. 77) is known solely from fragments. Judging from the relative measurements of corresponding parts, the skull of *Dorudon serratus* is slightly smaller than that of *Zygorhiza kochi*, but otherwise is quite similar in general appearance. The skull of

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1 The Mazyck plantation, according to Dr. C. Wythe Cooke, is probably that now known as Fair Spring and owned by a Mr. Dennis. It is located in Berkeley County, South Carolina, about one mile west of Macbeth and 1½ miles north of Moncks Corner.
D. serratus, however, has a higher rostrum, the vertical diameter at the level of the anterior edge of alveolus of 13 being 55.5 mm., while the corresponding measurement of Z. kochii is 44 mm. The posterior extremities of the nasals are widely divergent posteriorly, separated by the wedge-like narial process of the combined frontals, attenuated and vaulted. The anterior end of the jugal was mortised into the maxillary and terminated anteriorly above Pm4. A small elongated antorbital foramen is present on the lateral surface of the maxillary above Pm3. The sagittal and lambdoidal crests are not prominently developed.

Portions of both nasals are preserved. The correct positions of these nasals are reversed in the photograph published by True (1906a, pl. 2, fig. 1), since the edge which normally is mortised into the ascending process of the premaxillary is shown in contact with the corresponding edge of the opposite nasal. The hinder end, which is grooved on its under surface for contact with the frontal, faces the bottom of this plate. The inner edge of the hinder third of each nasal diverges widely from that of the opposite one; the nasals are separated for at least one-third of their length by the attenuated narial process of the frontals. The curvature of these nasal bones indicates that they were highly vaulted. The maximum length of the right nasal, as preserved, is 131 mm. The length of the incomplete left nasal is 89 mm.

![Diagram of Dorudon serratus](image)

**Fig. 77—Dorudon serratus** Gibbes. Lateral view of reconstructed skull, No. 8763, Museum of Comparative Zoology. × ½. ant.f., antorbital foramen; c., occipital condyle; fr., frontal; ju., jugal; la., lachrymal; max., maxillary; na., nasal; pa., parietal; pgl., postglenoid process of squamosal; pmx., premaxillary; s.or.pr., supraorbital process of frontal; sq., squamosal; zyg., zygomatic process of squamosal. Upper Eocene, Santee limestone marl, South Carolina.

<table>
<thead>
<tr>
<th>Table 43—Measurements (in millimeters) of right maxillary fragment</th>
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<tbody>
<tr>
<td>Greatest length, anterior face of anterior root of Pm2 to hinder end (region where jugal is mortised into maxillary)</td>
</tr>
<tr>
<td>Distance from antero-basal angle of right Pm2 to postero-basal angle of Pm4</td>
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<tr>
<td>Distance from antero-basal angle of right Pm3 to postero-basal angle of Pm4</td>
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<tr>
<td>Distance from postero-basal angle of crown of right Pm4 to antorbital foramen</td>
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</tbody>
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<tr>
<th>Table 44—Measurements (in millimeters) of left maxillary fragment</th>
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<tr>
<td>Greatest length</td>
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<tr>
<td>Distance from anterior edge of alveolus of Pm1 (two-rooted) to hinder face of hinder root of Pm2</td>
</tr>
<tr>
<td>Distance between alveolar margin of maxillary (externally) at center of Pm2 to apex of principal cusp of this tooth</td>
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<tr>
<th>Table 45—Measurements (in millimeters) of right premaxillary fragment</th>
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<tbody>
<tr>
<td>Maximum length</td>
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<tr>
<td>Maximum length of alveolus of 13</td>
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<tr>
<td>Maximum transverse diameter of alveolus of 13</td>
</tr>
</tbody>
</table>
Mandible

The horizontal ramus of the mandible (Gibbes, 1847, pl. 3, fig. 1) is rather slender and the symphysis apparently is extended backward to the level of the center of or possibly to the hinder face of the hinder root of Pm3. The section preserved of the left mandible measures 453 mm. in length, but all of the internal face is destroyed behind the level of the center of Pm4. The external face of the mandible becomes concave behind the level of Pm4. The hindermost mental foramen is located on the outer face of the mandible in the interval between Pm3 and Pm4. The vertical diameter of the left mandible behind the hinder root of Pm3 is 51.5 mm.; at center of Pm3 it is 53 mm.; and at level of center of Pm4 it is 59.5 mm. The fragment of the right mandible measures 238 mm. in length.

Dentition

The upper incisors (fig. 78) are caniniform and have long slender roots and no perceptible neck; the crown is sharp pointed, laterally compressed, recurved, with vertical carina on both anterior and posterior cutting edges, and enamel strongly rugose. The crown of the canine is no doubt similar in shape and in proportions to those of the incisors. On the lateral surface of the premaxillary, 22 and 28 mm., respectively, above the palatal surface and between the incisors, are small circular pits for the reception of the apices of the mandibular teeth. The incisors and premolars have the enamel surface of the crown ornamented more or less with vertical striæ that anastomose at intervals; on the premolars this ornamentation is coarser on the inner side of the crown than on the outer.

Unfortunately all of the enamel crown of the detached left I3 with the exception of a small fragment of the hinder basal border is destroyed. This fragment of the crown shows, however, that a low vertical carina was present on the hinder edge and that the enamel was striated vertically. The maximum antero-posterior diameter of the root of this incisor at the level of the alveolus is 21 mm. and the maximum transverse diameter is 14.5 mm.

The upper premolars of Dorudon serratus are distinguished from those of Zygorhiza kochii by the absence of a cingulum at the base of the crown and by the less conspicuous development of striæ on the enamel. Pm1 has two roots and the alveolus is pyriform in outline. The distance between the hinder rim of the alveolus of the left Pm1 and the anterior rim of the alveolus of Pm2 (15 mm.) is about half the corresponding interval (32 mm.) in Zygorhiza kochii. On the figures published by Gibbes (1847), the accessory denticles of the premolar teeth are too nearly erect and are somewhat exaggerated in size. All of the premolars have two roots. On the hinder premolars the posterior root is almost twice as thick transversely as the anterior one. The vertical furrow on the hinder face of the neck gives the false impression of a divided posterior root. These cheek teeth have
high, sharp-edged and pointed accessory denticles, which are quite large in comparison to
the principal cusp. The accessory denticles are smaller and are farther removed from the
apex of the principal cusp on the anterior cutting edge than on the posterior edge.

The left Pm2 is the largest of the upper cheek teeth. The nearly vertical anastomos-
ing striæ are most conspicuous on the internal surface of the basal half of the crown of the
left Pm2. There are three accessory denticles with carinate edges on the anterior edge
of the crown, the basal one being relatively small. The three accessory denticles on the
hinder cutting edge of the crown are larger than those on the anterior edge, although the
basal one of these is likewise quite small. The distal denticle on the hinder edge is nearer
the apex of the principal cusp than is the corresponding denticle on the anterior edge. It
is certain that the cingulum is not developed on the outer face of the crown nor above the
anterior root on the internal face. The base of the crown is broken off internally above the
hinder root. The maximum transverse diameter of the anterior root is 14.5 mm. and the
corresponding diameter of the hinder root is 17 mm. The two roots of this tooth diverge

![Diagram of Dorudon](image)

**Fig. 78—*Dorudon serratus* Gibbes. Ventral view of distal fragments
of right and left premaxillaries, No. 8673, Museum of Comparative
Zoology. × ½. *f. max.*, elongate fossa for anterior end
of maxillary; *pmx.*, premaxillary. Upper Eocene, Santee limestone
marl, South Carolina.

very strongly toward their extremities, where they are separated by an interval
of 42.5+ mm.

The accessory denticles on the hinder cutting edge of the crown of the right Pm2
are damaged, the anterior edge and all of the enamel on the internal face of the crown are
destroyed, and the apical portion of the principal cusp is broken off. The pulp cavity
of both roots is exposed on the internal face and this pulp cavity extends upward into the
principal cusp. The extremities of both roots are separated by an interval of 30 mm.

On the right side, Pm2 to Pm4 at least form a closed series.

On the hinder cutting edge of the crown of the right Pm3 there are four accessory
denticles, the largest being near the principal cusp and the smallest at the base of this edge.
A small basal tubercle is present on the anterior cutting edge, but the two larger accessory
denticles above it as well as most of the principal cusp are destroyed. On the outer face
of the crown the enamel is relatively smooth, but on the internal face above the hinder
root it is striated vertically. No cingulum is developed on either the inner or the outer
faces of the crown. The roots are attenuated distally and diverge from one another
toward their extremities. The maximum transverse diameter of the anterior root is 13.2
mm., and the corresponding diameter of the hinder root is 23.5 mm.
The right Pm4 has three accessory denticles and a small basal tubercle on the hinder cutting edge. There are three accessory denticles on the anterior cutting edge, the enamel on the one nearest the principal cusp being distinctly striated. The enamel on the outer surface of the crown is rather smooth and the striae are quite indistinct. The internal face of the crown is moderately rugose, the vertical striae being especially conspicuous above the hinder root. The distal denticle on the hinder edge is nearer the apex of the principal cusp than is the corresponding denticle on the anterior edge. No cingulum is developed on either the inner or the outer face of the crown. The roots of this premolar are less divergent than those of Pm2. The transverse diameter of the anterior root is 13.2 mm. and the corresponding diameter of the hinder root is 16.4 mm.

Gibbes (1847, pl. 3, fig. 1) figures the fragment of the left mandible, which is 453 mm. in length. At the anterior end of this fragment of the left mandible is the nearly complete alveolus of I3 and behind it are the alveoli for C and Pm1. The alveoli for C and Pm1

<table>
<thead>
<tr>
<th>Table 49—Measurements (in millimeters) of the teeth and alveoli</th>
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<tbody>
<tr>
<td>Maximum antero-posterior diameter of alveolus of left I2</td>
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<tr>
<td>Interspace between alveoli of left I2 and I3</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of alveolus of left I3</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of root of left I3</td>
</tr>
<tr>
<td>Maximum transverse diameter of root of left I3</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of alveolus of left Pm1</td>
</tr>
<tr>
<td>Maximum transverse diameter of alveolus of left Pm1</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of crown of left Pm2 at base.</td>
</tr>
<tr>
<td>Maximum transverse diameter of crown of left Pm2 at base</td>
</tr>
<tr>
<td>Vertical diameter of left Pm2, apex of crown to extremity of anterior root</td>
</tr>
<tr>
<td>Vertical distance between apex of crown of left Pm2 and point of junction of the two roots below neck</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of enamel crown of left Pm2 at middle, as preserved</td>
</tr>
<tr>
<td>Length of anterior cutting edge of principal cusp of left Pm2</td>
</tr>
<tr>
<td>Length of posterior cutting edge of principal cusp of left Pm2</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of crown of right Pm3 at base</td>
</tr>
<tr>
<td>Maximum transverse diameter of crown of right Pm3 at base</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of crown of right Pm4 at base</td>
</tr>
<tr>
<td>Maximum transverse diameter of crown of right Pm4 at base</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of alveolus of right M1</td>
</tr>
<tr>
<td>The fairly complete lower right incisor, with anterior edge and apex of crown restored with wax (True, 1909a, pl. 2, fig. 7):</td>
</tr>
<tr>
<td>Maximum length of tooth (apex of crown restored)</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of root</td>
</tr>
<tr>
<td>Maximum transverse diameter of root</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of crown at base</td>
</tr>
<tr>
<td>Maximum transverse diameter of crown at base</td>
</tr>
<tr>
<td>Detached incisor (True, 1909a, pl. 2, fig. 9):</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of root</td>
</tr>
<tr>
<td>Maximum transverse diameter of root</td>
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<tr>
<td>Detached incisor (True, 1909a, pl. 2, fig. 6):</td>
</tr>
<tr>
<td>Maximum length of tooth, as preserved</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of crown</td>
</tr>
<tr>
<td>Maximum transverse diameter of crown</td>
</tr>
</tbody>
</table>

measure about 24 mm. in diameter. These alveoli are 15 mm. apart and the latter is 15 mm. from the alveolus for Pm2. A portion of the crown of Pm2, which is shown in the figure published by Gibbes, is now missing. The crown of Pm2, if it has been correctly drawn by the artist, possesses an unusually large basal accessory denticle on the anterior cutting edge. In this detail it resembles most closely the Pm2 (No. 13774, U. S. N. M.) referred to Zygorhiza kochii. It is quite possible that this premolar is two rooted. The anterior root is preserved, but the jaw is fractured in the region of the assumed position of the hinder root and the gap has been filled with plaster of paris. Furthermore, it would appear that the crowns of Pm2 and Pm3 were almost in contact. In that event, Pm2 to M3 form a closed series. The crown of the two-rooted Pm3 is destroyed, with the excep-
tion of small fragments of the basal anterior and posterior angles. The antero-posterior diameter across the upper ends of the roots is 39 mm. Close behind this tooth is an imperfectly preserved alveolus of a somewhat larger Pm4. The maximum antero-posterior distance between the anterior face of the anterior root and the hinder face of the posterior root (estimated) is 56 mm. The condition of the alveoli for the succeeding cheek teeth is such that accurate measurements can not be taken. The dental formula seems to have been, \[ \frac{3}{1} \cdot \frac{4,2}{3,1} \cdot \frac{3}{1,4,5} \].

An isolated left M\(\text{T} \) (No. 2335, U. S. N. M.) from the Castle Hayne formation in North Carolina has a slight cinguloid ridge on the basal border of the inner and outer surfaces of the crown. The principal cusp has its apex and practically all of its grooved anterior face worn off. Wear has also removed the enamel near the base of the internal face of the principal cusp. The upper portion of the anterior root is similarly worn. The three accessory denticles on the hinder cutting edge of the crown diminish in size from the uppermost one to the basal one. The apex of the middle denticle, however, is worn far below the level of the apices of the uppermost and lowermost denticles. The anterior root is broken off at the level of the isthmus and the extremity of the posterior root is missing. The antero-posterior diameter of the crown at base is 31 mm. and the maximum transverse diameter of the crown at base is 13.5+ mm.

**VECTERBÆ**

**CERVICAL VERTEBÆ**

The comparatively thin atlas seems to have been characterized by having the outer expanded portion of the posterior articular facets directed obliquely, vertebrarterial canals nearly in line with outer margins of articular facets, anterior and posterior articular facets separated above by a narrow flat surface, and inferior fragment of transverse process inclined very slightly backward. The following measurements for the incomplete atlas are taken from True (1908a, p. 75, pl. 2, fig. 13): Breadth between outer margins of anterior articular facets, 104 mm.; greatest thickness of atlas, 33 mm.; least thickness of ventral face in median line, 24 mm.; and breadth of inferior portion of transverse process at base, 25 mm.

The remaining cervical vertebrae are unknown.

**CAUDAL VERTEBÆ**

Of the 12 posterior caudal vertebrae figured by Gibbes (1847, pl. 2, figs. 4–8), the six anterior ones are distinctly larger than the six hinder ones. The largest caudal vertebra measures 3\(\frac{1}{2} \) inches (88.9 mm.) in length and 4 inches (101.6 mm.) in breadth. The caudal vertebra near the anterior end of this series have rather large metapophyses (processus obliquomammillares), neural spines vestigial or absent, centrum somewhat contracted near the middle, short attenuated transverse processes which are perforated at the base and have the anterior margin nearly straight and the posterior margin oblique, anterior face of centrum concave, posterior face slightly convex, and posterior facets on ventral face for the chevron bones. The posterior caudals are distinctly compressed antero-posteriorly, the neural arches and transverse processes are not developed, and the lateral surface of the centrum is grooved vertically. A single foramen is present in the center of the ventral longitudinal depression on all of these caudal vertebrae. The total length of this series of 12 caudal vertebrae is estimated to be about 645 mm. according to the figure published by Gibbes.
DORUDON OSIRIS (Dames)


**Type locality**—Cliffs over Qasr-el-Sagha on escarpments north of the lake (Birket-el-Qurun), Fayum, Egypt. From Horizon II, 5 α = Carolina beds = Qasr-el-Sagha stage, upper Eocene.

**Lectotype**—Portions of right and left premaxillaries; and ramus of left mandible with six serrated cheek teeth and I2 in situ, as well as the alveoli for I1, I3, C, and Pm1. From an isolated hill, designated on Schweinfurth's map as §, 12½ kilometers west of the old temple and 3 miles west-south-west of Qasr-el-Sagha. The mandible was found in a violet-colored marl bed, which is characterized in part by the profusion of vertebrate remains and which is situated at about the lower third of the slope of this hill and in a geological horizon corresponding to "AAAβ-Schicht" of the Mokattam series.1 No. M. 16, Geologisch-Paläontologisches Institut und Museum der Universität, Berlin; collector, Georg Schweinfurth; winter of 1885–86.

Dames (1894, pp. 197–201) allocated an axis, two lumbar and two caudal vertebrae collected by Dr. Schweinfurth during the winter of 1885–86 to this species. The axis (Dames, 1894, pl. 31) is here referred to an immature Prozeuglodon ipsis, the larger (Dames, 1894, pl. 34) of the two lumbar vertebrae seems to represent some hitherto undescribed archaeocete, and the smaller one (Dames, 1894, pl. 35) of the two lumbarbs as well as the two caudal vertebrae (Dames, 1894, pl. 36) are tentatively referred to Dorudon intermedius.

**Referred specimens**—(1) A somewhat crushed skull that lacks the extremity of right supraorbital process, extremity of right zygomatic process, posterior end of right jugal, postero-external angle of left supraorbital process, left zygomatic process, left squamosal, and left exoccipital. The dentition is fairly complete. The left mandible lacks the condyle and the hinder lower angle; the anterior extremity is restored; and the tooth series is complete. The right mandible is somewhat crushed. This specimen lay isolated and broken in pieces on a terrace on the lower third of the plateau slope in gray and reddish-yellow marl [= "Stufe II 5a" of Blanckenhorn]. This is the bone horizon of the Carolina beds of the plateau rim of Qasr-el-Sagha, 2 miles west-south-west of Qasr-el-Sagha, and north of the lake (Birket-el-Qurun), Fayum, Egypt; Qasr-el-Sagha stage. No. 1902. XI. 59, Paläontologische Sammlung, Alte Akademie, München; collector, Ernst Stromer. (Mn. 1, Stromer, 1903c, p. 66, pl. 10, fig. 5; see also Stromer, 1903a, pp. 345–352, fig., and Blanckenhorn, 1902, p. 387.)

(2) Hinder half of a weathered left mandible. From a grayish clay [= "Stufe II 5a" of Blanckenhorn] at Gebel Achdar, 13 miles north-north-east of Qasr-el-Sagha, Fayum, Egypt; Qasr-el-Sagha stage. No. 1902. XI. 59a, Paläontologische Sammlung, Alte

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Akademie, München; collector, M. Blankenhorn; February 16, 1902. (Mn2, Stromer, 1903c, p. 70; see also Blankenhorn, 1903, p. 383.)

(3) An imperfect weathered skull that lacks the premaxillary portion of the rostrum, the zygomatic arches, the supraorbital processes of the frontals, the extremity of the left exoccipital and the tympanic bulla; the crowns of most of the milk teeth are broken off. The left mandible possesses four fairly complete serrate-edged teeth (Dpm2 – MI), but the coronoid process is damaged and the condyle and the hinder lower angle are missing. On the fragment of the right mandible, the erupting MI and M3 are preserved. Northern Fayum, Egypt; Qasr-el-Sagha stage. No. 1904. XII. 134, Paläontologische Sammlung, Alte Akademie, München; collector, Richard Markgraf; 1904 (Mn. 11, Stromer, 1908b, pp. 112–113).

(4) Isolated vertebrae, including atlas, axis, and dorsal vertebrae, probably belonging in part to this species. Northern Fayum, Egypt; Qasr-el-Sagha stage. No. 1904, XII. 134b, c, Paläontologische Sammlung, Alte Akademie, München; collector, Richard Markgraf; 1904 (Mn. 12, Stromer, 1908b).

(5) A tympanic bulla, two cervical vertebrae, and head of a humerus, probably belonging to this species. Northern Fayum, Egypt; Qasr-el-Sagha stage. No. 1904. XII. 134f, Paläontologische Sammlung, Alte Akademie, München; collector, Richard Markgraf; 1904.

(6) Two hinder premolars and a molar. Northern Fayum, Egypt; Qasr-el-Sagha stage. No. 1904. XII. f. 1, Paläontologische Sammlung, Alte Akademie, München; collector, Richard Markgraf; 1904.

(7) Cranium with natural endocranial cast exposed and two associated tympanic bullae. From the yellow sandstone with marine molluscs, north of east end of the lake (Birket-el-Qurun), Fayum, Egypt; Qasr-el-Sagha stage. No. 1914. I. 56, Paläontologische Sammlung, Alte Akademie, München; collector, Richard Markgraf; 1914 (Pompeckj, 1922, p. 71 ff., pl. 2, figs. 10–15).

(8) Ulna. North of Tamlitje, Fayum, Egypt; Qasr-el-Sagha stage. No. 1922. IX. 8, Paläontologische Sammlung, Alte Akademie, München; collector, Richard Markgraf; 1914.

(9) A consecutive series of 14 lumbar and caudal vertebrae, somewhat crushed. From the gray and red marl north of the lake (Birket-el-Qurun), Fayum, Egypt; Qasr-el-Sagha stage. No. 11237a, Württembergische Naturäiensammlung, Stuttgart; collector, Richard Markgraf; 1904 (St. 11, Stromer, 1908b, pl. 4, figs. 15, 16, 17).

(10) Right mandible, with anterior extremity missing and with posterior end fairly complete; the three molars, as well as Pm2 and Pm3, are in situ. Left mandible with anterior extremity missing, and with Pm2, Pm3, and Pm4 in situ; coronoid process and condyle fairly complete; lower hinder angle imperfect. Probably two species are represented. From the gypsumiferous marl near Dimê, north of the lake (Birket-el-Qurun), Fayum, Egypt; Qasr-el-Sagha stage. No. 11417, Württembergische Naturäiensammlung, Stuttgart; collector, Richard Markgraf; 1905.

(11) An almost complete skull, very slightly crushed dorso-ventrally, with damaged lambdoidal crests and with enamel on crowns of teeth destroyed. From the gypsumiferous marl near Dimê, north of the lake (Birket-el-Qurun), Fayum, Egypt; Qasr-el-Sagha stage. No. 11626, Württembergische Naturäiensammlung, Stuttgart; collector, Richard Markgraf; 1906 (St. 2, Stromer, 1908b, p. 110).

(12) A weathered left mandible with six serrate-edged cheek teeth and five single-rooted teeth; enamel destroyed on crowns of the teeth. From the gypsumiferous marl near Dimê, north of the lake (Birket-el-Qurun), Fayum, Egypt; Qasr-el-Sagha stage. No. 11627, Württembergische Naturäiensammlung, Stuttgart; collector, Richard Markgraf; 1906 (St. 14, Stromer, 1908b, p. 111).
(13) An uncrushed imperfect skull, without zygomatic arches, but with remarkably complete natural endocranial cast exposed dorsally and on the right side; the milk dentition is preserved. From the light-brown hard limestone north of the lake (Birket-el-Qurun), Fayum, Egypt; Qasr-el-Sagha stage. No. 11786, Württembergische Naturaliensammlung, Stuttgart; collector, Richard Markgraf; 1907 (St. 3, Stromer, 1908b, pl. 5, figs. 12–13). [See comments under endocranial cast of *Dorudon elliotsmithii*.]

(14) Eight teeth, including I₂, I₃, C, Pm₃, Pm₄, and M₁. Fayum, Egypt; Qasr-el-Sagha stage. No. 13138, Württembergische Naturaliensammlung, Stuttgart; collector, Richard Markgraf; summer, 1912.

(15) Left humerus, radius, ulna, and a rib. Fayum, Egypt; Qasr-el-Sagha stage. No. 13139, Württembergische Naturaliensammlung, Stuttgart; collector, Richard Markgraf; summer, 1912.

(16) Eight vertebrae, including atlas, axis, third and sixth cervicals, one lumbar and three caudal vertebrae. Fayum, Egypt; Qasr-el-Sagha stage. No. 13140, Württembergische Naturaliensammlung, Stuttgart; collector, Richard Markgraf; summer, 1912.


(18) Artificial endocranial cast of No. 10018, Geol. Mus., Cairo. No. M. 8150, Geological Department, British Museum (Natural History).

(19) A remarkably complete skull with exception of extremity of rostrum which has been restored; enamel crowns of the teeth are imperfectly preserved. Both periotics are present, but the tympanic bullae are lost. North of the lake (Birket-el-Qurun), Fayum, Egypt; Qasr-el-Sagha stage. No. M. 10228, Geological Department, British Museum (Natural History) (Andrews, 1923, p. 648).

(20) A weathered and crushed skull. One mile west of Qasr-el-Sagha, Fayum, Egypt. Qasr-el-Sagha stage. No. 13720, Department of Vertebrate Palaeontology, American Museum of Natural History; collector, Walter Granger; 1907.

(21) A skull that lacks most of the upper surface of the braincase, including the supraoccipital shield. Basocranium region nearly complete. The right I₂ and all of the cheek teeth, with the exception of both Pm₁, are in place. The remaining teeth are missing. The tympanic bullae and the periotics are attached to the skull. From a reddish-yellow sandstone, north of Qasr Qurun, Fayum, Egypt. Qasr-el-Sagha stage. No. 14382, Department of Vertebrate Palaeontology, American Museum of Natural History; collector, Richard Markgraf.

**SKULL**

The skull of *Dorudon osiris* (pls. 18–21) differs from that of *Dorudon intermedius* in having an unusually narrow and ventrally pinched-in supraoccipital shield, a narrower intertemporal region, the posterior ends of the nasals closely approximated and not widely separated by a long wedge-like narial process of the combined frontals, and the anterior extremity of the jugal much closer to antorbital foramen. The narrow supraoccipital shield is remarkable for its extreme narrowness as compared with its height, the lateral portions of the lambdoidal crests being sharply folded backward so that this deeply concave surface has the appearance of being pinched-in above the level of the condyles. The narrow supraoccipital contributes the posterior face of the upper lateral portions of the lambdoidal crest, the anterior face being constituted by the hinder borders of the parietal. The deep suture between these bones runs along the edge of the lambdoidal crest.

Parietals normal in relation to adjacent bones and meet on mid-line to form a high sagittal crest that extends forward as far as the suture that marks their contact with the frontals; dorsal profile rises abruptly behind level of orbit; each parietal contributes a
portion of the slightly convex lateral cranial wall and meets the squamosal in a dentate suture that runs downward and forward; squamosal rather large, its upper surface convex from before backward and contributing a considerable portion of the cranial wall; ventro-anterior or temporal margin of squamosal extended forward as a thin shelf; zygomatic process rather large, its ridge-like upper edge being continued backward and upward along outer and hinder edge of squamosal to join with lambdoidal crest and forming with the latter the posterior boundary of the enormous temporal fossa; maximum zygomatic breadth equivalent to 0.45 of the condylo-basal length of skull; exoccipital relatively narrow, with rather thick and rounded or obliquely truncated external edge; upper edge of exoccipital more or less separated from lambdoidal crest of squamosal; foramen magnum small; occipital condyles borne on short necks, broader above than below and convex from side to side; intertemporal region relatively narrow; lateral walls of intertemporal constriction are nearly vertical above elongated sphenorbital fissure; groove for optic nerve originating at optic foramen, which is situated anterior to and above level of sphenorbital fissure, extends forward and upward on lateral surface of orbitosphenoid and then curves outward on ventral face of supraorbital process of frontal; parietals and frontals quite thick in region of sutural union; forehead flattened; supraorbital process of frontal broadened, extended laterally beyond level of jugal and arched at extremity; postorbital projection of supraorbital process thick and curved downward, but preorbital angle is relatively thin; orbit of moderate size; anterior extremity of jugal mortised into outer face of maxillary and forming outer wall of the narrow groove for lachrymal duct; lachrymal wedged in between preorbital end of supraorbital process and the jugal, forming part of anterior wall of orbit and abutting also against hinder border of maxillary; lateral surface of maxillary strongly grooved below anterior extremity of jugal; nasals attenuated anteriorly, convex from side to side, and attain their maximum width posterior to proximal ends of ascending processes of the premaxillaries; posterior ends of nasals either closely approximated or very slightly divergent; anterior extremities of nasals constitute posterior border of dorsal nasal fossa, which they overhang to some extent; posterior border of dorsal nasal fossa lies over the interval between Pm1 and Pm2; rostrum seemingly relatively narrower than in Dorudon intermedius; the large premaxillaries attain their maximum depth at level of anterior ends of nasals; the two premaxillaries form the sides and the floor of the dorsal nasal fossa, as well as the extremity of the rostrum, and on their alveolar borders are located three incisors; ascending processes of premaxillaries lodged proximally in grooves on the upper internal borders of the maxillaries and terminated approximately on a level with center of Pm2; proximal end of maxillary abuts against supraorbital process of frontal superiorly and inferiorly projects backward below the latter; two molars are located on inferior process of maxillary; molar series set off from palatal surface by deep excavation; large antorbital foramen located above Pm3 or above interval between Pm2 and Pm3; flat oral surfaces of premaxillaries (fig. 79) prolonged backward as a narrow tongue-like wedge to the level of the anterior edge of Pm2, separating anterior extremities of maxillaries; bony palate prolonged backward by elongation of palatines and adjacent thin plates of pterygoids, forming an inclosed tube for internal choanae; a V-shaped elevation is present on palatal surface of this choanal tube; basioceiptal narrow, with large lateral descending plate-like processes; ventral surface of basisphenoid bounded laterally by thin hamular plates of pterygoids; large pterygoid fossa for accessory air sac of middle ear overspread ventrally by the pterygoid, the hamular process which constitutes the inner wall being bent or curved outward to meet the more nearly vertical postero-external limb of the pterygoid which in turn is suturally united with the bifid anterior end of the squamosal, and the roof is contributed by the alisphenoid and the underlying flat plate-like portion of the pterygoid; mandibular branch of trigeminal nerve passes outward from cranial cavity through deep notch on posterior border of alisphenoid and reaches temporal fossa through the
foramen ovale which is located in the fissure between the falciform process and the dorsal portion of anterior end of squamosal; zygomatic arches not bowed outward; anterior extremity of zygomatic process of squamosal continued forward as a thin splint-like projection on upper face of jugal almost to level of postorbital angle of supraorbital process of frontal; wide glenoid articular surface concave from end to end; downward and forward
The free upper border of the outer lip of the tympanic bulla (fig. 80) tends to curve inward. On this lip and near the middle of the length of the bulla, the processus sigmoideus is located. The distal end of the sigmoid process is twisted almost at right angles to the basal portion; the breadth exceeds the free height of this process. Although strongly compressed in an antero-posterior direction, the anterior, external, and posterior faces of the sigmoid process are curved and somewhat tumid. The slope of the anterior face of the sigmoid process is distinctly oblique, and its dorsal or distal extremity is not bent forward as in most odontocetes. The general form of this process is somewhat similar to that of Squalaodon and also to that of the mysticetes. Adjacent to and above the base of
this sigmoid process and on the dorso-internal edge of the outer lip, the fissura Glaseri is located. The extremity of the slender anterior process of the malleus was ankylosed to the outer lip of the bulla on the inner edge of this fissure.

The posterior conical apophysis or processus medius is limited to a 7- or 8-mm. broad, low convexity on the outer lip between the sigmoid process and the posterior process. The curvature of the processus medius is much steeper anteriorly than posteriorly. The pedicles of the posterior process were damaged on all of the tympanic bullae examined. A vertical cleft separates the thickened hinder edge of the outer lip from the involucrum. The slender outer pedicle of the horizontally expanded posterior process was ankylosed to the postero-internal angle of the outer lip at the epitympanic edge of this vertical cleft, while the somewhat larger inner pedicle was ankylosed to the postero-external angle of the involucrum on the opposite side of the cleft. Thus these two pedicles constitute the inner and outer walls of the dorsal continuation of this cleft. Through this cleft, according to Pompeckj, there existed some sort of a connection with an air sinus located between the tympanic bulla and the proc. paroccipitalis, and this sinus may have been extended dorsally in the fissura petroso-paroccipitalis. There are some indications that the connection between the posterior process of the tympanic bulla and the posterior process of the periatic was not particularly solid, or at least was not strengthened by ankylosis of the opposing contact surfaces.

The proc. sigmoideus, medius, and posterius form a frame for the attachment of the tympanic membrane and also externally contribute to the formation of a short osseous external auditory meatus. The attachment of the annulus tendineus, which encircles the tympanic membrane, is limited to a ridge which is extended dorsally on the posterior face of the sigmoid process and horizontally on the inner edge of the base of that process; behind the latter it was lodged in a fine groove which follows along the ventral edge of the inner face of the median process; posteriorly it was attached to the anterior edge of the outer pedicle of the posterior process.

Anterior to the sigmoid process and on the outer face of the outer lip of the bulla is a longitudinal groove, which has been identified as the sulcus for the chorda tympani. Opposite this groove is the base of the anterior process which rises like a tongue to a height of about 8 mm. Its outer face is strongly concave at the base and less so distally, and its fore and hinder margins are weakly tupid. The processus tubarius on extremity of the anterior process rests in the fossa epitubaria on the proximal end of the anterior process of the periatic.

The thick convex involuted portion of the tympanic bulla is slightly and unequally depressed below the level of the thin overarchling outer lip, and is constricted rather abruptly in front of the level of the anterior process. It is grooved transversely with fine furrows.

The ventral surface of the tympanic bulla is strongly curved. On the hinder fourth of this surface is a broad, deep median furrow. Viewed from behind, the inner surface of the tympanic bulla is somewhat flattened, while the outer surface is strongly curved.

<table>
<thead>
<tr>
<th>Table 51—Measurements (in millimeters) of the tympanic bulla</th>
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<tbody>
<tr>
<td><strong>No. 14382</strong></td>
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<tr>
<td><strong>Right</strong></td>
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<tr>
<td>Maximum oblique diameter of bulla</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of bulla</td>
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<tr>
<td>Maximum transverse diameter of bulla</td>
</tr>
<tr>
<td>Vertical distance from dorsal edge of median process (conical apophysis) to ventral face of bulla</td>
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<tr>
<td>Maximum transverse diameter of involucrum</td>
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</table>
PERIODIC

The periotic of *Dorudon osiris* resembles those of other archaeocetes in its essential structural features. It is characterized in part by the dorsal prolongation of the denser outer portion to form an inwardly curved plate-like superior process, which is applied to the squamosal on the inner wall of the cranium. The elongated posterior process (pl. 18, fig. 2) is firmly wedged in between the exoccipital and the squamosal, as in the Mysticeti. The long axis of the posterior process forms an obtuse angle with the antero-posterior axis of the *pars cochlearis*, and, although it is directed outward, it is distinctly curved backward toward its distal end. The ventral surface of the posterior process is traversed by long grooves and ridges which follow in the main the curvature of this process, and between them are intercalated shorter and finer grooves. Near the middle of its length, this process measures approximately 20 mm. antero-posteriorly. At the proximal end, this posterior process is abruptly truncated and the inner face rises obliquely from the posterior excavation for the stapedial muscle.

Viewed from the ventral side (Pompeckj, 1922, pl. 2, fig. 1), the *pars cochlearis* is seen to be distinctly narrowed anteriorly and measures antero-posteriorly about 36 mm. The ventral surface of the *pars cochlearis* is irregularly convex or vaulted, the maximum convexity being behind the middle. On the anterior half of this vaulted surface is a broad longitudinal furrow which perhaps may indicate the course of the internal carotid artery. Anteriorly the ventral surface of the *pars cochlearis* rises in a moderate curvature and is separated from the anterior process by a short fissure. The inner border of the ventral or tympanic surface of the *pars cochlearis* in some instances is somewhat roughened and this condition results from the presence of numerous fine short grooves, which are rather closely spaced. The inner side of the more convex region of the ventral face of the *pars cochlearis* ends rather abruptly, forming a sharp edge which projects inward to a slight extent beyond the level of the cerebral rim of the internal acoustic meatus. In front of and behind this region, the internal margin of the *pars cochlearis* is less sharply defined and the curved ventral surface is continuous above with the internal or cerebral surface of the periotic.

The *fenestra rotunda*, which is irregularly ovoidal in outline, is situated on the hinder surface of the *pars cochlearis* and somewhat above the level of the ventral surface of the posterior process. The *fenestra rotunda* is sunk below the level of the more or less convex hinder surface of the *pars cochlearis*; its long axis is somewhat horizontal, and its transverse and vertical diameters are, respectively, about 4.5 and 3 mm. On the extero-lateral surface of the *pars cochlearis*, near its upper limit and behind the middle of its length, the *fenestra ovalis* is situated. The rim of the *fenestra ovalis*, which receives the foot plate of the stapes, is sunk below the level of the lateral surface of the *pars cochlearis*, and its fore and hinder walls slope more obliquely to the rim than do the rather steep outer and inner walls. In outline, the *fenestra ovalis* is irregularly elliptical, and measures about 4 × 3.5 mm. On the roof of the *recessus epitympanicus* and above the level of the *fenestra ovalis* is the epitympanic orifice of the Fallopian aqueduct which opens into a narrow groove, about 1 mm. in width anteriorly and separated internally from the *fenestra ovalis* by the narrow elevated rim of the latter. This groove marks the course of the facial nerve. It widens somewhat posteriorly and terminates at about the level of the antero-internal angle of the posterior process. Behind this groove is a shallow depression, which in Recent Cetacea corresponds to the area for the attachment of the stapedial muscle. The area for the attachment of this muscle furthermore is extended downward internally upon the outer face of the *pars cochlearis*. This shallow fossa is sunk below the level of the hinder end of the groove for the facial nerve.

External to the groove for the facial nerve and a little behind the epitympanic orifice of the *aquaeductus Fallopii* is a rather deep irregular little pit, about the size of a small
pin head, which constitutes the *fossa incaudis*. In front of it is a considerably larger concavity, which is located on a protuberance and is bounded externally and anteriorly by a roughened raised edge, for the reception of the head of the malleus.

In front of the last-mentioned fossa, between the anterior process and the *pars cochlearis*, is a short narrow fissure, which marks the position of a former ventrally open groove. Internal to this nearly closed fissure and upon the antero-external face of the *pars cochlearis* is an oblique groove, which can hardly have any function other than to lodge the *tensor tympani* muscle whose hinder end was inserted upon the manubrium of the malleus.

In front of the fossa for the head of the malleus, a dorso-ventrally curved groove is present on the outer face of the anterior process, and forms a ventral hollow whose surface slopes outward and upward. The outer wall of this cavity is contributed by the free edge of the squamosal behind the basal portion of the falciform process of that bone. This cavity is considered by Pompeckj (1922, p. 58) to be the *fossa epityubaria* and, if correctly identified, it lodges the *processus tubarius* of the tympanic bulla. The ventral portion of the anterior process is somewhat compressed from side to side and there is a shallow narrow groove near the extremity. The anterior process curves forward and inward; its outer surface is rather strongly convex and its inner face slopes obliquely upward to about the level of the entrance to the Fallopian canal. Above this level, which corresponds to the region where the anterior process attains its maximum transverse diameter, the inner surface of the anterior process is somewhat concave and the curvature of this surface passes imperceptibly into that of the thin plate-like superior process.

Bordering the upper edge of the *processus superior* (Pompeckj, 1922, pl. 2, fig. 3) is a broad groove which traverses the inner wall of the squamosal and possibly corresponds to the channel for the *arteriae meningeae spinalis*. In the Canidae, the inner surface of the squamosal is similarly grooved along the superior margin of the periotic, and this channel leads anteriorly to the postglenoid foramen and posteriorly it is continuous with the *sulcus* and *canalis transversus* in the supraoccipital.

Viewed from the internal or cerebral side, the thin plate-like superior process of the periotic is sub-rectangular in outline. The dorsal margin is irregular and the curved cerebral surface is somewhat pitted and more or less roughened. Below this process is the ventrally placed *pars cochlearis*. On the cerebral surface of the *pars cochlearis* is the large irregularly ovoidal internal acoustic meatus which measures about 12.5 × 7 mm. The internal acoustic meatus is considerably smaller at its *fundus* than at its cerebral rim, and it is sunk about 9 mm. deep into the *pars cochlearis*. The small *tractus spiralis foraminosus* is well defined, with a minute *foramen centrale* at its anterior end, and it is located for the most part on the ventral side of the *fundus*. A thin *crista transversa*, which does not rise to the level of the cerebral rim of the internal acoustic meatus, separates the *fundus* from the cerebral entrance to the *aquaeductus Fallopii*. At the base of the anterior face of this thin osseous partition and adjacent to the *aquaeductus Fallopii* is the minute orifice of the *foramen singulare*. The cerebral orifice of the *aquaeductus Fallopii*, through which the facial nerve passes and then emerges again in the epitympanic recess, is located at the dorso-anterior angle of the rim of the internal acoustic meatus. Behind the posterior rim of the internal acoustic meatus is a sub-triangular fossa for the *soccultus endolympathicus* and in which is located the minute cerebral orifice of the *aquaeductus vestibuli*. Below the latter and slightly nearer to the posterior rim of the internal acoustic meatus is the small cerebral orifice of the *aquaeductus cochleae*.

The measurements of the right periotic (Senckenbergischen Museum, Frankfurt a.M.) are as follows: Maximum length of periotic, end of anterior process to end of posterior process, 110 mm.; maximum dorso-ventral depth of periotic, from most inflated portion of tympanic face of *pars cochlearis* to dorsal margin of superior plate-like process, 38
mm.; maximum transverse diameter of pars cochlearis behind level of fenestra ovalis, 19 mm.; greatest length of posterior process, 65 mm.

**OSSICULA AUDITUS**

A surprising resemblance exists between the configuration of the malleus (Pompeckj, 1922, pl. 2, figs. 10–15) of *Dorudon osiris* and that of *Balaenoptera borealis*, including not only the structural peculiarities of the body, but also the details of its attachment to the outer lip of the bulla. It would appear from the material available, however, that the body of the malleus was not rotated so that its long axis was transverse to the anteroposterior axis of the tympanic bulla, as is the case in *B. borealis*. In relation to the outer lip of the bulla, the long axis of the malleus of *Dorudon osiris* seems to have been slightly oblique. Viewed from the dorsal side, the body of the malleus is seen to consist of an anterior caput mallei and a posterior collum mallei, the two structures being separated by a slight constriction. The caput mallei is conspicuously swollen and the two facets for articulation with the incus are located on its upper surface. Of these the nearly vertical upper facet is considerably larger than the transverse lower facet. From the collum mallei, a short slender process, the manubrium mallei, projects forward and inward; the tympanic surface of the manubrium mallei was attached by fibrous tissue or ligament to the corresponding surface of the tympanic membrane. There is a small depression on the outer face of the collum mallei, which corresponds to the processus muscularis, and in it the tensor tympani tendon was inserted. The body of the malleus is borne on a slender stalk, the processus anterior (longus, gracilis, or Foktanus of authors), which is laterally compressed; the extremity of this stalk-like process is fused with the outer lip of the tympanic bulla on the inner edge of the fissura Glaseri. There is a little pit for the chorda tympani on the lateral surface of the caput mallei at the base of the processus anterior. Furthermore, the processus anterior is grooved lengthwise, thus providing a channel for the chorda tympani to the sulcus on the outer lip of the bulla.

An imperfect incus has been described by Pompeckj (1922, p. 75). It measures 4.5 mm. in length, 4 mm. laterally and 2 mm. transversely. The body of the incus is feebly developed, being absorbed by the crus longum. On its base is a saddle-shaped facet for articulation with the malleus. The crus longum is bluntly conical in shape, and on its distal end is a small facet for articulation with the stapes. The crus breve was not freed from the matrix, but judging from the depth of the fossa incudis on the periotic, it was a thin slender process.

The slender stapes measures about 3.5 mm. in height and the greatest diameter of its footplate varies from 3 to 4 mm. The intercrural aperture is oval. The footplate of the stapes is closely fitted to the rim of the fenestra ovalis and its contour forms a short oval; an oval concavity is present on its vestibular face. Whether or not a distinct scar or tubercle for the attachment of the stapedius muscle was present, is as yet uncertain. In case of *Zygophora kochii*, a small tubercle for the attachment of this muscle is present on the postero-internal angle of the head. The facet which marks the area of contact with the corresponding facet on the head of the crus longum of the incus is small, oval in outline and placed slightly oblique on the head of the stapes.

**MANDIBLE**

The mandible (pl. 23, figs. 3–4) of *Dorudon osiris* is characterized by a rather slender horizontal ramus, a moderately high coronoid process, and a somewhat reduced hinder lower angle. From before backward the horizontal ramus increases in depth quite gradually up to Pm³; the increase in depth becomes more perceptible behind this tooth, and Pm⁴ marks the transition to the somewhat steeply rising convex anterior edge of the coro-
noid process.Externally the horizontal ramus is convex in front, but becomes more flatttened posteriorly; on the internal face the flat symphysial surface extends backward to about the level of the middle of Pm2. There are two small mental foramina on the outer face of this ramus below I1, one under I2, and apparently another below I3. The posterior edge of the thin coronoid process is truncated almost vertically. The condyle is broad, somewhat curved dorso-ventrally, and scarcely if at all curved from side to side. On the internal face below the coronoid process is the large orifice of the alveolar canal.

The left mandible in the Stuttgart collection (No. 11417) is much larger than the right one bearing the same catalogue number. The distance from the anterior edge of Pm2 to the hinder face of the condyle is 593 mm. on the left mandible and 536 mm. on the right mandible. Both of these mandibles (pl. 23, figs. 1–2) when complete were longer than all other mandibles referred to this species. The larger one belonged to an individual with a skull longer than the one in London (No. M. 10228, B.M.). This left mandible is therefore tentatively referred to Dorudon osiris, since available evidence indicates that this species attained a larger size than the other smaller archaeocetes of the Qasr-el-Sagha stage.

**Table 52—Measurements (in millimeters) of mandibles**

<table>
<thead>
<tr>
<th></th>
<th>No. M. 11417 Berlin Left</th>
<th>No. 1932 XI. 59 Munich Right</th>
<th>No. 1934 XII. 154 Munich Left</th>
<th>No. 11527 Stuttgart Right</th>
<th>No. 11417 Stuttgart Left</th>
<th>No. 11417 Stuttgart Left</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of mandible, from hinder face of condyle to extremity</td>
<td>...</td>
<td>570±</td>
<td>711</td>
<td>718± 747±</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Vertical height of mandible through coronoid process</td>
<td>...</td>
<td>177</td>
<td>160</td>
<td>177± 256</td>
<td>263±</td>
<td>...</td>
</tr>
<tr>
<td>Vertical diameter of condyle</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Antero-posterior diameter of symphysis</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Vertical height of mandible at level of I2</td>
<td>30</td>
<td>38</td>
<td>25</td>
<td>47.5</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Vertical height of mandible at level of C</td>
<td>...</td>
<td>60</td>
<td>60</td>
<td>...</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Vertical height of mandible at level of Pm2</td>
<td>45</td>
<td>58</td>
<td>52</td>
<td>70.5 80.2 89.5</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Vertical height of mandible at level of Pm3</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>82.1 92</td>
<td>...</td>
</tr>
<tr>
<td>Vertical height of mandible at level of M3</td>
<td>...</td>
<td>115</td>
<td>...</td>
<td>174</td>
<td>174</td>
<td>...</td>
</tr>
<tr>
<td>Anterior edge of Pm2 to hinder edge of M3</td>
<td>210</td>
<td>235</td>
<td>240±</td>
<td>255</td>
<td>167</td>
<td>195</td>
</tr>
<tr>
<td>Posterior edge of M3 to hinder edge of coronoid process</td>
<td>...</td>
<td>180±</td>
<td>...</td>
<td>128.5</td>
<td>167</td>
<td>195</td>
</tr>
<tr>
<td>Posterior edge of M3 to hinder face of condyle</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>200</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Diastema between Pm2 and Pm3</td>
<td>10</td>
<td>22</td>
<td>16</td>
<td>7</td>
<td>...</td>
<td>...</td>
</tr>
</tbody>
</table>

**PERMANENT DENTITION**

The tooth formula is: \(4 \cdot 1.4.3 \cdot 6 \cdot 1.4.3\). The upper and lower dentition is not only heterodont, but also semi-aniisodont. At the anterior end of the upper tooth row, the pits for the reception of the apices of the mandibular grasping teeth are located on the outer side of the single-rooted teeth, while the larger fossae for the apices of the mandibular cheek teeth are on the inner side of the two-rooted teeth, showing that the upper and lower tooth series cross over when the jaws are closed. The distance from the anterior edge of alveolus of the first incisor to the anterior edge of alveolus of the second premolar is certainly greater above than below, and conversely the hinder portion of the lower tooth series is much longer than the corresponding portion of the upper. The incisors and the canine have a thin enamel coat on the crown, which is distinctly striated vertically. The first upper incisor, which is situated 18 to 20 mm. behind the anterior end of the premaxillary, curves downward and backward, while the first lower incisor, which is situated at the extreme end of the mandible, curves forward and upward. The implantation of the incisors and the canine in the mandible tends to accentuate their forward and upward curvature, while the corresponding single-rooted teeth in the upper jaws are directed more downward than backward. The crown of I2 is strongly compressed from side to side, and the apical portion curves backward and inward. The crowns of I3 and C are similar to that of I2.
The enamel on the crown of Pm1 is faintly striated. It is somewhat larger than the C, and below the base of the crown the root is pinched-in at the middle of its outer and inner faces, giving the appearance of two roots. The crown of Pm1 is less flattened from side to side than those of the following cheek teeth, and this tooth marks the transition between the attenuated crowns of the single-rooted grasping teeth and the laterally compressed serrated crowns of the shearing teeth.

The crown of Pm2 is distinctly longer than that of the corresponding lower premolar, and furthermore its anterior edge slopes less steeply than that of the latter. In addition to a high principal cusp, there are two accessory denticles and a small basal tubercle on the anterior cutting edge of the crown of Pm2, and three accessory denticles on the hinder cutting edge. The accessory denticles are smaller and farther removed from the apex of the principal cusp on the anterior cutting edge than on the posterior. The enamel on the outer face of the crown is faintly striated vertically. Distinct crenelations are occasionally present on the anterior cutting edge of the principal cusp. Pm3 to M2 form a closed series, and ordinarily there is an interval of 4 to 5 mm. separating Pm2 and Pm3.

Of the upper serrate-edged cheek teeth, the crown of Pm3 (pl. 22) is generally slightly longer than that of either Pm2 or Pm4. The crown of Pm3 is also somewhat shorter than that of the corresponding lower premolar. There are three accessory denticles on the anterior cutting edge of the crown and a rudimentary denticle at the base of the anterior edge of the principal cusp; three accessory denticles are present on the hinder cutting edge of the crown. These accessory denticles increase in size from the base to the apex of the crown.

Two large and one small basal accessory denticles are present on both the anterior and the posterior cutting edges of the crown of Pm4 (pl. 22), the upper one on the hinder edge being slightly nearer the apex of the principal cusp than the corresponding one on the anterior edge. The crown of Pm4 is smaller than that of Pm3, and the enamel on the outer face is faintly and sparsely striated vertically. A slight cinguloid ridge is developed above the anterior and posterior roots on the outer face of the crowns of Pm3 and Pm4. On both of these premolars, the hinder root is somewhat larger than the anterior one.

The first upper molar (pl. 22) is noticeably smaller than Pm4, and the principal cusp is relatively low. There are one large and one minute basal accessory denticles on the anterior edge of the crown and two large accessory denticles on the hinder edge. The enamel on the outer face of the crown is relatively smooth.

The second upper molar is much smaller than M1 and the uppermost one of the two accessory denticles on the hinder edge of the crown is about equivalent in size to the single accessory denticle on the anterior edge. The principal cusp is considerably larger than any of the accessory denticles. In the upper jaw, the serrate-edged cheek teeth are implanted slightly obliquely, so that the anterior basal portion of the crown of each tooth is placed on the outer side of the hinder basal angle of the preceding tooth.

The single-rooted Pm1 seems to have had a lower crown than that of Pm1 and there is no perceptible median furrow on the root. A small basal accessory denticle is present on the hinder face of the crown.

The high principal cusp of Pm2 is compressed from side to side; there are two small denticles on the anterior edge of the crown, and two large accessory denticles and a small basal denticle on the posterior edge. The interval between Pm2 and Pm3 is quite variable; on the type mandible (No. M. 16, Berlin) it is about half the length of the interval between C and Pm1, and also of the interval between Pm1 and Pm2, while on another mandible (No. 1902. XI. 59, Munich) the former interval is only a few millimeters shorter than either of the latter. On the type mandible, Pm3 to M3 form a closed series.

In the mandible, Pm3 is the largest tooth in the premolar-molar series. The high crown of this tooth is furnished with three accessory denticles on its anterior cutting edge,
### Table 53—Measurements (in millimeters) of premaxillary and maxillary teeth

<table>
<thead>
<tr>
<th></th>
<th>M2</th>
<th>M1</th>
<th>Pm4</th>
<th>Pm3</th>
<th>Pm2</th>
<th>Pm1</th>
<th>C</th>
<th>I3</th>
<th>I2</th>
<th>I1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Antero-posterior diameter at base of enamel crown</td>
<td>R.</td>
<td>L.</td>
<td>R.</td>
<td>L.</td>
<td>R.</td>
<td>L.</td>
<td>R.</td>
<td>L.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(No. 14882, A. M. N. H.)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vertical height of enamel crown, from level of line drawn between antero- and postero-basal angles and apex of principal cusp (No. 14882, A. M. N. H.)</td>
<td>18.7</td>
<td>27.5</td>
<td>27.5</td>
<td>38</td>
<td>41</td>
<td>41.2</td>
<td>39</td>
<td>36.6+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antero-posterior diameter at base of enamel crown (No. 1907. XI. 59, Munich)</td>
<td>11.7</td>
<td>15</td>
<td>26.2</td>
<td>31</td>
<td>31</td>
<td>29+32.2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum transverse diameter at base of enamel crown (No. 1907. XI. 59, Munich)</td>
<td>20</td>
<td>39</td>
<td>42</td>
<td>43</td>
<td>26</td>
<td>22</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antero-posterior diameter at base of enamel crown (No. M. 19228, Brit. Mus.)</td>
<td>12</td>
<td>18</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum transverse diameter at base of enamel crown (No. M. 19228, Brit. Mus.)</td>
<td>18+</td>
<td>39.7</td>
<td>38.4</td>
<td>48.4</td>
<td>48.3</td>
<td>48.3</td>
<td>30+32</td>
<td>22.3+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antero-posterior diameter at base of enamel crown (No. 11626, Stuttgart)</td>
<td>22</td>
<td>20</td>
<td>26</td>
<td>23</td>
<td>36</td>
<td>38.5</td>
<td>45</td>
<td>50</td>
<td>47</td>
<td>41.2</td>
</tr>
<tr>
<td>Maximum transverse diameter at base of enamel crown (No. 11626, Stuttgart)</td>
<td>13±</td>
<td>20±</td>
<td>16</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

### Table 54—Measurements (in millimeters) of the mandibular teeth

<table>
<thead>
<tr>
<th></th>
<th>M3</th>
<th>M2</th>
<th>M1</th>
<th>Pm4</th>
<th>Pm3</th>
<th>Pm2</th>
<th>Pm1</th>
<th>C</th>
<th>II</th>
<th>III</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum transverse diameter at base of enamel crown (No. M. 16, Berlin)</td>
<td>28</td>
<td>25</td>
<td>30</td>
<td>45</td>
<td>45</td>
<td>35</td>
<td>25</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antero-posterior diameter at base of enamel crown (No. 1902. XI. 59, Munich)</td>
<td>34</td>
<td>26</td>
<td>28</td>
<td>27</td>
<td>50.2</td>
<td>53</td>
<td>49</td>
<td>36.4</td>
<td>26</td>
<td></td>
</tr>
<tr>
<td>Maximum transverse diameter at base of enamel crown (No. 1902. XI. 59, Munich)</td>
<td>13</td>
<td>15</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>16.5</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>Antero-posterior diameter at base of enamel crown (No. 11627, Stuttgart)</td>
<td>29.3</td>
<td>27.3</td>
<td>31.5</td>
<td>50.6</td>
<td>59.3</td>
<td>43.3</td>
<td>24.4</td>
<td>29</td>
<td>29</td>
<td>30.5</td>
</tr>
<tr>
<td>Maximum transverse diameter at base of enamel crown (No. 11627, Stuttgart)</td>
<td>18</td>
<td></td>
<td>18</td>
<td></td>
<td>14</td>
<td>18</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1. Dpm4.
and three larger ones as well as a small basal one on its posterior edge. The anterior and posterior cutting edges of the principal cusp are often crenelated. The principal cusp of Pm₄ projects a little higher than that of Pm₃, and the three accessory denticles on the anterior cutting edge do not extend as far upward on the crown as the four on the posterior edge. The enamel on the two hinder premolars, especially on the inner side of the crown, is ornamented with a series of more or less vertical striæ which anastomose at intervals; this ornamentation does not extend over upon the fairly smooth surface of the posterior accessory denticles. The transverse diameter of the anterior and posterior roots of the two hinder lower premolars are more nearly equal in contrast to the marked disparity in the size of the roots of the corresponding premolars in the upper jaw.

The three molars in the mandible (Dames, 1894, pl. 1, fig. 1a) have a large anterior principal cusp. The anterior face of the principal cusp of M₁, M₂, and M₃ is also characterized by the presence of a broad vertical groove, into which is fitted the hinder edge of the preceding tooth. Three large accessory denticles are present on the hinder edge of M₁. There are at least three accessory denticles on the hinder edge of the crown of M₂ and four on M₃. The antero-posterior diameter of the crown of M₂ is slightly shorter than that of either M₁ or M₃. The slope of the posterior cutting edge of the crown increases in steepness from the first to the hindermost molar. The molars are situated on the rising anterior edge of the coronoid process.

DECIDUOUS DENTITION

The deciduous dental formula is: Di \( \frac{1.2.3}{1.2.3} \), De \( \frac{1}{1} \), Dpm \( \frac{1.2.3.4}{1.2.3.4} \). The tooth succession of this species is fairly well known and it is of interest that the replacement of the deciduous dentition is completed rather late in the animal's growth. The following comments are based on three specimens (Nos. 11786 and 11626, Stuttgart; and No. 1904. XII. 134, Munich), which retain a considerable portion of the deciduous dentition.

As regards the premaxillary and maxillary teeth, the deciduous single-rooted teeth are similar in conformation to the corresponding permanent teeth. In the Di and De, at least, the enamel on the outer surfaces of the crown is smooth.

Dpm₁ has a somewhat laterally compressed conical crown, with sharp anterior and posterior cutting edges, a small anterior and a slightly larger posterior basal accessory denticle, and rather smooth enamel. On Dpm₂ the sharp anterior cutting edge is somewhat steeper than the posterior edge, and it has a basal accessory denticle; there are two accessory denticles on the posterior cutting edge. The enamel on the crown of this tooth is smooth externally and somewhat wrinkled behind internally. The Dpm₃ is similar to Pm₃, but it has three accessory denticles on the anterior cutting edge. The crown of this tooth is thickened internally and the enamel extends downward here somewhat farther than on the external surface. This deciduous tooth is three rooted. The enamel crown of Dpm₄ is smooth externally and there are two accessory denticles on the anterior cutting edge and two larger ones in addition to a small basal tubercle on the posterior cutting edge. This tooth certainly has three roots and Stromer (1908b, p. 113) has recognized a remnant of a fourth root in another tooth (No. 1904. XII. 134, Munich).

It is impossible to interpret the presence of three distinct roots on the hinder upper deciduous teeth, Dpm₃ and Dpm₄, otherwise than another confirmation of the extensive remodeling which the archaeocete tooth has been subjected to, in addition to the lateral compression of its crown and the accompanying development of serrated cutting edges. Their successors in the permanent dentition, Pm₃ and Pm₄, have two roots but the hinder one is somewhat thickened.

In the mandible, Di and De are distinguished from the corresponding permanent teeth chiefly by their smaller size. The Dpm₁ is not preserved on any of the mandibles.
Dpm² has two roots and is slightly shorter than Pm². A trifling difference in size exists between Dpm³ and Pm³, but otherwise there are no salient differences. Dpm⁴ is quite similar in appearance to Pm⁴. The anterior cutting edge of Dpm⁴ is somewhat steeper than the hinder edge. There are four accessory denticles and a weak basal swelling on the anterior edge, while three large accessory denticles and a quite small one are present on the posterior edge.

ENDOCRANIAL CAST

Imperfections in the artificial endocranial cast (No. M. 8150, B. M.), which was described and figured by Elliot Smith (1903), resulting possibly from the imperfect cleaning of the inner surface of the cranium, distort the general features of this brain mass. The artificial cast of the cranial cavity of another skull (No. M. 10228) in the British Museum (Nat. Hist.) lacks the anterior portions of the olfactory peduncles and likewise the anterior portions of the trigeminal apparatus. The shrivelled and shrunken appearance of this endocranial cast indicates an obvious dwindling of the brain substance, not only in the olfactory and trigeminal regions, but also in the cerebrum, cerebellum, and medulla oblongata.

The remarkably complete cast of the whole interior of the right side of the brain case, including the olfactory peduncle from its origin in the olfactory bulb to its insertion on the ventral surface of the cerebrum, has been exposed in a juvenile skull in the Stuttgart collection (No. 11786). This has been described and figured by Stromer (1905b, pl. 5, figs. 12, 13). The olfactory peduncles are quite slender and terminate anteriorly in an enlarged olfactory bulb. The length of the slender olfactory peduncle (diameter 5 mm.) is not quite twice the antero-posterior length of the brain mass, the actual distance from the base of the cerebrum anteriorly to the distal end of the olfactory bulb being 145 mm. The cast of the slender optic nerve (diameter 3 mm.), which is quite distinct at the level of the point of divergence of the anterior divisions of the trigeminal from their contact with the olfactory peduncle behind the level of the sphenoidal fissure, extends forward to the optic foramen, and thence continues forward and outward along the under surface of the supraorbital process of the frontal. The endocranial portion of the optic nerve extends forward below the level of the olfactory peduncle. The anterior portion of the ophthalmic division of the trigeminal has been destroyed; the maxillary division emerges from the cranium through the sphenoidal fissure. The maxillary trunk of the trigeminus measures 6 mm. in width and 18 mm. in height near its base. Dart (1923, p. 618) contends that this endocranial cast (No. 11786, Stuttgart) has been incorrectly identified and that it "more nearly resembles the Prozeuglodon atrox Andrews or is intermediate between Prozeuglodon atrox and the Zeuglodon intermedius." The cranial and dental characters of this juvenile skull are, however, clearly those of Dorudon osiris.

Some of the peculiarities displayed in these casts of the brain mass, especially the size and relative proportions of the different parts, have resulted in part from the effects of crushing and of distortion of the cranium and in part from differences in size and age of the skulls. The skull in the British Museum (No. M. 10228) is the largest of the five that have been described and is slightly larger than the largest specimen in the Stuttgart collection (No. 11626). The juvenile skull in the Stuttgart collection (No. 11786) with the exposed endocranial cast is slightly smaller than the skull in the Munich collection (No. 1902. XI. 59) and the latter is approximately the same size as the skull in the Geological Museum at Cairo (No. 10018) for which there is a cast in the British Museum (No. M. 8150).

In view of the intimate relation of the olfactory bulb with the inner cavity of the naso-turbinal, which in turn is bounded externally by the frontal sinus, and since the hinder ends of the nasal bones lie approximately at the level of the middle of the frontal sinuses,
a comparative estimate of the relative antero-posterior lengths of the brain mass and olfactory apparatus of these two specimens is afforded by the relative distances between the posterior ends of the nasal bones and the apex of the supraoccipital shield. In the case of the British Museum specimen (No. M. 10228) this distance is 292 mm. and in the Stuttgart specimen (No. 11786) it is 225.5 mm. The total length of the endocranial cast in the British Museum, including the brain mass, olfactory peduncles and olfactory bulb, when complete should be approximately 283 mm., and the distance from the anterior surface of the cerebrum at base to the distal end of the olfactory bulb about 185 mm.

The "gouged-out" appearance of the anterior face of the diminutive cerebrum (Dart, 1923, fig. 16), a modification which is more marked in the larger artificial endocranial cast (No. M. 10228, B. M.) than in the smaller natural endocranial cast (No. 11786, Stuttgart), reveals the degenerate condition of this region. The atrophy of the olfactory region of the cerebrum is more pronounced than in the other smaller archaeocetes. Each cerebral hemisphere is bounded medially on the dorsal aspect by the sagittal sinus, posteriorly by the cerebellum, and ventro-laterally by the Gasseri ganglion. Behind the prominence of the sagittal sinus is a well-marked median tentorial depression from which a narrow and deep transverse tentorial sulcus extends laterally, separating the cerebellum and the cerebrum. The prominence of the sagittal sinus on the natural endocranial cast is bounded laterally by a long furrow and it also increases posteriorly to a width of 15 mm. The Gasseri ganglion (Dart, 1923, fig. 15) is relatively small in comparison to the other Fayum forms, and its stranded position lateral to the cerebrum is held by Dart (1923, p. 632) to show that this form is descended from a type in which the trigeminal apparatus was a more significant structure. The cast of the middle cerebral vessels fills the Sylvian depression. The flattening of the brain mass accentuates the extreme disproportion between the large cerebellum and the diminutive cerebrum. The cerebellum is large but crumpled, and is elevated 15 to 20 mm. above the cerebrum along the tentorial sulcus. The lobus medius cerebelli is quite asymmetrical, but is poorly developed. On the natural endocranial cast (No. 11786, Stuttgart), the convolutional pattern of the lobus medius cerebelli is quite distinct. Each of the two hinder divisions of the lobus medius cerebelli on this natural endocranial cast measure about 34 mm. in transverse diameter.

The laterally placed paraflocculi do not bulge out over the acoustic region, but are contracted toward the lobus medius cerebelli. These paraflocculi constitute the greatest part of the cerebellar mass. Dart (1923, p. 632) considers that the space between the middle cerebral vessels and the jugular leashes, lateral to the paraflocculus, is devoid of brain substance and that it seems to have been occupied by venous sinuses. The posterior view (Dart, 1923, fig. 17) reveals best of all the general flattening of the brain and also the dorso-ventral compression of the medulla oblongata. The cast of the medulla oblongata on the natural endocranial cast (No. 11786, Stuttgart) at the foramen magnum measures 34 mm. transversely and 23 mm. vertically. The increased thickening of the roof of the cranium and the accompanying elevation of the sagittal crest is apparently correlated with this dorso-ventral flattening of the brain mass. The transverse furrow below the lobus medius cerebelli on the posterior aspect of the cerebellum, which marks the position of the secondary tentorial bony projection, is very wide and scalloped out, indicating that this shelf became greatly reinforced in thickness internally coincident with the pinching-in of the lambdoidal crests. This thickened transverse tentorial bony projection has been exposed on the juvenile skull (No. 11786) in the Stuttgart collection.

The boundaries of the jugular leashes are not sharply delimited on this cast. The cubic capacity of the artificial endocranial cast (No. M. 10228) in the British Museum is approximately 480 c.c. For the dimensions of these endocranial casts see table 55 (p. 200).
Table 55—Measurements (in millimeters) of endocranial casts

<table>
<thead>
<tr>
<th></th>
<th><em>D. caeris</em> No. 11786, Stuttgart</th>
<th><em>D. ellioti-oebeli</em> No. 12055, B. M.</th>
<th><em>D. sensitsinus</em> No. 12123, B. M.</th>
<th><em>D. intermedius</em> No. 11786, B. M.</th>
<th><em>P. oyro</em> (in text) No. 12066, B. M.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Distance from hinder face of cerebellum to extremity of olfactory lobe</strong></td>
<td>219</td>
<td>219</td>
<td>120.5</td>
<td>155</td>
<td>122.3</td>
</tr>
<tr>
<td><strong>Greatest antero-posterior diameter, as preserved</strong></td>
<td>127.7</td>
<td>127</td>
<td>127</td>
<td>124</td>
<td>124</td>
</tr>
<tr>
<td><strong>Greatest transverse diameter of brain mass</strong></td>
<td>100±</td>
<td>90±</td>
<td>127±</td>
<td>141.3</td>
<td>122.4</td>
</tr>
<tr>
<td><strong>Greatest length of brain mass</strong></td>
<td>100±</td>
<td>90±</td>
<td>127±</td>
<td>141.3</td>
<td>122.4</td>
</tr>
<tr>
<td><strong>Greatest transverse diameter of cerebrum</strong></td>
<td>94±</td>
<td>96±</td>
<td>89.5</td>
<td>90±</td>
<td>98±</td>
</tr>
<tr>
<td><strong>Greatest inter-parafloccular width</strong></td>
<td>193</td>
<td>127±</td>
<td>136.4</td>
<td>177</td>
<td>153.5</td>
</tr>
<tr>
<td><strong>Length of cerebellar hemisphere (measured to tentorial suture)</strong></td>
<td>52</td>
<td>47±</td>
<td>64</td>
<td>56</td>
<td>47</td>
</tr>
<tr>
<td><strong>Height of cerebellar projection above cerebrum along tentorial suture</strong></td>
<td>15-20</td>
<td>10</td>
<td>10-20</td>
<td>20-25</td>
<td>20-25</td>
</tr>
<tr>
<td><strong>Width of median lobe of cerebellum—</strong></td>
<td>60±</td>
<td>57</td>
<td>53</td>
<td>65</td>
<td>64</td>
</tr>
<tr>
<td></td>
<td>1. in the region of Area B</td>
<td>60±</td>
<td>100</td>
<td>91</td>
<td>66</td>
</tr>
<tr>
<td></td>
<td>2. in the region of Area C</td>
<td>57</td>
<td>53</td>
<td>65</td>
<td>64</td>
</tr>
<tr>
<td><strong>Greatest height of brain-mass, from base of lateral projections to lobus medius cerebelli</strong></td>
<td>65.9</td>
<td>63±</td>
<td>68.8</td>
<td>92.5</td>
<td>96</td>
</tr>
<tr>
<td><strong>Greatest antero-posterior diameter of cerebrum, measured midway along tentorial suture</strong></td>
<td>41</td>
<td>38</td>
<td>28</td>
<td>30</td>
<td>43</td>
</tr>
<tr>
<td><strong>Anterior end of sagittal sinus to level of hinder face of lobus medius cerebelli</strong></td>
<td>83.6</td>
<td>79±</td>
<td>100</td>
<td>91.5</td>
<td>85±</td>
</tr>
<tr>
<td><strong>Anterior surface of right Gasserian ganglion to posterior face of paraflocculus</strong></td>
<td>63.9</td>
<td>31.2</td>
<td>85</td>
<td>76</td>
<td>82.5±</td>
</tr>
<tr>
<td><strong>Antero-posterior diameter of right paraflocculus</strong></td>
<td>41</td>
<td>31.2</td>
<td>35.6</td>
<td>43</td>
<td>46.7±</td>
</tr>
<tr>
<td><strong>Transverse diameter across posterior projections of lobus medius cerebelli</strong></td>
<td>41.4</td>
<td>34</td>
<td>61.5</td>
<td>69.5</td>
<td>58</td>
</tr>
<tr>
<td><strong>Width of medulla oblongata at foramen magnum</strong></td>
<td>20</td>
<td>23</td>
<td>310 cc.</td>
<td>490 cc.</td>
<td>785 cc.</td>
</tr>
</tbody>
</table>

1 Left.

Narial Cavity

The sinuses and canals which comprise the narial cavity are exposed on the juvenile skull in the Stuttgart collection (No. 11786). The paired naso-pharyngeal ducts commence at the hinder opening of the rather wide internal choanae (Stromer, 1908b, pl. 5, fig. 13, w) and slope obliquely upward. On the hinder part of the exposed cast is the large frontal sinus (f). The longitudinal grooves on the dorsal surface of the frontal sinus mark the position of its inner chambers which are enclosed by the scroll-like ethmoturbinals. Below the frontal sinus is a small sinus with two thin lamellae, which Stromer (1908b, pl. 5, fig. 13, w) identified as the sinus sphenoidalis. In the median line adjacent to the frontal sinus is the cast of the slender nasoturbinal (g). The lower maxillary sinus (e) has a more rounded lateral angle than in *Dorudon zittelli*. The cast of the relatively long lachrymal canal (c) which widens out near the middle, shows that it originates in the narial cavity and that it is gradually attenuated toward its orifice in the lachrymal bone. The lachrymal canal lies above the somewhat wider longitudinal infraorbital canal (b).

Vertebrae

Cervical Vertebrae

To this species are referred an atlas and an axis (No. 1904, XII. 134c, Munich), as well as the atlas, axis, third and sixth cervical vertebrae of another individual1 (No. 13140, Stuttgart). The atlas is quite similar to that of *Dorudon stromeri* and its dimensions are approximately the same. The measurements of the atlas in the Munich collection are as

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1 The description of these cervical vertebrae, which was being prepared by Prof. J. Pompeckj, apparently was not completed prior to his untimely death on July 8, 1930. These vertebrae were neither studied critically nor measured by the writer during his stay in Berlin during April 1930.
follows: Vertical diameter, 122 mm.; greatest breadth, 196.5 mm.; distance between outer edges of anterior articular facets, 128 mm.; and distance between outer edges of posterior articular facets, 116.7 mm.

The axis has a transverse oval neural canal, thin transverse processes perforated at the base by a vertebrarterial canal, a weak median ridge near hinder end of ventral face of centrum, and a short neural spine with posteriorly flattened extremity. The measurements of the axis (No. 1904. XII. 134c, Munich) are as follows: Length of centrum, 25± mm.; length of odontoid process, 30 mm.; transverse diameter of posterior face of centrum, 51 mm.; vertical diameter of posterior face of centrum, 37 mm.; transverse diameter of neural canal anteriorly, 30 mm.; and vertical diameter of neural canal anteriorly, 27 mm.

Dorsal Vertebrae

So far as known the dorsal vertebrae (No. 1904. XII. 134b, Munich) of this species are essentially similar to those of Dorudon stromeri. The measurements of one of the posterior dorsal vertebrae are as follows: Antero-posterior diameter of centrum, without epiphyses, 50 mm.; vertical diameter of centrum, 61.5 mm.; distance between ends of transverse processes, 118 mm.; and antero-posterior diameter of neural spine at base, 53.2 mm.

Lumbar Vertebrae

Six lumbar vertebrae (No. 11237a, Stuttgart) are tentatively referred to this archaeocete. They seem to be too small to have belonged to an archaeocete the size of Dorudon stromeri. These vertebrae and one additional vertebra were used by Stromer (1908b, pl. 4, fig. 1) in his reconstruction of a Dorudon skeleton.

Assuming that this archaeocete has the same number of lumbar vertebrae as Zygorhiza kochii, then these six lumbers belong at the hinder end of the series. Stromer (1908b, p. 122) also states that the six lumbar and the eight caudal vertebrae constitute a consecutive series. Granting that this interpretation is correct, the first vertebra is then the tenth in the lumbar series. The measurements of the tenth lumbar vertebrae are as follows: Length of centrum, 54 mm.; transverse diameter of centrum anteriorly, 53 mm.; and vertical diameter of centrum anteriorly, 53 mm.

The fourth in the series studied by Stromer is here designated as the thirteenth lumbar. This vertebra (Stromer, 1908b, pl. 4, fig. 15) is the largest in the series; the measurements are as follows: Length of centrum, 60 mm.; transverse diameter of neural canal, 20± mm.; vertical diameter of neural canal, 15± mm.; and height of neural spine, 48± mm.

The basal portions of the neural spines are preserved on the tenth and eleventh lumbar vertebrae, and indicate that these processes are rather wide antero-posteriorly on the hinder lumbers. The anterior edge of both pedicles of the neural arch at the base is nearer the anterior end of the centrum than the posterior edge is to the hinder end. The dorsoventrally flattened transverse processes arise below the middle of the lateral surface of the centrum. On the tenth lumbar the transverse processes are 80± mm. long. On the tenth to the thirteenth lumbers at least, these processes are attenuated toward the extremity, and are directed outward and downward. At the base the hinder edges of the transverse processes are nearer the posterior end of the centrum than the anterior edges are to the anterior end. The ends of the centra are transversely oval in outline and the ventral profile viewed from the side exhibits a slight concave curvature from end to end. All of these hinder lumbers have two foramina on the ventral face of the centrum. A weak median longitudinal carina is present on the ventral face of the centrum of the fourteenth (? first sacral) and the fifteenth (? second sacral) lumbar vertebrae.
Distinct and rather closely approximated prezygapophyseal facets, which are flat and oval in outline, are present on the tenth and eleventh lumbar vertebrae. The postzygapophyseal facets seem to be present on the tenth lumbar, but they are certainly vestigial on the twelfth lumbar vertebra. The elongated metapophyses of the hinder lumbar vertebrae are slender, flattened from side to side, and project upward and forward beyond the level of the anterior end of the centrum.

Of the two lumbar vertebrae collected by Schweinfurth on the eastern island (El Kenissa) of Birket-el-Qurun and referred to Dorudon osiris by Dames (1894, pp. 199–200), one (Dames, 1894, pl. 34, figs. 1a, 1b) is certainly too large to have belonged to this species, and the other (Dames, 1894, pl. 35, figs. 1a–1c) belonged to an individual somewhat larger than the vertebrae (No. 11237, Stuttgart) described above. Stromer (1908b, p. 124) has already expressed the same opinion.

**Caudal Vertebrae**

Eight caudal vertebrae (No. 11237a, Stuttgart), belonging to the same individual as the preceding lumbar vertebrae, are likewise figured by Stromer (1908b, pl. 4, fig. 1). The length of this consecutive series of fourteen lumbar and caudal vertebrae is stated by Stromer (1908b, p. 122) to be about 900 mm.

On the second in this caudal series, the rather wide transverse processes are 60 ± mm. long and are truncated at the extremity.

The transverse processes of the third in this caudal series are pierced at the base near the anterior edge by a foramen. In the caudal series of Zygorhiza kochi, however, it is certain that no foramina are present in the transverse processes of the five anterior caudals and there is evidence to indicate that the eighth in this series is the first one with perforated transverse processes. Since the twelve hinder caudal vertebrae of Dorudon serratus (Gibbs, 1847, pl. 2, fig. 8) are not duplicated among these caudal vertebrae of D. osiris, the perforation of the transverse processes of the anterior caudals may constitute another distinction between Dorudon and Zygorhiza. Centrum of third caudal is 56 mm. long.

On the fourth to the eighth caudal in this series, the transverse processes are pierced near the center of the base by a foramen. A vertical groove that leads to this foramen is present on the lateral surface of the centra of the sixth to the eighth caudals in this series.

All of these eight caudal vertebrae have two prominences at the hinder end of the ventral face of the centrum for articulation with the chevron bones. The two hinder ones also have an additional pair of such prominences at the anterior end of the ventral face of the centrum. The centrum of the eighth caudal measures 52 mm. antero-posteriorly and 45 ± mm. transversely at the anterior end.

The first and second caudal vertebrae have short neural spines. The neural spines are, however, reduced to a carinate ridge on the third to sixth caudal vertebrae, inclusive. The fourth caudal has a very low neural canal. On the fifth caudal (Stromer, 1908b, pl. 4, figs. 16–17) the greatly reduced neural canal is wider than high, the antero-posterior diameter of the short transverse processes is slightly less than the length of the centrum, and the metapophyses project forward beyond the level of the anterior end of the centrum. The six anterior caudals, at least, have a shallow depression, corresponding in position to that of the prezygapophyseal facets, which connects the basal portions of the elongated metapophyses. The hinder caudal vertebrae in this series have an attenuated process projecting backward from the roof of the neural arch.

The two imperfectly preserved caudal vertebrae, which were collected by Schweinfurth on the eastern island (El Kenissa) of Birket-el-Qurun and which were referred to Dorudon osiris by Dames (1894, p. 200, pl. 36, figs. 1a–1c), probably belong to some slightly larger species. It is quite possible that the smaller of the two lumbers referred to previously and these two caudals may belong to Dorudon intermedius.
FORELIMB

So far as known, no forelimb bones have been found associated with a skull of this archaeocete. The isolated bones hereinafter described are tentatively allocated to this species. Judging from the number of skulls that have been collected, *Dorudon osiris* appears to be the most abundant archaeocete in the Qasr-el-Sagha stage and the probabilities are that some of these limb bones belong to this archaeocete. Included among the bones referred to *Dorudon osiris* are the left humerus, radius, and ulna of one individual (No. 13139, Stuttgart), and an isolated ulna (No. 1922. IX. 8, Munich). The configuration of the scapula, which is unknown, is probably similar to that of *Dorudon stromeri* and *D. zitteli*.

HUMERUS

The humerus is characterized by the lateral flattening of the shaft, by the width of the proximal end, and by the curvature of the prominent deltoid crest. At the distal end of the shaft, the posterior olecranon fossa is rather small, but the anterior supratrochlear fossa is well defined. The measurements of the left humerus are as follows: Greatest length, 237.5 mm.; antero-posterior diameter of proximal end, including greater tuberosity, 79.5 mm.; antero-posterior diameter of shaft through distal portion of deltoid crest, 79 mm.; and antero-posterior diameter of outer condyle, 35 mm.

RADIUS

The shaft of the radius is compressed from side to side, but the external and internal faces are slightly convex. The antero-posterior expansion of the shaft below the head is less pronounced than in *Zygaphiza kochii* and the angle thus formed is less prominent. The articular facet on the proximal end for articulation with the trochlea of the humerus is transversely oval in outline and shallowly concave. The radius referred to *Dorudon stromeri* (p. 211) may belong instead to this species.

ULNA

In all essential features, the ulnae tentatively referred to this species are quite similar to that (No. 11239a, Stuttgart) described under *Dorudon stromeri*. Hence no further discussion is necessary in view of the present uncertainty as regards the allocation of isolated limb bones. One of these ulnae (No. 1922. IX. 8, Munich), which is eroded at both ends, measures: Length, 146+ mm.; dorso-ventral diameter of greater sigmoid cavity, 37.5 mm.; and transverse diameter of distal end of shaft, 43.2 mm.

DORUDON STROMERI (Kellogg)


Type locality—Fayum, Egypt. From a grayish-green fine-grained soft sandstone belonging to the Qasr-el-Sagha stage. Upper Eocene.

Type specimen—An almost complete and very slightly crushed skull of an immature individual, which lacks both jugals, both lachrymals, the anterior extremity of the left zygomatic process, the postero-external portion of the left supraorbital process, and the hinder ascending processes of the premaxillaries. The first and second incisors, the canine, the first premolar, and the second molar are missing in both upper jaws. The erupting third upper incisors are visible in the alveoli. The crowns of the serrate edged deciduous cheek teeth are damaged and the enamel is destroyed. The tympanic bullae and the periotics are attached to the skull. Both mandibles lack the anterior extremity and the
hinder lower angle. The right mandible has alveoli for I₂, I₃, C, and Pm₁; the following serrate edged cheek teeth are present: Dpm₂, Dpm₃, Pm₄ (apex of crown visible in alveolus, erupting), M₁ and M₃. The left mandible has alveoli for I₂, I₃, C, and Pm₁; the following serrate edged cheek teeth are present: Dpm₂, Dpm₃, Pm₄ (apex of crown visible in alveolus, erupting), and M₁. Eight detached teeth, including five single-rooted teeth with compressed conical crowns, two Dpm₄ and the left M₂ were also found. Associated with the skull are also the stylohyal, six cervical vertebrae, seven dorsal vertebrae, seven ribs, the manubrium of the sternum, the right scapula, and the right humerus with detached head. No. 1904. XIl. 134e, Paläontologische Sammlung, Alte Akademie, München; collector, Richard Markgraf; 1904 (Mn. 9, Stromer, 1908b).

Referred specimens—To this species are tentatively referred a right radius and ulna; another right radius without distal epiphysis; an isolated xiphisternum; isolated teeth; and a left tympanic bulla. North of the lake (Birket-el-Qurun), Fayum, Egypt; Qasr-el-Sagha stage. Nos. 11239, 11239a, Württembergische Naturwissenschaftliche Sammlung, Stuttgart; collector, Richard Markgraf; 1904 (St. 13, 13a, 13b, Stromer, 1908b, pl. 5, figs. 2, 10, 11, 14, 23, 26.)

SKULL

General conformation of skull (pls. 24–25) similar to that of Dorudon osiris, except that the rostrum is somewhat more robust and less abruptly widened behind level of anterior extremities of nasals, intertemporal region slightly wider, anterior extremity of jugal much closer to orbit, and supraoccipital shield relatively wider.

Parietals normal in relation to adjacent bones, contributing the roof for the cranium and the major portion of the intertemporal constriction, and meeting on the mid-line to form a high sagittal crest that extends forward to hinder edges of frontals; dorsal profile rises gradually behind level of center of orbit; each parietal contributes a portion of slightly convex lateral cranial wall and meets the squamosal in a dentate suture that runs downward and forward; squamosal rather large, its upper surface convex from before backward; ventro-anterior or temporal margin of squamosal extended forward as a thin shelf; zygomatic process thin, short, with pointed extremity, and with its ridge-like upper edge continued backward and upward along outer edge of squamosal to join with lambdoidal crest and forming with the latter the posterior boundary of the enormous temporal fossa; supraoccipital shield broad, strongly concave transversely, with vertical median ridge, and bounded laterally by the prominent lambdoidal crest, of which the anterior face is contributed by the corresponding parietal and the posterior face by the supraoccipital; exoccipital relatively wide, with rather thick and somewhat rounded external edge; upper edge of exoccipital more or less free, and not confluent with lambdoidal crest of squamosal, but slightly below the latter; foramen magnum large; occipital condyles semi-oval in outline, considerably broader above than below, slightly convex from side to side, and borne on very short condylyar processes; intertemporal region moderately broad and short; lateral walls of intertemporal constriction are nearly vertical above elongated sphenoidal fissure; groove for optic nerve originating at optic foramen, which is situated anterior to and above level of sphenoidal fissure, extends forward and upward on lateral surface of orbitosphenoid and then curves outward on ventral face of supraorbital process of frontal; parietals and frontals quite thick in region of sutural union; supraorbital process of frontal broadened, extended laterally beyond level of jugal and arched at extremity; postorbital projection of supraorbital process unusually thick and preorbital angle relatively thin; orbit relatively large; the lachrymal and jugal have dropped out on both sides; the grooves and sutures for these bones show that the anterior end of laterally flattened jugal was mortised into outer face of maxillary as in Dorudon osiris and that the lachrymal was
wedged in between preorbital end of supraorbital process and the jugal, forming part of anterior wall of orbit, and abutting against hinder border of maxillary; an open groove for lachrymal duct present; lateral surface of maxillary strongly grooved below anterior extremity of jugal; nasals attenuated anteriorly, slightly convex from side to side, and attain their maximum width posterior to hinder ends of ascending processes of premaxillaries; posterior extremities of nasals widely divergent and separated by wedge-like process of combined frontals; anterior extremities of nasals constitute posterior border of dorsal narial fossa, which they overhang to some extent, the posterior end of dorsal narial fossa being on a level with interval between Dpm1 and Dpm2 and the anterior end being above I3; premaxillaries contribute the floor and the lateral walls of dorsal narial fossa; ascending process of premaxillary lodged in groove on upper internal border of maxillary and terminated posteriorly above interval between Dpm3 and Dpm4; proximal end of maxillary abuts against supraorbital process of frontal superiorly, and inferiorly projects backward below the latter; two molars are located on inferior process of maxillary; molar series set off from palatal surface by deep excavation; the large antorbital foramen lies above interval between Dpm2 and Dpm3; flat oral surfaces of premaxillaries prolonged backward behind level of I3 as a narrow wedge-like tongue, separating anterior extremities of maxillaries; major portion of palatal surface contributed by more or less flattened horizontal plates of maxillaries, but between the opposite C and Dpm1 a longitudinal furrow is formed; bony palate prolonged backward by elongation of palatines and adjacent thin plates of pterygoids, forming an enclosed tube for internal choanae; vertical plate of vomer projects backward beyond level of posterior margins of palatines; suture between basioccipital and basisphenoid obliterated; median basi-cranial region bounded laterally in front by hamular plates of pterygoids and behind by lateral descending plate-like processes of basisioccipital; pterygoid fossa for accessory air sinus of middle ear oval in outline, bounded internally by hamular plate of pterygoid, anteriorly by pterygoid, and externally by the postero-external limb of pterygoid and the bifid anterior end of squamosal; large foramen ovale for exit of mandibular branch of trigeminal nerve located at hinder end of fissure between falciiform process and dorsal portion of anterior end of squamosal; ventral surface of attenuated zygomatic process of squamosal furnished with concave oval glenoid articular surface; a short postglenoid process; a well-defined channel for the external auditory meatus, which originates on postero-external margin of the ventral surface of squamosal, continues its course outward behind the base of the postglenoid process of that bone; parasphenoid process rather large, with anterior concavity, but separated from hinder edge of lateral descending process of basioccipital by the wide notch for jugular leash; posterior process of periotic wedged in between exoccipital and hinder border of squamosal.

For measurements of this skull, see table 62 (p. 246).

TYMPANIC BULLA

Its main features, the tympanic bulla (pl. 24, fig. 2) of this species agrees with that of *Dorudon osiris*, but is distinguished from that of the latter by its somewhat greater width. Viewed from below, the bulla is seen to be rounded anteriorly and strongly arched ventrally. There is a broad deep median furrow on the hinder half of this surface which is bounded laterally by a narrow outer and a broader inner convexity.

Near the middle of the external face of the thin outer lip of the bulla a vertical groove extends to the dorsal edge. Behind this groove the large twisted sigmoid process arises from the upper edge of the outer lip, projecting upward and somewhat backward. The posterior conical apophysis or processus medius may be described as a low broad convexity which is situated on the outer lip of the bulla between the sigmoid process and the outer pedicle of the posterior process. The edges of the tympanic membrane were attached to
these three structures. The upper surface of the involucrum is relatively smooth, broad, and curved; it is narrowed anteriorly and depressed below the level of the overarching thin outer lip. Between the involucrum and the thin outer lip, an elongated cavum tympanicum is formed and its rounded anterior end corresponds to the eustachian orifice. The left tympanic bulla measures 83.5 mm. antero-posteriorly and 64.6 mm. transversely.

PERIOTIC

Both periotic bones are largely concealed by the closely appressed tympanic bullae. In so far as can be determined from the surfaces that are exposed, the periotic of this species is quite similar to that of *Dorudon osiris*. The posterior process is large and is firmly wedged in between the exoccipital and the squamosal.

MANDIBLE

The elongated mandible (pl. 27, figs. 1–2) has a slender and rather narrow horizontal ramus. From before backward, the horizontal ramus increases in height rather gradually up to Dpm3, and Pm4 marks the transition to the somewhat steeply rising convex anterior edge of the coronoid process. External surface of horizontal ramus somewhat convex, internal surface flattened; the small unequally spaced mental foramina disappear behind Dpm2; unankylosed symphysis extends backward to level of Dpm2; coronoid process rather low, its posterior edge being truncated obliquely; entrance to alveolar canal extraordinarily wide; and condyle convex dorso-ventrally, somewhat broader than high, its upper surface being on a level with the base of crown of M1. The measurements of the right mandible are as follows: Length, hinder face of condyle to extremity, 700 mm.; vertical height through coronoid process, 193 mm.; vertical diameter of condyle, 43.5 mm.; antero-posterior diameter of symphysis, 268 mm.; posterior edge of M3 to hinder face of condyle, 203 mm.; vertical height of mandible at level of Dpm2, 63 mm.; and vertical height of mandible at level of M3, 120 mm.

PERMANENT DENTITION

All of the anterior upper grasping teeth, including the incisors, with the exception of I3 which is erupting, the canine, and the first premolar have dropped out of their respective alveoli. The alveoli of the anterior teeth (D1 to Dpm2) in the upper tooth row are separated by interspaces of varying width. The maximum interspace occurs between I3 and Dc, and the minimum between Dpm2 and Dpm3. The hinder upper cheek teeth (Dpm3 to M1) form a closed series. The four hinder upper cheek teeth (Dpm2 to M1) possess two roots.

The anterior molar, M1, is distinctly smaller than Dpm4. The principal cusp of M1 is acutely pointed and the two accessory denticles on the posterior cutting edge are slightly larger than the two on the anterior edge. The antero-posterior diameter of the base of the crown of this molar is 31.2 mm. M2 is not preserved in either maxillary.

The anterior faces of the crowns of the three lower molars are grooved for the reception of the posterior edge of crown of the preceding tooth. Viewed from the side, the curvature of the anterior edge of the principal cusp of M1 is seen to be more convex than that of M2. The principal cusp of this molar is slightly larger than the highest of the three accessory denticles on the posterior cutting edge. The principal cusp of M2 (pl. 26, fig. 3) is noticeably larger than the largest of the three accessory denticles on the posterior cutting edge. A vertical groove with sharp lateral margins occupies most of the anterior cutting edge of the crown. The crown of M3 is similar to that of M2. The antero-posterior diameters of the crowns of these three molars are respectively in the right and left mandibles: M1, 44.4 and 45.5 mm.; M2, — and 37.5 mm.; and M3, 40 and — mm.
DECIDUOUS DENTITION

At the anterior end of the upper tooth row (Di1 to behind Dpm1), the pits for the reception of the lower teeth are located on the outer side of the single-rooted teeth, while the larger fosse for the lower deciduous cheek teeth are on the inside of the two-rooted teeth. On the mandible, however, the pits for the reception of the upper deciduous teeth are located entirely on the outer side of the entire tooth row, but are quite indistinct behind Dpm3. Thus it is certain that the upper and lower tooth series cross over when the jaws are closed.

The three deciduous incisors (pl. 26, fig. 3) differ from one another in the size and length of their roots. All have laterally compressed crowns. One can not be certain whether they were detached from the skull or from the mandibles.

Two deciduous canines are associated with this specimen. The longer of the two seems to have belonged in the mandible, since the laterally flattened crown is curved rather strongly backward. The other canine has the upper portion of the root more noticeably widened antero-posteriorly and the crown is less strongly curved backward. This tooth resembles the upper canine.

The anterior deciduous premolar has dropped out of both maxillaries. The apex of the principal cusp is damaged on both Dpm2. The steep anterior cutting edge of this tooth may have been devoid of accessory denticles. Three fairly large accessory denticles are present on the posterior cutting edge.

The crown of Dpm3 is slightly larger than that of either Dpm2 or Dpm4. The two accessory denticles on the anterior cutting edge of Dpm3 are smaller and farther removed from the apex of the principal cusp than the three on the posterior cutting edge. The basal accessory denticle on the posterior cutting edge is quite small. The hinder root of Dpm3 is transversely widened and internally forms a narrow buttress supporting the hinder portion of the crown. In position it resembles somewhat the enamel-covered postero-internal buttress on Dpm3 of Prozeuglodon isis.

As compared with Dpm3, the entire crown as well as the principal cusp of Dpm4 are slightly smaller. The anterior and posterior cutting edges of Dpm4 are provided with three accessory denticles. The hinder root of Dpm4 is likewise transversely widened, forming a distinct postero-internal buttress.

In the left maxillary the antero-posterior diameters of the alveoli are respectively as follows: Dc, 25± mm.; Dpm1, 27± mm. The antero-posterior diameters of the base of the crown of the three hinder deciduous premolars are as follows: Dpm2, 44.7 mm.; Dpm3, 46.7 mm.; and Dpm3, 41.9 mm.

It is unfortunate that the anterior single-rooted deciduous teeth are not preserved in situ in either mandible. The alveoli (see, Stromer, 1908b, p. 142) for Di2, Di3, Dc, and Dpm1 indicate the size of the roots and inferentially the proportions of the crown.

As contrasted with that of Dpm3, the crown of Dpm2 is quite small. The principal cusp of Dpm2 is rather low and the two accessory denticles on the anterior cutting edge are rather minute in comparison with the two larger ones on the posterior edge of the crown. Besides the latter there is a small basal tubercle on the hinder cutting edge.

Dpm3 is the largest of the deciduous cheek teeth in the mandible. The three accessory denticles on the anterior cutting edge of the crown are farther removed from the apex of the rather high principal cusp than the four large ones on the posterior edge.

Dpm4 has been dislodged in both mandibles, but both were found associated with this specimen (pl. 26, fig. 3). The crown of Pm4 can be seen in the alveolus in both mandibles. Regressive processes associated with the development of the permanent Pm4 have brought about the destruction of the major portion of the posterior root of Dpm4, although the anterior root does not appear to have been altered. The crown of Dpm4
is lower than that of Dpm3 and the principal cusp is not so prominent. The sharp and rather steep anterior cutting edge is furnished with four small accessory denticles and there are four accessory denticles on the posterior edge which progressively diminish in size toward the base of the crown.

The antero-posterior diameters of the base of the crown of the deciduous cheek teeth in the right and left mandibles are respectively: Dpm2, 38.2 and 38.3 mm.; Dpm3, 59.3 and 58 mm. The antero-posterior diameters of the alveoli of Dpm1 are, respectively, 24 and 26 mm.

HYOID BONE

Only one of the hyoid bones (Stromer, 1908b, p. 114) was found associated with the skull and this has been identified as the stylohyal. This tongue bone is shown behind the condyles of the skull (pl. 24, fig. 2). It is quite slender, slightly curved from end to end, and somewhat thickened at its extremities. The length of the stylohyal is 180 mm. and its width varies from 7 to 8 mm.

VERTEBRAE

CERVICAL VERTEBRAE

The combined length of the seven free cervical vertebrae is estimated to be equivalent to about one-fourth of the greatest length of the skull.

Atlas—The atlas (Stromer, 1908b, pl. 4, fig. 9) has concave articular facets for the occipital condyles of the skull and these facets are connected ventrally by a flat surface. The neural spine on the rather narrow neural arch is reduced to a low tubercle. The short transverse processes project outward and slightly backward, and are truncated distally. The ventral hypapophysis is small and pointed. The hinder facets for the axis are flat and vertically oval. The greatest vertical depth of this atlas, from tip of neural spine to ventral face of centrum, is 112.5 mm., and the maximum transverse diameter is 180.5 mm.

Axis—This cervical vertebra (Stromer, 1908b, pl. 4, fig. 8) has a blunt rounded odontoid process, rather high oval and nearly vertical articular facets for the atlas, and well-developed postzygapophyses. The short plate-like transverse processes project outward and slightly backward, and are perforated at the base by a vertebral arterial canal. The neural spine is directed obliquely backward. Viewed from behind, the neural spine has a spatulate shape. The antero-posterior diameter of the centrum is shorter than its odontoid process and its posterior face is shallowly concave. A weak median ridge is present on the ventral face of the centrum. The greatest vertical diameter of the axis, from tip of neural spine to ventral face of centrum, is 152.3 mm., and the maximum transverse diameter between ends of transverse processes is 135.3 mm.

The centra of the hinder cervical vertebrae, some of which lack epiphyses, are compressed antero-posteriorly and possess faint longitudinal ridges on their ventral surfaces. The articular ends of the centra of the third to fifth cervical vertebrae, inclusive, are oval in outline, but on the sixth they are almost circular.

Third Cervical—The transverse processes of the third cervical vertebra are short and resemble those on the axis. The neural spine is short and attenuated. The greatest vertical diameter of the third cervical, from tip of neural spine to ventral face of centrum, is 108.6 mm., and the maximum transverse diameter between ends of transverse processes is 109 mm.

Fourth Cervical—The transverse processes of the fourth cervical vertebra have a thin slender process which projects forward and downward from the ventral edge. The neural spine is low, but is broader at the base than on the third cervical. The greatest vertical diameter of the fourth cervical, from tip of neural spine to ventral face of centrum, is
105.8 mm., and the maximum transverse diameter between ends of transverse processes is 101 + mm.

Sixth Cervical—The centrum of the sixth cervical (Stromer, 1908b, pl. 4, figs. 13–14) is shorter than that of the seventh, its antero-posterior diameter being 26.8 mm. The diapophysis and parapophysis unite to form a broad, nearly vertical, lateral process, which is continuous above with the outer buttress on the pedicle of the neural arch. This lateral process is perforated at the base by a small vertebrarterial canal. The stout parapophyses project downward and outward, considerably below the level of the ventral face of the centrum. The horizontal axis of the distally expanded and laterally flattened parapophysis exceeds the maximum longitudinal diameter of the centrum. The pre- and post-zygapophyses are large and their facets are oval in outline. The neural spine of this vertebra is destroyed. The greatest vertical diameter of the sixth cervical, from the broken base of the neural spine to ventral face of the centrum is 106.8 mm., and the maximum transverse diameter is 121 mm.

Seventh Cervical—This vertebra has a longer neural spine and shorter transverse processes than any of the preceding cervical vertebrae. On the reconstruction of the skeleton published by Stromer (1908b, pl. 4, fig. 1) it is shown as the fifth in the cervical series. The greatest vertical diameter of this cervical, from tip of neural spine to ventral face of centrum, is 128.2 mm., the maximum transverse diameter is 136.6 mm., and the antero-posterior diameter of its centrum is 28.8 mm.

Dorsal Vertebrae

Of the seven dorsal vertebrae, which belong to this specimen, five are from the anterior end of the series, one from near the middle, and one from the hinder end. Although the total number of vertebrae included in the dorsal series is unknown, it is quite likely that 15 vertebrae comprised the full complement. In allocating these vertebrae to their position in the series, comparisons were made with those of Zygorhiza kochii and Basilosaurus cetoides, for which the entire dorsal series is known. These seven dorsal vertebrae are identified as the first, second, third, fourth, fifth, eighth, and fourteenth. These allocations, however, should be considered as tentative until a consecutive dorsal series of Dorudon stromeri is found. As compared to those of Zygorhiza kochii, they differ chiefly in the relative lengths of the centra, in the shape of the articular facets for the tubercula of the ribs, and in the proportions and direction of the neural spines.

The vertebra assumed by Stromer (1908b, p. 121, pl. 4, fig. 12) to be the seventh cervical is quite unlike the corresponding cervical of Dorudon zitteli and of Basilosaurus cetoides, but does resemble an anterior dorsal of Zygorhiza kochii. The neural canal is quite high and narrow. The pre- and post-zygapophyses are widely separated. The neural spine is narrow and directed obliquely backward. The neural arch is rather robust, with a lateral diapophysis on each side, at the extremity of which is a large articular facet for the tuberculum of the rib. The usual facet for the capitulum of the rib is situated on the lateral surface of the centrum at the base of the neural arch. This is identified as the first dorsal.

It is certain that the centra of these dorsal vertebrae increase in length toward the posterior end of the series, for the posterior ones are distinctly longer than the anterior ones. From the anterior to the hinder end of the series there is a progressive decrease in the width of the interval separating the outer margins of the postzygapophyseal facets. On the anterior dorsals (Stromer, 1908b, pl. 4, fig. 10), the outer articular ends of the diapophyses are ovoidal in outline and project considerably above the level of the prezygapophyseal facets. On the eighth dorsal, however, the outer articular end of the diapophysis is relatively narrow and its antero-ventral surface curves to meet the anterior projecting metapophysis and
prezygapophysis. On the anterior dorsal vertebrae, the rather slender neural spine is attenuated distally and slopes backward. On the middle and hinder dorsals, however, these neural spines are much broader at the base and are more nearly vertical. The pedicles of the neural arches of the anterior dorsals, especially those of the second and third, are rather narrow antero-posteriorly and slender, but rapidly increase in width up to the middle of the series.

The hinder dorsal (Stromer, 1908b, pl. 4, fig. 11), which is identified as the fourteenth, has a rather wide neural spine, measuring about 46 mm. antero-posteriorly at the base, wide neural arches, reduced postzygapophyses, and rather strong metapophyses. The transverse processes, which project from the side of the centrum, are attenuated distally and their extremities are furnished with an oval facet for articulation with the single headed rib.

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<tr>
<th>Table 56—Measurements (in millimeters) of the dorsal vertebrae</th>
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<td>Greatest vertical depth, from tip of neural spine to ventral face of centrum</td>
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<tr>
<td>Distance between outer ends of diapophyses</td>
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<td>Distance between outer ends of parapophyses</td>
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<td>Antero-posterior diameter of centrum, without epipophyses</td>
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<td>Dorso-ventral diameter of centrum</td>
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<td>Distance from tip of prezygapophysis to tip of postzygapophysis</td>
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<td>Transverse diameter of neural canal, anteriorly</td>
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<td>Vertical diameter of neural canal, anteriorly</td>
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1 Extremity of neural spine missing.

FORELIMB

The rather stout forelimb has the usual ball-and-socket shoulder joint and a hinged elbow joint. The vertical diameter of the scapula is approximately equal to the greatest length of the humerus. The humerus differs from that of Zygophisza kochii and Dorudon zittelii in having a deltoid crest that reaches farther distally, a distinctly stouter shaft, and no obvious antero-posterior constriction of the shaft above the level of the outer condyle. These characters in part may be associated with immaturity. The scapula and humerus associated with the skull (No. 1904. XII. 134e, Munich) are distinctly smaller than those of Zygophisza kochii. The radius and ulna (No. 11239a, Stuttgart) tentatively referred to this species belonged to a larger individual.

SCAPULA

The right scapula (Stromer, 1908b, pl. 5, fig. 4) has a strongly convex vertebral edge, a somewhat curved posterior edge, and a nearly straight anterior edge. The prescapular fossa is separated from the large postscapular fossa by a ridge which increases in height toward the base of the acromion. The acromion is thin, flat, and rather long, and is crushed downward and forward. The concave articular head has an almost straight inner and a convex outer edge. The slender pointed coracoid process projects about 30 mm. beyond the head. The greatest antero-posterior diameter of the right scapula (No. 1904, XII. 134e, Munich), including the restored anterior angle, is 231 mm. The greatest vertical diameter of this scapula, from vertebral edge to ventral face of articular head below the coracoid process, is 215 mm., and the distance from the posterior face of the head to the extremity of the coracoid process is 88 mm.
HUMERUS

The detached head and the shaft of the right humerus (Stromer, 1908b, pl. 5, figs. 5-6) were found. The articular head of the humerus is separated from the greater and lesser tuberosities by a shallow furrow. The shaft of the right humerus, without the proximal epiphysis, measures about 177 mm. in length. The deltoid crest is unusually long. The hinder face of the shaft is narrow and rounded. The trochlear surface at the distal end is quite similar to that of Zygorhiza kochii. A distinct olecranon fossa is present on the hinder face of the shaft above the trochlea and a small excavation, the coronoid or anterior supratrochlear fossa, can be recognized on the anterior face.

The measurements of this humerus (No. 1904. XII. 134e, Munich) are as follows: Greatest length, including unankylosed proximal epiphysis, 209 + mm.; antero-posterior diameter of proximal end, including greater tuberosity, 73.5 mm.; greatest antero-posterior diameter of head, 54 mm.; transverse diameter of head, 47 mm.; antero-posterior diameter of shaft through distal portion of deltoid crest, 72.5 mm.; transverse diameter of shaft at same level, 24 mm.; antero-posterior diameter of outer condyle, 38.4 mm.; antero-posterior diameter of inner condyle, 39 mm.; and transverse diameter of combined trochlea and capitulum, 28 mm.

RADIUS

The allocation of this radius and the ulna hereinafter described (No. 11239a, Stuttgart) to this species is open to question inasmuch as four and possibly five species have been described from the Qasr-el-Sagha stage. The general conformation of this right radius (Stromer, 1908b, pl. 5, figs. 10, 11) is somewhat similar to that of Zygorhiza kochii, but differs from the one tentatively referred to Dorudon zitteli in that the profile of the anterior face is bent to form an obtuse angle in contrast to the rather regular convex curvature of the corresponding face of the latter. Viewed from the side, the anterior face of the proximal third of the shaft slopes forward and, then turning abruptly, slopes backward on the distal two-thirds. The hinder face exhibits a concave curvature. The proximal end of this radius is roughly rhomboidal in outline and is occupied by a large concave articular surface, but the areas for the trochlea and capitulum of the humerus are not sharply differentiated. The proximal epiphysis, with its facets for the scaphoid and lunar, is missing. The internal surface of the neck of the shaft below the proximal end is somewhat roughened by the presence of osseous excrescences. The ulnar facet is limited to the roughened area on the hinder surface of the neck.

The measurements of this radius are as follows: Greatest length, 128 + mm.; antero-posterior diameter of proximal facet at middle, 21 mm.; transverse diameter of proximal facet, 29 mm.; antero-posterior diameter of shaft at level of anterior angle, 34 mm.; transverse diameter of shaft at same level, 15 mm.; antero-posterior diameter of distal end, 32 mm.; and transverse diameter of distal end, 19 ± mm.

ULNA

An imperfect left ulna (No. 11239a, Stuttgart), weathered at both ends and laterally crushed, may possibly belong to this species. This ulna has been figured and described by Stromer (1908b, p. 125, pl. 5, figs. 14, 26). The anterior and posterior edges of the rather broad olecranon process curve backward. The external margin of the greater sigmoid cavity is regularly curved from end to end, but the internal margin is deeply notched as in Zygorhiza kochii; the short narrow groove, which leads inward and downward, terminates in a small cavity which is situated medially on the anterior face of the sigmoid cavity. The lesser sigmoid articular surface occupies the anterior face of the shaft below the distal edge of the greater sigmoid cavity. The distal epiphysis is missing.
The measurements of this ulna are as follows: Greatest length, 190 ± mm.; antero-posterior diameter of proximal end of olecranon process, 70 mm.; length of anterior edge of olecranon process, proximo-anterior angle to greater sigmoid cavity, 47 mm.; length of greater sigmoid cavity, 35 mm.; transverse diameter of distal portion of greater sigmoid cavity, 25 mm.; and greatest antero-posterior diameter of shaft near distal end, 59 mm.

RIBS

Four complete ribs and three others which lack the distal extremity were associated with this specimen. The anterior ribs (Stromer, 1908b, pl. 5, fig. 24) are about 250 mm. long and strongly bent downward at the angle. The upper portions of the shafts of the anterior ribs are antero-posteriorly flattened and the torsion or twisting of the shaft makes the widened distal portion face outward. No pronounced enlargement of the shaft near the distal end, such as characterizes the anterior ribs of Zygohesperus kochii, is present on any of the ribs. The anterior ribs have a much thicker neck than those behind the middle of the series. The ribs behind the middle of the series (Stromer, 1908, pl. 5, fig. 25) are longer than the anteriormost ribs, measuring perhaps 340 mm. in length, and are rather slender.

STERNUM

The manubrium (Stromer, 1908b, pl. 5, fig. 22) is the sole sternal segment associated with this specimen. The hinder end of the manubrium is almost twice as thick as the anterior end. The ventral face is slightly curved transversely. Behind the rounded antero-external angles are concave attachment areas for the anterior pair of ribs. The measurements of the manubrium (No. 1904. XII. 134e, Munich) are as follows: Antero-posterior diameter, medially, 86 mm.; transverse diameter anteriorly, 76 mm.; and transverse diameter posteriorly, 63 mm.

The xiphisternum (Stromer, 1908b, pl. 5, fig. 23) tentatively referred to this species consists of a quadrangular anterior portion, from which a long spatulate xiphoid process projects backward. The hinder end of the xiphoid process is not deeply notched. On the hinder half of each rough lateral surface of the dorso-ventrally flattened anterior portion of the xiphisternum are two closely approximated indentations for the attachment of the sternal cartilages of two ribs. Stromer (1908b, p. 124) considers that the concavities on the ventral face are pathological. The measurements of the xiphisternum (No. 11239a, Stuttgart) are as follows: Antero-posterior diameter, medially, 175 mm.; transverse diameter anteriorly, 85 mm.; and vertical diameter anteriorly, 38 mm.

DORUDON ZITTELI (Stromer)


Type locality—An isolated hill, designated on Schweinfurth’s map as §, 123 kilometers west of the old temple, and 3 miles west-southwest of Qasr-el-Sagha on the escarpments north of the lake (Birket-el-Qurun), Fayum, Egypt. From “Stufe II. 5a” of Blanckenhorn—Qasr-el-Sagha stage. Upper Eocene.

Type specimen—Weathered remains of a skeleton, consisting chiefly of a natural stone cast of the nasal and frontal sinuses with adherent fragments of nasals, premaxillary, and maxillary, in addition to an anterior premaxillary fragment with alveoli for three single-
rooted teeth, and imperfect cervical vertebrae, including the atlas, axis, third and fourth cervicals. Several fragments of ribs were associated with these remains. About 30 paces distant, a mandibular fragment and a lumbar vertebra were found. All of these bones lay more or less exposed on the marl terrace. No. 1902. XI. 60, Paläontologische Sammlung, Alte Akademie, München; collector, Ernst Stromer; 1902 (Mn. 3, Stromer, 1903c; see also Blanckenhorn, 1903, p. 391).

Referred specimens—(1) Dorsal, lumbar, and caudal vertebrae, in part very well preserved, besides other skeletal remains. From the schistose clay ("Stufe II. 5a" of Blanckenhorn) of the plateau, half day's journey north-north-east of Qasr-el-Sagha, Fayum, Egypt; Qasr-el-Sagha stage. No. 1902. XI. 60a, Paläontologische Sammlung, Alte Akademie, München; collector, Ernst Stromer; February 8, 1902 (Mn. 4, Stromer, 1903c, pl. 11, figs. 4–10; see also Blanckenhorn, 1903, p. 382; Stromer, 1908b, p. 126).

(2) A nearly complete skull of an adult individual, which is strongly crushed from side to side, and both mandibles; the enamel is destroyed on the crowns of the teeth. Associated with this skull are seven cervical vertebrae, and a consecutive thoracic series consisting of the first to the eleventh dorsal vertebrae, inclusive. A left scapula and several rib fragments belong with this individual. From "Stufe II. 5a" of Blanckenhorn at a collecting site west of Dimê, Fayum, Egypt; Qasr-el-Sagha stage. No. 11235, Württembergische Naturaliensammlung, Stuttgart; collector, Richard Markgraf; 1904 (St. 4, Stromer, 1908b, p. 126).

(3) Right and left humeri tentatively referred to this species. From "Stufe II. 5a" of Blanckenhorn at a collecting site west of Dimê, Fayum, Egypt; Qasr-el-Sagha stage. No. 11417b, Württembergische Naturaliensammlung, Stuttgart; collector, Richard Markgraf (St. 12, Stromer, 1908b, pp. 126, 140).

(4) A right humerus and associated radius are allocated with reservations by Stromer to this species. From a very fine-grained white sandstone at Uadî Ro'jan on the northern steep cliff of the Fayum basin, Egypt; Qasr-el-Sagha stage. No. 11951a, Württembergische Naturaliensammlung, Stuttgart; collector, Richard Markgraf; December 1906–January 1907 (St. 14, Stromer, 1908b, p. 126, pl. 5, figs. 7–9, 16–19).

SKULL

Long exposure to the weather had largely destroyed the type skull. Only fragments of the rostrum and of the frontal region are preserved. The anterior premaxillary fragment has alveoli for the three incisors, of which the anterior and posterior alveoli are only partially complete. The proportions of this end of the premaxillary are similar to Dorudon osiris. The vertical diameter of the premaxillary anteriorly is more than 35 mm., thus agreeing with Dames' original specimen (1894, p. 191). It differs from Dorudon osiris, however, in having the cavity for the reception of apex of mandibular i3 placed closer behind i2. The hinder upper jaw fragment consists of the ascending portion of the premaxillary and the corresponding portion of the maxillary, in which are found incomplete alveoli for C. and Pm2, and the roots of Pm1. In the right maxillary both roots of Pm1 are visible, but in the left maxillary the two roots are united at the base. The diastema between C and Pm1, as well as that between Pm1 and Pm2, is slightly shorter than in Dorudon osiris (No. 1902. XI. 59, Munich). On the dorsal surface, are the weathered remnants of the maxillaries, the hinder portions of both nasals, and the hinder ends of the premaxillaries. Behind them were remnants of the frontals which were united by a distinct median suture. The posterior extremities of the nasals were separated by the narrow narial process of the combined frontals. The ascending processes of the premaxillaries overlie the lateral edges of the nasals and of the maxillaries like in Dorudon serratus. A

portion of the hinder end of the supraorbital process of the left frontal is preserved and its curvature is more flattened than in *Dorudon osiris*.

The measurements of this specimen (No. 1902. XI. 60, Munich) are as follows: Breadth of premaxillary at level of I₂, 50± mm.; breadth of maxillary at level of Pm₁, 64± mm.; greatest breadth of combined nasals, posteriorly, 43 mm.; diastema between C and Pm₁, 23 mm.; diastema between Pm₁ and Pm₂, 19 mm.; length of alveolus of I₂, 21-23 mm.; breadth of alveolus of I₂, 12.5 mm.; length of crown of Pm₁, 28-27.5 mm.; and breadth of Pm₁, 10± mm.

The skull (pl. 26, fig. 1) of the referred specimen (No. 11235, Stuttgart) is crushed from side to side. Aside from the more flattened curvature of the hinder margin of the supraorbital process of the frontal and the shape of the supraorbital shield which can not be determined, this skull agrees in most respects with that of *Dorudon osiris* and hence a detailed description is not necessary. The ventral surface of this skull was not examined, but it would appear from a statement in Stromer's account (1908b, p. 126) that the region around the tympanic bullae, and the paroccipital processes also, resemble *Dorudon stromeri*. The large size of the tympanic bullae seemingly constitutes one of the diagnostic features of this species. The dimensions of the right and left bullae, however, are not the same, the greatest lengths being 88 and 94 mm., while the greatest breadth of both is 55± mm.

The hinder ends of the nasals, however, are not separated by a narial process of the frontals.

The diagnostic characters of this species, so far as known, seem to be confined to a slight difference in the curvature of the hinder margin of the supraorbital process of the frontal, the presence of two roots on Pm₁, unusually large tympanic bullae, a high coronoid process on the mandible, and a scapula with a narrow precapular fossa.

For measurements of the skull, see table 62 (p. 246).

**Narial Cavity**

More important than these remnants of cranial bones is the fine-grained natural stone cast of the narial cavity and associated sinuses, which has been figured by Stromer (1903c, pl. 10, fig. 2; pl. 11, figs. 1-3). The painstaking removal by Stromer of the weathered bones overlying this cast has revealed in remarkable detail the paired air sinuses, which are connected directly or indirectly with the narial cavity. This stone cast, unfortunately, is incomplete laterally and inferiorly, both in front and behind.

The hinder portion of this natural cast, as seen from above, is clearly divided into two chambers or frontals sinuses. As a whole, each frontal sinus (Stromer, 1903c, pl. 10, fig. 2, g) is convex above and laterally. Each of these sinuses is divided into smaller elongate chambers which are inclosed by thin scrolls of bone, the ethmoturbinals. At least nine smaller chambers can be distinguished in each frontal sinus and they are separated by the thin longitudinal lamellae of these scrolls. The broken edges of these lamellae can be seen in the furrows on the upper surface of this natural cast. An examination of the anterior and posterior ends of these chambers of the frontal sinus shows that these ethmoturbinals were involuted. Each frontal sinus is bounded below anteriorly by the *lamina terminalis*, internally by the osseous narial septum and the nasoturbinal, and superiorly by the frontal.

On the dorsal surface and at the posterior end of this cast, there are impressions of a number of terminal branches of the olfactory nerves. No remnants of the transverse cribriform plate, which separates the narial cavity from the cranial cavity, are preserved. The median vertical septum, the mesethmoid, which divides the narial cavity into two lateral chambers, each almost filled by the scroll-like ethmoturbinals, is conspicuously narrowed superiorly, but is rather wide inferiorly. In Recent carnivores this mesethmoid is ankylosed to or in contact with the frontals and nasals dorsally along their median
sutural contact, its lower edge rests in the trough of the vomer, and its posterior edge is fused with the cribiform plate along the vertical median line. In this natural cast, however, the anterior portion of the longitudinal trough of the vomer is filled with stone (Stromer, 1903c, pl. 11, fig. 3. a) and it is obvious that the anterior extension of the mesethmoid was not ossified. Stromer (1903c, pp. 72, 73), therefore, concludes that the anterior portion of the nasal septum was cartilaginous at least as far backward as the level of the hinder ends of the premaxillaries. It was certainly ossified posteriorly.

The median stone cast (Stromer, 1903c, pl. 11, fig. 3. a), which is sheathed laterally and ventrally by the vomer, becomes reduced in size posteriorly and disappears in front of the level of the frontal sinuses. This may correspond to the mesorostral cartilaginous plug which fills the trough of the vomer in many cetaceans.

A lateral transverse cleft (Stromer, 1903c, pl. 10, fig. 2, SI), which may possibly correspond to the ethmoidal cleft, partially separates each frontal sinus from the adjoining maxillary sinus.

The maxillary sinuses are larger than the frontal sinuses. The left maxillary sinus (Stromer, 1903c, pl. 10, fig. 3. f) is roughly three-sided, as viewed from above, and is rather flat. The projecting outer angle of the maxillary sinus extends into the hindermost part of the maxillary. This sinus extends backward to the lateral transverse cleft (Stromer, 1903c, pl. 10, fig. 2. SI) and its anterior limit is located approximately at the level of a line drawn through the opposite antorbital foramina. This sinus is bounded internally by the nasoturbinal and the ventral wall or floor is formed by the thin lateral extension of the nasoturbinal. No remnants of the maxilloturbinal bones were found.

Under each nasal bone and adjacent to the median line is a broad longitudinal ridge (Stromer, 1903c, pl. 10, fig. 2. e) which ends posteriorly behind the level of the transverse cleft and extends forward beyond the level of the antorbital foramen. These longitudinal ridges are closely approximated posteriorly but diverge anteriorly. Each of these longitudinal ridges is considered by Stromer (1903c, p. 74) to represent a cast of an involuted nasoturbinal bone. The broken edges of this thin nasoturbinal can be seen in the grooves which form the lateral boundaries of the longitudinal broad ridge. In front of the orbit, a thin horizontal plate of the nasoturbinal extends outward below the maxillary sinus, completely isolating it, but anterior to this level this horizontal plate is abruptly narrowed (Stromer, 1903c, pl. 11, figs. 2–3).

The anterior portion of the transverse oval lachrymal canal (Stromer, 1903c, pl. 10, fig. 2. d), which empties into the nasal cavity, is preserved. It is wider anteriorly and passes backward within the maxillary above the level of the somewhat larger infraorbital canal.

The choanae (Stromer, 1903c, pl. 11, fig. 2. b) are rather broad, approximately high oval in cross-section, and extend backward almost horizontally. Each of these passages is confluent above in front with the maxillary sinus, but posteriorly is completely cut off above from the frontal sinus by the more or less horizontal and transverse lamina terminalis, which in turn is united internally with the vertical sagittal partition, the mesethmoid. The lateral stone plate (Stromer, 1903c, pl. 10, fig. 2. c) below the frontal sinus, which is continuous internally with the cast of the corresponding narial passage represents a natural cast of the under surface of the supraorbital process of the frontal at its base and, judging from its relative position, one may conclude that a large sphenopalatine foramen was at least partly responsible for the formation of this angular projection.

MANDIBLE

The imperfect type mandible is slightly smaller than Dames' type of Dorudon osiris. The lower border of this mandible is missing below the level of the entrance to the alveolar
canal. The roots of $\text{Pm}^2$ and $\text{Pm}^3$ and a portion of the crown of $\text{Pm}^4$ are preserved. The diastema between $\text{Pm}^2$ and $\text{Pm}^3$ seems to be slightly longer than in *Dorudon osiris* (No. M. 16, Berlin) and the symphysis extends farther backward.

The coronoid process of the left mandible belonging to the referred skull (No. 11235, Stuttgart) is relatively higher than in mandibles of *Dorudon osiris* of approximately the same size. The measurements of the left mandible are as follows: Length of mandible, from hinder face of condyle to extremity, 660 mm.; vertical height of mandible through coronoid process, 223 mm.; vertical height of mandible at level of I$^2$, 39 mm.; vertical height of mandible at level of $\text{Pm}^2$, 67 mm.; vertical height of mandible at level of $\text{M}^3$, 115 mm.; anterior edge of $\text{Pm}^2$ to hinder edge of $\text{M}^3$, 230 ± mm.; posterior edge of $\text{M}^3$ to hinder face of condyle, 190 ± mm.; diastema between I$^1$ and I$^2$, 10 mm.; and diastema between $\text{Pm}^2$ and $\text{Pm}^3$, 10 ± mm.

**DENTITION**

The upper and lower jaws of the referred specimen (No. 11235, Stuttgart) are not only tightly closed, but also, unfortunately, the hinder rostral region and the supraorbital processes of the frontals are depressed, partially concealing the hinder upper and lower cheek teeth. The enamel is not preserved on the crowns of the teeth.

In the mandible (pl. 26, fig. 1), the incisors, the canine, and the anterior premolars are similar to those of *Dorudon osiris*. There is a conspicuous vertical furrow on the outer surface of the root of the canine. The root of $\text{Pm}^1$ may possibly be bifurcated. The sharp cutting edges of the crown of $\text{Pm}^1$ lack accessory denticles. The antero-posterior diameter of $\text{Pm}^2$ is greater than that of the corresponding tooth of *Dorudon osiris*, and the diastema between $\text{Pm}^2$ and $\text{Pm}^3$ is quite short.

With regard to the upper dentition, little can be said, except that the formula apparently is: I$^3$. C$^1$. $\text{Pm}^4$. M$^2$. It is quite certain, however, that $\text{Pm}^1$ has two roots. The serrated upper cheek teeth are approximately the same size as those of *Dorudon osiris*. The measurements of the teeth have been published by Stromer (1908, pp. 143, 145).

**VERTEBRÆ**

**CERVICAL VERTEBRÆ**

The major portion of the skeleton of the type specimen was rendered worthless by weathering and consequently only four of the cervical vertebrae were collected. Although imperfect, these cervicals (Stromer, 1903c, pl. 10, fig. 1) reveal the essential features of the neck. The weathered left half of the atlas has a damaged transverse process and the adjoining portion of the neural arch is lacking. The anterior facet is concave and the posterior facet is sharply set off from the hinder surface of the atlas. The axis has a rather broad odontoid process with a somewhat concave dorsal face, its anterior facets are transversely convex with rather sharply defined upper lateral margins, the neural canal is approximately as high as broad, and the well-developed postzygapophyses have flat circular facets. The third and fourth cervical vertebrae have normal pre- and postzygapophyses, their transverse processes are perforated at the base by a vertebrarterial foramen, and a median carina is developed on the ventral face of the centrum.

The centra of the axis, the third and the fourth cervical vertebrae lack epiphyses, and furthermore the end surfaces of the centra do not exhibit the usual coalescence ridges and furrows for ankylosis with the epiphyses. The fact that the epiphyses of these cervical vertebrae are not as yet ankylosed to the centra is another indication of immaturity. It has been shown by Wheeler (1930, p. 418) that in the case of the finback, *Balaenoptera physalus*, the epiphyses begin to fuse with the centra of the vertebrae at both ends of the vertebral column about the same time. At the anterior end of the vertebral series, the
progressive ankylosis of the epiphyses with the centra does not continue much beyond the cervical series. At the hinder end of the series, ankylosis of the epiphyses with the centra progressively proceeds forward with age through the caudal and lumbar series, and is completed among the anterior dorsals.

A consecutive series of seven cervicals (pl. 26, fig. 2) were attached to the referred skull (No. 11235, Stuttgart). Of the latter, the atlas and axis are imperfectly preserved. These cervical vertebrae are distinctly larger than those belonging to the type individual, but are smaller than those of *Dorudon stromeri*. The atlas is characterized by the oblique oval posterior facets, and the axis by the truncated odontoid process and by the high oval neural canal. On the six hinder cervicals, a median carina is present on the ventral surface of the centrum. The seventh cervical vertebra has rib facets, the neural canal is broader than high, and the transverse processes arise from the neural arches and from the side of the centrum. The cervical series may have measured perhaps 220 mm. in length.

**Dorsal Vertebrae**

Stromer (1908b, p. 127) concluded that the anterior dorsal was missing from the Stuttgart specimen (No. 11235), and that this dorsal series comprised the second to the twelfth, inclusive. If this dorsal series (pl. 26, fig. 2) is considered to consist of the first to the eleventh, then the ninth in the series becomes the transitional dorsal like in *Zygorhiza kochii* and *Basilosaurus cetoides*. On this transitional dorsal the facets for the capitulum and tuberculum are separated by a short interval, and on the tenth they coalesce to form a single short transverse process.

The length of this series of eleven dorsal vertebrae is 510 mm. along the ventral surface. The centra of these vertebrae are not quite so broad although they are slightly longer than those of *Dorudon stromeri*. The neural canals of the anterior dorsals are also narrower than on those of *Dorudon stromeri*. Beginning on the anterior dorsals and as far backward as the tenth dorsal, the hinder edges of the pedicles of the neural arch slope obliquely forward and upward. The neural spines of the nine anterior dorsals are relatively slender and are inclined backward. The neural spines of the third and fourth dorsals appear to be the longest in the series. On the tenth and eleventh dorsals the neural spines are broader at the base and apparently are more nearly vertical.

With the exception of the extremities of some of the neural spines, all of these eleven dorsal vertebrae are practically complete. The centra increase in length from the first to the eleventh. The ninth dorsal is the transitional vertebra. It has paired lateral facets for articulation with the tuberculum and capitulum of the corresponding rib. From the first to the eleventh dorsal there is a progressive decrease in width of the interval between the outside margins of the postzygapophysial facets. The postzygapophyses become progressively shorter toward the hinder end of the dorsal series. The prezygapophyial facets are nearly horizontal on the anterior dorsals, while those on the hinder dorsals are concave, somewhat oblique in position, and are strengthened by the lateral metapophyses. Anteriorly the diapophyses arise high up on the neural arch and gradually shift their position to a lower level from the second to the eighth, but on the ninth the shift is more noticeable. The diapophysis arises from the side of the neural arch and the closely approximated short parapophysis from the side of the centrum. On the anterior five dorsals the diapophyses are elongated and the facet for articulation with the tuberculum of the rib projects above the level of the prezygapophysial facets. On each side of the centrum of the first to sixth dorsals, inclusive, below the level of the pedicles of the neural arch and at the postero-superior angle, there is a well-defined facet for the head of the following rib. The antero-superior facet on the lateral surface of the centrum is less sharply defined. The greatest vertical diameters of these dorsal vertebrae, tip of neural
spine to ventral face of centrum, are as follows: Third dorsal, 212.5 mm.; seventh dorsal, 205 mm.; eighth dorsal, 199 mm.; and ninth dorsal, 207 + mm.

Stromer (1908b, p. 126) refers the anterior and the hinder dorsal which he figured in 1903c (pl. 11, figs. 4, 7–8) to this species.

**Lumbar Vertebrae**

An isolated lumbar vertebra (Stromer, 1903c, p. 76) was found in the matrix attached to the mandible associated with the type specimen. Although imperfectly preserved, most of the structural peculiarities of this lumbar (No. 1902. XI. 60, Munich) can be determined. The centrum is broader than long, the neural canal is almost as high as broad, the neural spine is nearly vertical, and the diameter of the dorso-ventrally flattened transverse process at the base is nearly equal to the length of the centrum. The epiphyses are not ankylosed to the centrum.

The incomplete lumbar vertebra (No. 1902. XI. 60a, Munich) referred by Stromer (1903c, pl. 11, fig. 5; 1908, p. 127) to this species has a centrum about 52 mm. in length, and its breadth (58 mm.) anteriorly is greater than its vertical diameter (49 ± mm.). The transverse processes are directed outward and strongly downward. Anteriorly, the breadth (28 mm.) of the neural canal is greater than the vertical diameter (13.5 mm.). The widely separated and divergent postzygapophyses are smaller than those of the hinder dorsal vertebrae. Another hinder lumbar with slightly longer centrum (56 mm.) was associated with the preceding vertebra.

**Caudal Vertebrae**

One of the caudal vertebrae referred by Stromer (1903c, pl. 11, figs. 9–10; 1908, p. 127) to this species may possibly be the third in the caudal series. This large caudal vertebra (No. 1902. XI. 60a, Munich) has elongated and laterally flattened metapophyses projecting forward beyond the level of the anterior end of the centrum, no vestige of a neural spine, a very low and relatively small neural canal, and no obvious backward projection from roof of neural arch. The short transverse processes are truncated obliquely at their extremities and are pierced at the base near the anterior edge by a small foramen. The measurements of this caudal are as follows: Length of centrum, 55 mm.; breadth of centrum anteriorly, 61 mm.; vertical diameter of centrum anteriorly, 54 mm.; breadth of neural canal anteriorly, 12 mm.; and vertical diameter of neural canal anteriorly, 10 mm.

The vertebra (Stromer, 1903c, pl. 11, fig. 6) tentatively identified as the sixth or seventh in the caudal series has short metapophyses, a long and rather broad process projecting backward from roof of the neural arch, very short transverse processes perforated near center of base by a small foramen, and a weak median longitudinal ridge on the ventral face. The facets for the chevron at the hinder end of the ventral surface of the centrum are quite prominent. The measurements of this caudal are as follows: Length of centrum, 55 mm.; breadth of centrum anteriorly, 60 ± mm.; vertical diameter of centrum anteriorly, 50 ± mm.; breadth of neural canal anteriorly, 11.5 mm.; and vertical diameter of neural canal anteriorly, 3 mm.

**Forelimb**

Any attempt to elucidate the successive structural alterations that have been effected in the forelimbs of the smaller archaeocetes must be held in abeyance until more complete forelimbs are available for at least one individual of each of the several species referred to this genus. A left scapula was associated with the referred skull (No. 11235, Stuttgart). The right and left humeri (No. 11417b, Stuttgart) and the right humerus with associated
radius (No. 11951a, Stuttgart) assigned with reservations to this species, if correctly identified, show that the forelimb of this archaeocete is somewhat similar in general conformation to that of *Dorudon stromeri*. As compared to the latter, the most obvious differences are the narrower supraspinous fossa of the scapula, the shorter deltoid crest and more obvious constriction of the shaft of the humerus above the level of the condyles, and the bowed forward shaft of the radius without any obvious anterior angle.

**Scapula**

The vertebral border of the left scapula (Stromer, 1908b, pl. 5, fig. 15) is incomplete, the distal end of the acromion is missing, and the coracoid process is destroyed. As compared with that of *Dorudon stromeri*, this scapula has a narrower supraspinous or prespinous fossa, a narrower neck, a convex hinder margin, a slightly broader acromion, and an articular head that is long oval in outline. The measurements of the left scapula (No. 11235, Stuttgart) are as follows: Greatest vertical diameter, from vertebral edge to ventral face of articular head, 215 mm.; greatest antero-posterior diameter, 230 + mm.; antero-posterior diameter of articular head, 43 mm.; and transverse diameter of articular head, 38 mm.

**Humerus**

Three humeri are tentatively referred to this species by Stromer (Nos. 11951a and 11417b, Stuttgart). They have a somewhat broader head than in *Dorudon stromeri*, the greater tuberosity is laterally flattened, the lesser tuberosity is more prominent, and the bicipital fossa is smaller. The right humerus (pl. 27, figs. 3–4) has a prominent deltoid crest, and the posterior profile of the shaft, viewed from the side, is abruptly indented at the lower end. The conformation of the trochlear surface is similar to that of *Zygorrhiza kochii*.

| Table 57—Measurements (in millimeters) of the humeri |
|---------------------------------|---------------------------------|
|                                  | No. 11951a                      | No. 11417b                      |
|                                  | Stuttgart Right | Stuttgart Right | Stuttgart Right | Stuttgart Right |
| Greatest length                  | 230                           | 230                           |
| Antero-posterior diameter of proximal end, including greater tuberosity | 80 | 76 |
| Greatest antero-posterior diameter of head                         | 58 | 57 |
| Transverse diameter of head                                           | 53 | 51 |
| Antero-posterior diameter of shaft through distal portion of deltoid crest | 38.7 | 37 |
| Transverse diameter of shaft at same level                          | 23 | 24 |
| Antero-posterior diameter of outer condyle                          | 38.8 | 33 |
| Antero-posterior diameter of inner condyle                         | 44 ± | 35 |
| Transverse diameter of combined trochlea and capitulum                | 29 | 29 |

**Radius**

The right radius (No. 11951a, Stuttgart) figured by Stromer (1908b, pl. 5, figs. 16–19) is likewise tentatively referred to this species. It is barely possible that this radius and the associated right humerus mentioned above may belong to *Dorudon osiris*. The anterior and inner faces are slightly eroded and the distal epiphysis is not completely ankylosed to the shaft. The laterally flattened shaft of this radius is bowed forward. There are on the distal end two distinct facets for articulation with the corresponding carpal bones, the anterior of which presumably articulated with the scaphoid, and the posterior one, which is oval in outline and shallowly concave, with the lunar. The facet on the hinder surface of the proximal end, which articulated with the ulna, is not sharply defined. The areas for articulation with the trochlea and capitulum of the humerus are slightly differentiated on the proximal end of this radius.
DORUDON ELLIOTSMITHII (Dart)

Type locality—Fayum, Egypt. Horizon unknown, possibly Qasr-el-Sagha.


ENDOCRANIAL CAST

The pronounced general flattening of this small endocranial cast (Dart, 1923, fig. 6) brings into prominence certain structural peculiarities which distinguish it from Dorudon sensitivus, particularly the increased bi-parafloccular width, the general triangular outline as seen from above, and the transversely widened cerebellum. The actual length, height, and bulk of the brain-mass are considerably less than in the latter. As with D. sensitivus, the endocranial cast of this species reveals the presence of a greatly enlarged cerebellum which tends to grow forward over the cerebrum, the trigeminal apparatus is markedly enlarged, and the flattened diminutive cerebrum is bounded behind by the cerebellum, superiorly in the mid-line by a well-marked sagittal sinus, and inferiorly by the Gasserian ganglion and the trigeminal apparatus.

The olfactory peduncles are broken off near their bases. The ventral surface of this cast is largely destroyed. However, the remnant of the trigeminal apparatus, which is preserved at the anterior end of this cast, indicates that the enlargement of these trunks is not quite so pronounced as in D. sensitivus. The smooth cerebrum (Dart, 1923, fig. 5) is noticeably flattened, and slopes upward and backward toward the cerebellum. Behind the sagittal sinus is a shallow median tentorial depression and the sharply defined transverse tentorial sulci separating the cerebrum and the cerebellum. The lateral Sylvian depression or longitudinal furrow which marks the boundary between the cerebral hemisphere and the Gasserian ganglion is partially filled with the cast of the middle cerebral vessels. The cast of the Gasserian ganglion is not complete and hence these structures do not appear quite so prominent as in D. sensitivus.

The cerebellum is only slightly elevated above the cerebrum and the lobus medius cerebelli is symmetrical. Each lateral paraflocculus is expanded, forming a large buttress. Measurements by Dart indicate that the bulk of this endocranial cast is approximately 310 c.c.

The lack of information in regard to the exact horizon from which this cast came, except for the statement of Elliott Smith (1903, p. 322) that it was “found in the same locality” as the skull of D. osiris (No. M. 8150, British Museum), adds to the uncertainty in regard to the type of archaeocete to which it may have belonged. The small size of the brain mass and the probability that it was found in the Qasr-el-Sagha deposits, may not justify the inference that it belonged to D. sittelii. It is true, nevertheless, that the measurements of the fragmentary type skull of D. zettelii show that it was very little if any larger than the juvenile skull of D. osiris in the Stuttgart collection (No. 11786). The degree of likeness between the natural endocranial cast of D. elliotsmithii and the natural endocranial cast of the juvenile skull (No. 11786) in the Stuttgart collection is quite marked, not only in the dimensions of the corresponding parts, but also in the contours of the brain mass. A careful comparison of a duplicate of the endocranial cast of D. elliotsmithii with that of the juvenile D. osiris may show that the differences between the brain masses of these two are less trenchant than are indicated by the descriptions and illustrations.

For the dimensions of the endocranial cast of D. elliotsmithii, see table 55 (p. 200).
DORUDON SENSITIVUS (Dart)


*Type locality*—Near a hill called Gar-el-Gehannem, west-south-west of the lake (Birket-el-Qurun), Fayum, Egypt. Exact horizon unknown; Wadi Rayan beds occur in this region and to the west are the Birket-el-Qurun and Ravine beds.

*Type specimen*—Natural endocranial cast. No. M. 12123, Geological Department, British Museum (Natural History); collector, H. J. L. Beadnell.

**ENDOCRANIAL CAST**

This natural endocranial cast is characterized by the large bulging Gasserian ganglia, the rounded cerebral hemispheres, the enlargement of the trigeminal apparatus, the unusually expanded paraflocculi, and the great transverse width of the medulla oblongata.

The olfactory peduncle is attached to the cerebral hemisphere (Dart, 1923, fig. 3) on its ventral surface in front of the area occupied in part by the tubercula olfactoria. Behind the level of the area of attachment of the olfactory peduncle is a longitudinal furrow in the lower and anterior part of the lateral aspect of the cerebral hemisphere which Dart identifies as the Sylvian depression. At the hinder end of each of these lateral depressions, the cast of the middle cerebral vessels is preserved.

The exposed surface of each bulging cerebral hemisphere (Dart, 1923, fig. 2) is essentially smooth. Each hemisphere is bounded medially on the dorsal aspect by the sagittal sinus and posteriorly by the cerebellum. The knob-like elevations along the sagittal sinus seemingly represent veins entering the brain from the diploe of the skull. Behind the prominence of the sagittal sinus is the deep median tentorial depression from which a tentorial sulcus runs laterally on each side, separating the cerebral hemisphere and the cerebellum.

The huge bulging lateral mass identified by Dart (1923, fig. 5) as the Gasserian (semilunar) ganglion, which hems in laterally and anteriorly the cerebral hemisphere at its ventral margin, rivals the cerebral hemisphere in size and gives rise to three proportionately large trunks—the ophthalmic, maxillary, and mandibular divisions of the trigeminal nerve. These two ganglia also participate in the modeling of the lateral walls of the cranial cavity.

The irregular mass of the cerebellum, which is characterized by its convolutional pattern, is elevated about 15 mm. above the cerebrum and is separated from the latter by the tentorial sulcus. On the lateral aspect the unusually expanded floccular lobe, comprising the flocculus and the paraflocculus, is quite prominent. The paraflocculus is bounded above by the lobus medius cerebelli; anteriorly it abuts on the cerebral hemisphere and the huge Gasserian ganglion; inferiorly it rests upon the acoustic nerve (VIII), the petrous portion of the squamosal, and the jugular leash which leaves the cranial cavity through the foramen lacernum posterius; and posteriorly it is in contact with the exoccipital bone. The elevated lobus medius is markedly asymmetrical.

On the ventral aspect of this natural endocranial cast it is seen that the ophthalmic trunk of the trigeminal nerve is in contact with the optic nerve inferiorly and the olfactory peduncle superiorly. These three structures parallel one another until the tuberculum olfactorium is reached. At the level of the tuberculum, the maxillary division of the trigeminal is attached to the Gasserian ganglion. Each optic nerve is wedged in between the ophthalmic trunk of the trigeminal nerve and the latero-basal angle of the corresponding olfactory peduncle. Although the optic nerve is not visible between the Gasserian ganglion and the tuberculum olfactorium as a distinct elevation, it must have followed the lateral aspect of the tuberculum to its posterior margin and there bent inward to meet its fellow of the opposite side in the assumed position of the optic chiasma at the posterior end of
the inter-tubercular sulcus. The small single median elevation behind this point has been identified as the tuber cinereum and the hypophysis. The mandibular division of the trigeminal is attached to the postero-medial angle of the Gasserian ganglion.

Behind the level of the tuber cinereum, the Gasserian ganglia diverge widely, giving rise at first to a slight central depression and then to a broad flat surface. Dart (1923, p. 623) has suggested that the wide divergence of the Gasserian ganglia may have resulted from the forward projection on each side of a tuberculum quinti which was correlated in size with these enormous ganglia. The roll-like longitudinal swelling on each side of the median transverse depression where the pons should lie is likewise considered by Dart to have resulted possibly from the expansion of the substantia gelatinosa of the medulla oblongata. The pons was probably quite small. Posteriorly the base of the brain (Dart, 1923, fig. 4) passes gradually into the medulla oblongata, which is characterized by its great transverse width. No trace of the origin of the third, fourth, or sixth cranial nerves is left on the cast. Likewise the origin of the seventh and eighth cranial nerves is obscure, although the portion of the latter that traverses the petrous portion of the squamosal is preserved. From its position it is inferred that the cochlear portion of the acoustic nerve is preserved. The cast is broken off in front of the emergence of the ninth, tenth, and eleventh complex of cranial nerves.

Posterior to the acoustic nerve and the parafloccular lobe is an ill-defined mass, the so-called jugular leash, which represents the cast of the jugular vein and associated nerve structures which emerge through the foramen lacerum posterius.

Since the dimensions and contours of this natural endocranial cast indicate that it was formed within a fairly large braincase, there is a strong possibility that it may have belonged to a type similar to D. stromeri.

For the dimensions of this endocranial cast, see table 55 (p. 200).

DORUDON INTERMEDIUS (Dart)


Type locality—Fayum, Egypt. The matrix indicates that the type skull came from the Birket-el-Qurum beds (Oberculina-Nummulite beds) "at the western end of the lake and from a horizon intermediate between those from which the other species were obtained (Andrews, 1923, p. 648). Lower upper Eocene.

Type specimen—An incomplete skull, which lacks the distal extremities of both premaxillaries, the distal ends of both nasals, both zygomatic arches, the extremity of the right exoccipital, the basioccipital, the right periotic, both tympanic bullae, and the major portions of both pterygoids. The crowns of all the teeth, with the exceptions of M2, are damaged. Also an artificial endocranial cast of this skull. No. M. 10173, Geological Department, British Museum (Natural History).

Referred specimen—An incomplete, but uncrushed skull, which lacks the anterior extremities of both premaxillaries, the anterior ends of both nasals and an adjacent section of the left maxillary, the right zygomatic arch, the posterior half of the right and the outer border of the left supraorbital process. The edges of the lambdoidal crest on the supraoccipital shield are incomplete in places, and all of the teeth are missing except M2 and M1 in the left maxillary, M1, Pm4 and a damaged Pm1 in the right maxillary, and an incomplete canine in the right premaxillary. From a red ironstone belonging to the Birket-el-Qurum stage, Fayum, Egypt. No. 1904. XII. 134a, Paläontologische Sammlung, Alte Akademie, München: collector, Richard Markgraf; 1904 (Mn. 10, Stromer, 1908b).
(2) One imperfect hinder lumbar vertebra (Dames, 1894, pl. 35) and two imperfect anterior caudal vertebrae (Dames, 1894, pl. 36). From “Schicht B” of the eastern island (El Kenissa) of Birket-el-Qurun, Fayum, Egypt. Nos. 18–20, Geologisch-Paläontologisches Institut und Museum der Universität, Berlin; collector, Georg Schweinfurth; winter of 1885–86.

**SKULL**

General conformation of skull (pls. 28–31) similar to *Dorudon osiris*, except that the rostrum is less abruptly widened behind level of anterior extremities of nasals, the posterior extremities of nasals are deeply forked and are separated by the narial process of combined frontals, the supraoccipital shield is higher, the middle portion of the lambdoidal crest is much less strongly folded backward and is not noticeably pinched-in, and the occipital condyles are larger.

Parietals normal in relation to adjacent bones, contributing the roof for the cranium and the major portion of the intertemporal constriction, and meeting on the mid-line to form a high sagittal crest that extends forward to hinder edges of frontals; dorsal profile rises abruptly behind level of anterior margin of orbit; each parietal contributes a portion of slightly convex lateral cranial wall and meets the squamosal in a dentate suture that runs downward and forward; squamosal rather large, its upper surface convex from before backward; ventro-anterior or temporal margin of squamosal extended forward as a thin shelf or projecting ledge; zygomatic process slender, presumably short (the anterior extremity of this process is restored on the referred specimen), with its ridge-like upper edge continued backward and upward to join with unusually high lambdoidal crest along outer and hinder edges of squamosal, and forming with the latter the posterior boundary of the enormous temporal fossae; supraoccipital shield (Andrews, 1923, fig. 23) broad and high, strongly concave transversely, with vertical median ridge, and bounded laterally by the prominent lambdoidal crest, for which the anterior face is contributed by the corresponding parietal and the posterior face by the exoccipital; width of supraoccipital shield less in proportion to its height than in *Dorudon stromeri*, its width being about 0.6 of its maximum vertical diameter above the foramen magnum; middle portion of the lambdoidal crest is not abruptly folded backward as in *Dorudon osiris*; exoccipital of moderate width, with sinuous and fairly thick external edge; upper edge of exoccipital free externally, but in contact with lambdoidal crest of squamosal dorso-internally; foramen magnum large; occipital condyles semielliptical in outline, considerably broader at apex than at base, slightly convex from side to side, and set off from exoccipital surface by shallow groove; paroccipital processes large, conspicuously prolonged downward; intertemporal region moderately long and broad; lateral walls of intertemporal constriction are nearly vertical above elongated sphenorbital fissure; groove for optic nerve originating at optic foramen, which is situated anterior to and above level of sphenorbital fissure, extends forward and upward on lateral surface of orbitosphenoid and then curves outward on ventral face of supraorbital process of frontal; parietals and frontals quite thick in region of sutureal union; supraorbital process of frontal broadened, extended laterally beyond level of jugal and arched at extremity; postorbital projection of supraorbital process noticeably thickened and preorbital angle relatively thin; orbit of moderate size; lachrymal wedged in between preorbital end of supraorbital process and the jugal, forming part of anterior wall of orbit and abutting against hinder border of maxillary; anterior end of jugal mortised into outer face of maxillary as in *Dorudon osiris* and terminated on the type skull not more than 46 mm. in front of preorbital angle of supraorbital process; an open groove for lachrymal duct present; lateral surface of maxillary not grooved below anterior extremity of jugal, but sloping obliquely inward to alveolar margin; nasals elongated, strongly attenuated anteriorly, slightly convex side to side, and attain their maximum width posterior to hinder ends
of ascending processes of premaxillaries; posterior extremities of nasals widely divergent and separated by a long wedge-like process of combined frontals; anterior extremities of nasals constitute posterior border of dorsal nasal fossa, which they overhang to some extent, the posterior end of the nasal fossa being on a level with the interval between Pm1 and Pm2, and the anterior end being between I3 and C; premaxillaries contribute the floor and the lateral walls of dorsal nasal fossa; ascending process of premaxillary lodged in groove on upper internal border of maxillary and terminated posteriorly above Pm3; proximal end of maxillary abuts against supraorbital process of frontal superiorly and inferiorly projects backward below the latter; two molars are located on inferior process of maxillary; molar series set off from palatal surface by a deep excavation; the large antorbital foramen lies above interval between Pm2 and Pm3; flat oral surfaces of premaxillaries prolonged backward behind level of I3 as a narrow tongue-like wedge, separating anterior extremities of maxillaries; major portion of palatal surface contributed by the more or less flattened horizontal plates of maxillaries, but between the opposite C and Pm1 a longitudinal furrow is formed; bony palate prolonged backward by elongation of palatines and adjacent thin plates of the pterygoids, forming an enclosed tube for the internal choanae; a V-shaped elevation is present on palatal surface of this tube; vertical plate of vomer does not project backward beyond level of posterior margins of palatines; suture between basioccipital and basisphenoid obliterated on referred specimen; median basi-cranial region bounded laterally in front by hamular plates of pterygoids and behind by lateral descending plate-like processes of basioccipital; pterygoid fossa for accessory air sinus of middle ear pyriform in outline, bounded internally by hamular plate of pterygoid, anteriorly by pterygoid, and externally by postero-external limb of pterygoid and bifid anterior end of squamosal; a large foramen ovale for exit of mandibular branch of trigeminal nerve located at hinder end of fissure between falciform process and dorsal portion of anterior end of squamosal; zygomatic processes apparently bowed outward; ventral surface of zygomatic process of squamosal furnished with broad concave glenoid articular surface; a short, thin, curved postglenoid process; a well-defined channel for external auditory meatus, which originates on postero-internal surface of squamosal, continues its course outward behind the base of the postglenoid process of that bone; paroccipital process large, with anterior concavity, but separated from hinder edge of lateral descending process of basioccipital by the wide notch for the jugular leash; posterior process of parietal wedged in between exoccipital and hinder border of squamosal.

For measurement of these skulls, see table 62 (p. 246).

**TYMPANIC BULLA**

No tympanic bullae were found associated with the type skull. Both of them are attached to the referred skull (pl. 28, fig. 1). When contrasted with those of *Dorudon stromeri* and *Dorudon osiris*, the tympanic bulla of this species is seen to be slightly smaller, but otherwise quite similar. From a ventral view, it is almost as wide anteriorly as posteriorly. The ventral face is strongly arched and there is a short broad median furrow on the hinder third of this surface. The usual vertical groove is located near the middle of the external face of the thin outer lip of the bulla. Behind this groove, the large dorsally projecting sigmoid process arises from the thin outer lip and its distal extremity is twisted almost at right angles to the longitudinal axis of the bulla. The posterior conical apophysis or *processus medius* is limited to a low broad convexity, which is almost in contact with the sigmoid process in front. The posterior pedicle is damaged on both periotics. The left tympanic bulla measures 76 mm. antero-posteriorly, 52 mm. transversely, and 55 mm. from extremity of sigmoid process to ventral face.
PERMANENT DENTITION

The crowns of all the teeth, with the exception of M2, are damaged on the type skull. Since the alveolar border of the left maxillary is complete, one can state with certainty that the tooth formula of the upper jaw is I 3. C 1. Pm 4. M 2. The roots alone of the four anterior teeth (C to Pm3) are preserved, portions of the crown of Pm4 and M1 remain, while M2 is nearly complete with the exception of the outer enamel surface of the principal cusp. Five of the upper cheek teeth (Pm2 to M2) have two roots. It is quite certain that Pm1 has but one root. The antero-posterior diameters of the crowns of the hinder cheek teeth in the left maxillary are as follows: M2, 26 mm.; M1, 30 mm.; and Pm4, 44.5+ mm.

On the referred skull, all of the anterior teeth are missing, with the exception of the damaged canine in the right premaxillary. Of the posterior cheek teeth, M2 and M1 are preserved in the left maxillary, and M1 and Pm4 in the right maxillary. The crown of the fourth upper premolar is approximately the same size as the corresponding teeth of *Dorudon osiris*. The anterior and posterior cutting edges of crown of Pm4 are each furnished with three accessory denticles, those on the anterior edge being smaller and farther removed from the apex of the principal cusp than those on the posterior edge. The first upper molar is distinctly smaller than Pm4; it has a much lower principal cusp and the two accessory denticles on the posterior cutting edge are slightly larger than the two on the anterior cutting edge. The second upper molar has a small principal cusp and the two accessory denticles on its posterior cutting edge are larger than the single one on its anterior edge. The three hinder upper cheek teeth (Pm4 to M2) possess two roots. The antero-posterior diameters of the crowns of the molars in the left maxillary, the two premolars and the canine in the right maxillary are as follows: M2, 22 mm.; M1, 29 mm.; Pm4, 39.5 mm.; Pm1, 27± mm.; and C, 27 mm.

ENDOCRANIAL CAST

The resemblances between *Dorudon intermedius* and *Prozeuglodon atrox* [= imm. *P. isis*] both cranially and endocranially are so pronounced that it is doubtful if such striking similarities would exist in the absence of some phyletic relationship between these two forms. The structural peculiarities which distinguish the endocranial cast of *D. intermedius* on one hand from that of *Prozeuglodon atrox* and on the other from that of *D. osiris* serve to emphasize the intermediate position of this species in the phyletic series. As compared with *Prozeuglodon atrox*, the endocranial cast of this archaeocete (Dart, 1923, fig. 12) is characterized by a better marked sagittal sinus, larger Gasserian ganglia, and a greater outward and backward thrust of the paraflocculus. It differs from the endocranial cast of *D. osiris* (No. M.10228, British Museum) in having the dorsal surface of the cerebrum strongly depressed below the prominence of the sagittal sinus, the Gasserian ganglia are relatively larger, and the flattening of the entire brain is less pronounced.

The olfactory peduncles are hemmed in laterally by the huge divisions of the trigeminal nerve. Parallel longitudinal grooves on the dorsal surface of the cast (Dart, 1923, fig. 13) mark the boundary between the medially placed olfactory peduncles and the externally placed trigeminal trunks. The ophthalmic and maxillary divisions of the trigeminal nerve, which are attached ventrally to the Gasserian ganglia, are not differentiated on the cast. Inasmuch as the casts of the anterior nerves are confluent on the ventral surface, the optic nerves are not visible.

The cerebral hemispheres are relatively quite small and the lateral bulging which is so conspicuous in *D. sensitivus* is entirely absent. The prominence of the sagittal sinus is quite high, but the median tentorial depression is less prominent. The cast of the middle
cerebral vessels, which lie in the Sylvian depression, is quite large and partially conceals the Gasserian ganglion when the cast is viewed from above.

The lateral thrusting of the brain mass accentuates the great width of the cerebellum. The *lobus medius cerebelli* is abruptly elevated above the cerebral surface. The contour of the brain mass is further affected by the backward thrusting of the paraflocculus. The posterior view (Dart, 1923, fig. 14) is instructive in revealing a transversely running furrow that subdivides the central mass of the cerebellum and laterally separates the paraflocculus above from the jugular leash below. This furrow marks the position of a secondary tentorial bony projection from the internal surface of the supraoccipital bone. Dart (1923, p. 631) suggests that this bony strut is perhaps associated with the increasing width of the occipital region.

The *medulla oblongata* is not widened in correlation with the increased width of the cranium and the lateral expansion of the brain mass. The slight dorso-ventral crushing of the cranium may have modified the contours of the *medulla oblongata* to a minor degree, but would not necessarily have altered the ellipsoidal outline of the transverse section.

The cubical capacity of this cast has been determined by Dart to be 785 cc. For the dimensions of this endocranial cast, see table 55 (p. 200).

**KEKENODON**


1908. *Xekekenodon* Stromer, Beiträge Paläont. u. Geol. Österreich-Ungarns u. d. Orienten, vol. 21, pp. 147, 152. (Errone typo.)

Permanent dental formula apparently: I \(1^{1,2,3,4}_{1,2}, C \frac{1}{1}, Pm \frac{1,2,3,4}{1,2,3,4}, M \frac{1,2,3,4}{1,2,3,4}; \) canines have a vertical carina on anterior and posterior cutting edges of their sharp-pointed conical crowns, and the enamel is fluted or ornamented with vertical ridges; upper serrate-edged cheek teeth have laterally compressed crowns ornamented with vertical striae, accessory denticles on their anterior and posterior cutting edges, and the cingulum either weak or absent; two of the upper premolars (? Pm3 and ? Pm4) have three roots; roots of all the cheek teeth united for a considerable portion of their length and usually closely approximated at their extremities; form of skull unknown.

**KEKENODON ONAMATA** Hector


**Type locality**—The “upper Eocene strata of the Waitaki Valley in Otago,” New Zealand. McKay (1882, p. 68) states that the type specimen was found in slightly calcareous greensand in the Waitaki Valley in the immediate vicinity of Wharekauri and on the bank of the Waitaki River “where the middle part or lower third of the fossiliferous portion of the *Kekenodon* beds are exposed so as to be washed by the river when in high flood——.” The *Kekenodon* beds described by McKay underlie the Otakaaika limestone. Ototaran stage, lower Miocene.
**KEKENODON**

*Type specimen*—The original description was based upon “fragments of the lower jaw and some ten teeth,” including six serrate-edged cheek teeth, two of which are three-rooted and two single-rooted teeth. Hector also figures a tympanic bulla and a periostium. Cat. No. Ma. 69, Dominion Museum at Wellington, New Zealand; collector, Alexander McKay; 1881.

McKay (1882, p. 68) describes this occurrence as follows: “Amidst a pile of débris (which probably represented an entire head), portions of a lower jaw, with several perfect and numerous fragments of teeth, were found. . . . Lying close to these remains vertebral centra were observed which probably belonged to the same individual.” These vertebrae ranged from 3½ to 4 inches in length. Furthermore, McKay (1882, p. 104) mentions an atlas and fragments of ribs which were not described by Hector.

*Referred specimens*—McKay (1882, p. 104) records the finding of the following additional remains of *Kekeodon onamata* in the Wharekuri basin: (1) A nearly entire skeleton, 23 feet in length, which “sustained damage during its carriage to Wellington, so that it is not now possible to put the parts together so as to form an entire skeleton;” (2) fragments of a skull but no teeth, tympanic bulla, both scapulae, sternum, numerous vertebrae (including an atlas and axis), and ribs; (3) cervical vertebrae, including the axis, and ribs; and (4) vertebrae, principally caudals, which were found near the type specimen.

According to Park (1905), remains of *Kekeodon onamata* have been collected at the following localities in South Canterbury, New Zealand: (1) The Kakanui calcareous greensand in the steep cliffs on the sea-coast north of the quarry near Kakanui Township (Park, p. 511); (2) the Marawhenua glauconitic greensand (a compact calcareous greensand) at the base of the Waitaki stone, ½ mile east of Marawhenua, in the cliffs facing the railroad (Park, p. 522); (3) the loose calcareous greensand exposed on the south bank of the Waitaki River, ½ mile below the junction of the Wharekuri stream (Park, pp. 523, 525); and (4) the Upper Waihao marly greensand immediately underlying the Waitaki stone at Waihao Forks (Park, p. 529).

The investigations of James Park (1905) have yielded much information, which is new, concerning the occurrence of *Kekeodon* in the Tertiary strata of New Zealand. According to Park, the bones of *Kekeodon* are generally found in loose or compact calcareous greensands which are often glauconitic, in shelly sands, or in soft calcareous sandstone. The vertical range of *Kekeodon* in the horizon in which it is found is very limited. Park states that the *Kekeodon* bed always occurs at the base of the Waitaki or Ngapara stone, which belongs to the lower Hutchinsonian or upper Ototaran stage of the Oamaru system. The Ototaran stage is considered to be lower Miocene by Thomson (1920, p. 323), while Park contends that the *Kekeodon* horizon can not be older than the middle Miocene.

**TYMPANIC BULLA**

The left tympanic bulla figured by Hector (1881, pl. 18, figs. 9,9) is incomplete. The upper border of the thin outer lip and the structures that arise from it, including the posterior process, the conical apophysis, the sigmoid process, and the anterior process are destroyed. Since the anterior end of the involucrum and the opposite portion of the thin outer lip are broken off, it is impossible to determine the peculiarities of the aperture for the eustachian tube. Otherwise, the general configuration and proportions of this bulla are quite similar to those of *Dorudon intermedius*.

The dorsal surface of the thick involuted portion of the bulla (pl. 32, fig. 9) exhibits a gently convex undulation. A broad furrow crosses the dorsal surface of the involucrum in an oblique direction anterior to the level of the sigmoid process. The involucrum is rather wide posteriorly, being equal to about two-thirds of the transverse diameter of the bulla, and is abruptly attenuated in front of the above mentioned furrow. The posterior
process consists of two pedicles which are separated by a vertical cleft. The larger of these pedicles arises from the hinder angle of the dorsal surface of the involucrum and the outer one projects from the thickened hinder edge of the outer lip.

The ventral face of the tympanic bulla is rather wide. On the hinder half of this surface is a broad median furrow. The internal profile is nearly straight and the external profile is strongly convex.

PERIOTIC

The left periotic figured by Hector (1881, pl. 18, fig. 10) is characterized in part by the deep external notch which is formed at the base of the anterior process and in front of the antero-external angle of the broad fossa for the head of the malleus, by the broad furrow on the anterior half of the ventral surface of the pars cochlearis, by the reduction of the groove for the tensor tympani muscle, and by the unusual proportions of the fossa for the reception of the head of the malleus. In other respects this periotic (pl. 32, fig. 10) possesses the usual features which characterize periotics of archaeocetes.

The pars cochlearis is relatively narrow and the anterior half of the ventral surface is occupied by a broad oblique furrow, which may indicate the course of the internal carotid artery. Anteriorly, the ventral surface of the pars cochlearis rises steeply and is separated from the anterior process by the very narrow groove for the tensor tympani muscle. The adjacent furrow, which is still open on the periotic of Dorudon ater, is almost entirely obliterated on this periotic, although its former position is indicated by a very fine groove. The ovoidal fenestra rotunda is placed rather far forward on the ventral face of the pars cochlearis. The fenestra ovalis is located on the external lateral surface of the pars cochlearis, near the upper limit of the latter and at about the middle of its length. The slender stapes is preserved and its foot plate is lodged in the fenestra ovalis. External and slightly anterior to the fenestra ovalis, the epitympanic orifice of the Fallopian aqueduct opens into a shallow excavation which is bounded externally by the laterally placed fossa incudis. The facial nerve crossed this excavation and followed the usual channel to the posterior face of the periotic. Behind the fenestra ovalis, a low transverse ridge marks the anterior limit of the rather broad hollow for the stapedial muscle. The outer portion of the posterior process of this periotic is destroyed. The hiatus epitympanicus is relatively narrow.

The broad fossa for the reception of the head of the malleus, which lies anterior to the fossa incudis, has abruptly elevated anterior and external edges. Viewed from the ventral side, the anterior process is rather broad at the base, its lateral surfaces are strongly convex, and it is abruptly attenuated anteriorly.

DENTITION

Two one-rooted teeth are included among the teeth belonging to the type specimen. One of these teeth (pl. 32, figs. 2, 15) lacks the apical portion of the crown and the distal end of the root. The measurements of this tooth indicate that it is probably the canine from the left maxillary, as suggested by Hector. The root is gradually enlarged below the neck and the enamel surface of the crown is fluted in a vertical direction.

All of the serrate-edged cheek teeth have the enamel surface of the laterally compressed crown ornamented with vertical striae, and the conical accessory denticles on the cutting edges progressively increase in size from the base of the crown toward the principal cusp. At least two of the upper premolars have three roots, a large anterior and two smaller posterior ones, but the other premolars have only two roots. The roots of the cheek teeth are always closely oppressed except at their extremities and generally are united for a considerable portion of their length. The allocation of all of these teeth is uncertain, since they were separated from the corresponding jaw bones. The following allocations must be considered as tentative.
The internal and posterior views of the left Pm2 (pl. 32, figs. 4, 4') show that the two roots of this tooth curve slightly forward. Both roots are noticeably enlarged below the neck and are closely appressed for almost their entire length. The principal cusp of the crown is distinctly larger than any of the accessory denticles, of which there are two on the anterior cutting edge and four in addition to a rather minute basal one on the posterior cutting edge.

A three-rooted tooth, which seems to be the right Pm3 (pl. 32, figs. 7, 14), has, in addition to the principal cusp, four accessory denticles on the posterior and three on the anterior cutting edges. The basal denticle on the posterior cutting edge is quite small. The neck of the combined roots below the base of the enamel crown is noticeably constricted, and the three roots are united for about half their length. The posterior pair of roots are broken off near the middle of their length.

On the other three-rooted tooth, which is identified as the left Pm4 (pl. 32, figs. 3, 11), the apices of the principal cusp and two of the accessory denticles are destroyed. There are two small accessory denticles on the upper half of the anterior cutting edge and one large and three smaller ones on the posterior cutting edge. The crown of this tooth curves inward. Two of the three roots of this tooth seem to have been united for their entire length, but the extremity of the anterior root seems to have been free.

The following measurements of these teeth were furnished by W. R. B. Oliver, director of the Dominion Museum.

<table>
<thead>
<tr>
<th>Table 58—Measurements (in millimeters) of the teeth</th>
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<tbody>
<tr>
<td>Greatest</td>
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<tr>
<td>length of tooth</td>
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<tr>
<td>of neck</td>
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<tr>
<td>below</td>
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<tr>
<td>crown</td>
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<tr>
<td>One-rooted tooth, left upper canine (pl. 33, fig. 15), apex of crown and end of root missing</td>
</tr>
<tr>
<td>Three-rooted cheek tooth, right Pm3 (pl. 33, fig. 14), anterior root complete</td>
</tr>
<tr>
<td>Three-rooted cheek tooth, left Pm4 (pl. 33, fig. 11), extremities of three roots destroyed</td>
</tr>
<tr>
<td>One-rooted tooth, right lower canine (pl. 33, fig. 17), practically complete</td>
</tr>
<tr>
<td>Two-rooted cheek tooth, right Pm3 (pl. 33, fig. 10), extremities of both roots destroyed</td>
</tr>
<tr>
<td>Two-rooted cheek tooth, right Pm4 (pl. 33, fig. 12), crown and portion of neck of roots</td>
</tr>
<tr>
<td>Two-rooted cheek tooth, right M2 (pl. 33, fig. 13), posterior root broken off below neck and extremity of anterior root destroyed</td>
</tr>
</tbody>
</table>

The tooth with one root (pl. 32, figs. 1, 17), which is identified by Hector as the canine from the right mandible, is practically complete. It has a curved root, which is noticeably expanded near the middle of its length, and the sharp pointed conical crown measures 1½ inches (38.1 mm.) in height. The enamel surface of the crown is fluted with vertical ridges and there is in addition a vertical carina on the anterior and posterior faces.

The tooth identified as the right Pm3 (pl. 32, figs. 5, 16) is somewhat better preserved than most of the others. It has two rather large and unusually long roots, which are at least three times as long as the crown and are separated distally for more than half of their length. The apex of the principal cusp as well as the summits of most of the accessory denticles on the cutting edges of the laterally compressed crown are worn; there are three accessory denticles on the anterior cutting edge and four on the posterior cutting edge.

One of the serrate-edged cheek teeth (pl. 32, figs. 6, 12) figured by Hector is considered to be a mandibular tooth, presumably the right Pm4. The crown of this two-
rooted tooth consists of a principal cusp, which is not especially large, and four accessory
denticles on both the anterior and the posterior cutting edges. The basal denticles on
both cutting edges are quite small.

A two-rooted tooth, which lacks accessory denticles on the anterior cutting edge, is
identified as M2 (pl. 32, fig. 13). The principal cusp is slightly larger than the adjacent
accessory denticle on the posterior cutting edge. There are in all four accessory denticles
on the posterior cutting edge. The posterior root is broken off below the neck and the
anterior one lacks the distal extremity.

PHOCOCETUS

vasconum Delfortrie)

Since this genus and its type species are based on a single premolar tooth, which ex-
hibits a remarkably close resemblance to a premolar of Kekenodon onamata, one can not
be certain from the material at hand whether slight differences in the ornamentation of
the enamel on the crown have any diagnostic significance. With the existing inadequacy of the material, it would be
difficult to justify the suppression of the generic name Phococetus. Until it can be demonstrated conclusively from com-
parable dental and skeletal remains that onamata and vasconum belong in the same genus, the generic names Kekenodon
and Phococetus may be recognized provisionally. In case later discoveries prove that these two species are congeneric,
Phococetus will have priority over Kekenodon.

PHOCOCETUS VASCONUM (Delfortrie)

1873. Zeuglodon vasconum Delfortrie, Actes Soc. Linneenne de
Bordeaux, ser. 3, vol. 9, pp. 113–117, figs. A–D; Brandt,
21, No. 6, pp. iv, 47; Delfortrie, 1874, Journ. Zool., Paris,
London for 1892, pt. 4, p. 561; Stromer, 1903, Beiträge
Paläont. u. Geol. Österreich-Ungarns u. d. Orientes, vol. 15,
p. 87.

1, p. 70; Van Beneden and Gervais, 1880, Ostéographie
des Cétacés vivants et fossiles, Paris, pp. 453, 519; Abel,
1913, Denkschr. k. Akad. Wiss. math.-naturw. Kl., vol. 90,
62, p. 86.

1908. Zeuglodon (= Phococetus) vasconum Stromer, Beiträge Paläont.
 u. Geol. Österreich-Ungarns u. d. Orientes, vol. 21,
p. 147.

Type locality—The soft calcareous sandstone at Saint-
Médard-en-Jalle, about 8 kilometers northeast of Bordeaux,
France. The “molasse ossifière” is referred to the lower Burdigalian by Dollfus (1909, pp.
385, 397). Lower Burdigalian stage, lower Miocene.

Type specimen—A single imperfect premolar tooth. Museum d’Histoire Naturelle
de Bordeaux, France. [Artificial cast, No. 11754, Academy of Natural Sciences of Phila-
delphia.]

DENTITION

The conformation of the crown and the arrangement of the accessory denticles indi-
cate that this tooth (fig. 81) is a Pm3 from a right mandible. Besides the median principal
cusp, which is not especially enlarged, there are three accessory denticles and a very small
basal tubercle on the anterior cutting edge, and four large accessory denticles and a small
basal one on the posterior cutting edge. On each of these cutting edges, the accessory
denticles progressively decrease in size from the upper to the lower one. No distinct cinguloid ridge is developed on the base of the rather low and laterally compressed crown of this tooth. The enamel surface around the base of the crown is ornamented with short vertical striae. The enamel on the accessory denticles is, however, rather smooth. Although the distal portions of the two laterally flattened roots of this tooth are broken off, it is quite obvious that the posterior root is larger than the anterior root. Delfortrie did not give the measurements of the type tooth. The measurements of the cast are as follows: Maximum antero-posterior diameter at base of crown, 35.5 mm.; maximum transverse diameter at base of crown, 12.8 mm.; and vertical diameter of enamel on crown at level of principal cusp, 23.5 mm.

Stromer (1903c, p. 87) has pointed out that this tooth is characterized by certain peculiarities, particularly the conformation of the crown and the union of the roots, which are quite like those exhibited by the premolars of *Kekenodon onamata* (see pl. 32, fig. 6). Abel (1914, p. 209) likewise remarks that the agreement between the cheek teeth of *Kekenodon onamata* and that of *Phococetus vasconum* is remarkably close, not only in the size and shape of the crown, the position and number of accessory cusps, but also in the union of the roots. The lateral vertical groove, that marks the line of union of the roots is, however, much more conspicuous in *K. onamata* than in *P. vasconum.* The lack of additional teeth of *Phococetus vasconum* hinders detailed comparisons with those of *Kekenodon onamata.*

**PROTOCETIDAE**


Archaeocetes of large and small size; permanent dental formula probably: I \( \frac{1.5.3}{1.5.3} \), C \( \frac{1}{1} \), Pm \( \frac{1.5.3}{1.5.3} \), M \( \frac{1.5.3}{1.5.3} \); crowns of cheek teeth distinctly secodont, without step-like cusps on either the anterior or the posterior cutting edges; Pm1 has two roots and laterally compressed conical crown; crowns of hinder upper premolars (Pm3 and Pm4) have a large principal cusp and a single large basal cusp on posterior cutting edge.

The genera included in this family seem to comprise an unnatural assemblage, although so far as known all possess cheek teeth that have not as yet acquired step-like cusps on the anterior and posterior cutting edges of the crown. In the case of *Pappocetus,* the crowns of the molars (M1 to M3) in the mandible consist of one large anterior cusp and a smaller posterior cusp; the crowns of the hinder mandibular cheek teeth (Dpm3 to M3) have a more or less complete cingulum. It will be observed also that the vertebrae of *Protocetus* are carnivore-like, having relatively short centra, and the large articular facets on the postzygapophyses of the hinder dorsal and of the lumbar vertebrae are nearly vertical in position. The pre- and post-zygapophyses constitute a firm articular connection between successive vertebrae. In striking contrast, the centra of the disproportionately large lumbar vertebrae of *Eocetus* are noticeably elongated and the vestigial articular facets on the postzygapophyses are nearly horizontal in position. The reduction of these postzygapophysial facets and the absence of articular connections between successive lumbar vertebrae is a specialization that also characterizes the Basilosauridae.

**EOCETUS**


Permanent dental formula: I \( \frac{1.5.3}{1.5.3} \), C \( \frac{1}{1} \), Pm \( \frac{1.5.3}{1.5.3} \), M \( \frac{1.5.3}{1.5.3} \); Pm1 to Pm4, inclusive, have two roots; Pm3 to M3 form a closed series; cutting edges of crowns of hinder upper premolars and of upper molars crenelated, but lack step-like accessory denticles; no remnant of a postero-internal cusp on Pm2, Pm3 or Pm4, but the enamel on the crown extends
further downward upon the inner side of the root than upon the outer; crowns of Pm2, Pm4 and M3 have a large principal cusp and a single hinder basal cusp on posterior cutting edge; M3 possibly has three roots; skull large and elongated; rostrum elongated, constituting about three-fifths of condylobasal length of skull; dorsal narial fossa not moved as far backward, relatively, as in Prozeuglodon; forehead flattened; intertemporal region relatively long and narrow; sagittal crest high; supraoccipital shield relatively narrow, bounded by prominent lambdoidal crests; temporal fossæ large; and the large lumbar vertebrae have distinctly elongated centra.

**BOCETUS SCHWEINFURTHI** (Fraas)


**Type locality**—Lower Mokattam series near Cairo, Egypt; about 8 meters below the upper limit of the lower Mokattam in a hard grayish-white limestone, below which *Schizaster* is very abundant.

According to Fraas, this horizon corresponds to the upper region of "A 1 a" of Schweinfurth (1883, p. 730), which later was designated by Blanckenhorn (1903, p. 372) as the "Untere Mokattamstufe I, 5, zweite Mauer." It is the uppermost member of the lower Mokattam. Andrews (1906, p. 245) correlates this horizon with the bed of the Birket-el-Qurun series in which *Prozeuglodon atrox* occurs. Upper middle Eocene.

**Type specimen**—An imperfectly preserved and somewhat crushed skull which lacks practically all of the occipital region with the exception of the right upper half of the supraoccipital shield, a considerable portion of the left parietal, all of the left squamosal, including the zygomatic process, the left jugal, and the basicranial bones. The tympanic bullae and the periostes are likewise missing, and all the teeth with the exception of I2 and I2 have the crowns either damaged or destroyed. The anterior extremity of the right zygomatic process is broken off, a portion of the anterior end of the right jugal is missing, both supraorbital processes are fractured, the rostrum is broken at two places, and the edge of the lambdoidal crest is incomplete. No. 10986, Württembergische Naturaliensammlung, Stuttgart; collector, Richard Markgraf; 1904.

**Referred specimens**—(1) Two imperfectly preserved lumbar vertebrae. Mokattam series near Cairo, Egypt. No. 10934, Württembergische Naturaliensammlung, Stuttgart; collector, Richard Markgraf; 1902 (9a, 9b, Stromer, 1903c, fig. 1, p. 84).

**SKULL**

Conformation and relations of bones in cranium and rostrum (pl. 33) similar to other archaeocetes; parietals normal in relation to adjacent bones, contributing the roof for the cranium and meeting on the mid-line to form a high sagittal crest; upper portion of supraoccipital shield relatively narrow and bounded by a prominent lambdoidal crest which is continued outward along posterior edge of squamosal; squamosal contributes a large portion of upper lateral wall of braincase; squamosal region of braincase somewhat inflated; zygomatic process quite slender; narrow intertemporal constriction relatively long; parietals and frontals quite thick in region of their sutural union; supraorbital process of frontal broadened, extended laterally beyond level of jugal and arched at extremity; postorbital projection of supraorbital process well developed, and preorbital angle thickened; orbit
relatively smaller than in Prozeuglodon isis; anterior end of laterally flattened jugal mortised into outer face of maxillary as in Dorudon; lachrymal wedged in between preorbital end of supraorbital process of frontal and the jugal, forming part of anterior wall of orbit, and abutting against hinder border of maxillary; no visible groove for lachrymal duct; nasals elongated and relatively wider anteriorly than in Prozeuglodon isis; dorsal narial fossa placed slightly farther forward than in Prozeuglodon isis, its posterior limit being above the hinder part of Pm1; the two premaxillaries form the sides and floor of the dorsal narial fossa, as well as the extremity of the rostrum, and on their alveolar borders are located the three incisors; ascending processes of premaxillaries terminate above Pm3; proximal end of maxillary abuts against supraorbital process of frontal superiorly and inferiorly projects backward below the latter to accommodate the posterior molars. The ventral surface of the braincase is destroyed.

The skull was much larger than those of Zygorhiza kochii and Dorudon osiris, and much smaller than those of Prozeuglodon isis and Basilosaurus cetoides. The dorso-ventral crushing of the forehead and the narial region has markedly altered the lateral aspect of this skull. As a result of this crushing, the rostrum appears to be proportionately longer than in other archaeocetes. Actually the rostrum constitutes about 60 per cent of the estimated condylobasal length of the skull. The distance between the anterior end of the right premaxillary and the anterior edge of the orbit is 570 ± 2 mm., and the length of the skull from the anterior end of the right premaxillary to the posterior surface of the apex of the supraoccipital shield is 910 mm. In the case of Prozeuglodon isis and Dorudon osiris, the length of the rostrum constitutes approximately 58 to 60 per cent of the condylobasal length of the skull. The anterior ends of the nasals, which constitute the posterior boundary of the dorsal narial fossa, are approximately 312 mm. distant from the anterior end of the rostrum, and the ratio of this portion of the rostrum to the total length of the skull is about 33 per cent. In Prozeuglodon isis this portion of the rostrum constitutes 37 per cent of the total length of the skull.

Although the skull had already acquired the typical archaeocete construction, the backward migration of the dorsal narial fossa had not reached its maximum, the cheek teeth had not as yet acquired step-like cusps on the anterior and posterior cutting edges, but the inner portion of the crown of the hinder premolars and the molars had been lost or at least was vestigial. The development of these accessory denticles is, however, foreshadowed in the development of a crenelated carina on the cutting edges of the cheek teeth. Furthermore, the lateral extension and widening of the supraorbital processes of the frontals had reached the stage characteristic of all later archaeocetes, a high supraoccipital shield bounded by prominent lambdoidal crests had been developed, the temporal fossae had been greatly enlarged, and the glenoid articular surfaces of the zygomatic processes had acquired the essential features present in succeeding types.

For measurements of this skull, see table 62 (p. 246).

DENTITION

The cheek teeth, which are in place, are so badly damaged that one can neither be certain of all their peculiarities nor of the complete tooth formula. In the right premaxillary I1 and I2 are present, and of these I2 is the larger. The third incisor has dropped out on both sides. At the base of the enamel crown, the antero-posterior diameter of I1 is 28.8 mm. and of I2 it is 33.5 mm. The incisors have a backwardly curved conical crown, the enamel is ornamented with fine vertical ridges, and a weak carinate cutting edge is present. The root of the right canine is broken off at the base of the enamel crown.

So far as known, the premolars and molars of this archaeocete do not possess a crown with markedly serrated cutting edges. Pm1, which lacks the crown, seems to have had
two roots. At the alveolar level, the roots of Pm1 measure 40 mm. antero-posteriorly and 16 mm. transversely. The diastema between Pm1 and Pm2 is approximately 29 mm. That portion of the crown of Pm2 which is preserved indicates that in addition to the principal cusp at least one well-formed hinder basal cusp was present. The antero-posterior diameter of the two-rooted Pm2 when complete was approximately 55 mm. The hinder half of the crown of Pm4 (Fraas, 1904a, pl. 11, fig. 10) is preserved, but the apical portion of the principal cusp is destroyed. It has one large posterior accessory cusp. The enamel on the inner side of the crown extends farther downward upon the root than on the outer side. This premolar apparently had only two roots. Behind Pm3 the upper premolars and molars form a closed series.

The crown of an isolated M3 (Fraas, 1904a, pl. 11, fig. 11), apparently from the left maxillary of this individual, is rather small, measuring 28 mm. antero-posteriorly and 15 mm. transversely at the base. The principal cusp is large and strong, and a small basal posterior cusp is present. There is a strong carina bearing vestigial denticles on the anterior cutting edge. The vertical diameter of the enamel crown of M3 on the inner side is 35 mm. and only 21 mm. on the outer side. Whether or not this molar had two or three roots is uncertain. It is apparent that the cheek teeth of this archaeocete did not have step-like accessory denticles on the anterior and posterior cutting edges. The resemblance otherwise between these cheek teeth and those of Protocetus atavus is remarkably close.

LUMBAR VERTEBRAE

Stromer (1903c, pp. 83–85) has described two lumbar vertebrae which were found in the Mokattam white nummulitic limestone near Cairo, Egypt. He has figured (1903c, fig. 1, p. 84) the best-preserved one (No. 10934, Stuttgart) of the two vertebrae. The anterior epiphysis of this lumbar is missing and the posterior epiphysis is not firmly ankylosed to the centrum. The length of the centrum of this lumbar is 245 mm., the transverse diameter at the posterior end is 140 mm. and the vertical diameter is 130 mm. The antero-posterior diameter of the neural arch is 116 mm. Anteriorly, the vertical diameter of the neural canal is about 25 mm., while the transverse diameter is 70 mm. The maximum vertical diameter of the neural spine is 108 mm., and the antero-posterior diameter of the transverse process near the base is about 155 mm. The wide blade-like neural spine has rather sharp anterior and posterior edges, and the extremity is curved; its antero-posterior diameter is greater than its vertical diameter. The transverse processes are placed rather low on the centrum and the anterior margin is much closer to the anterior epiphysis than is the hinder margin to the posterior epiphysis. The distal ends of these processes are destroyed. The large metapophyses are flat and rather smooth above, but bear no facets, and their outer surfaces are somewhat curved. The damaged postzygapophyses are greatly reduced and almost parallel one another; they do not project backward to the level of the hinder end of the centrum. Since the postzygapophyses terminate in front of level of hinder end of centrum, it is obvious that there can be no articulation between successive lumbar vertebrae. No obvious median longitudinal depression is present on the ventral face of the centrum. The centrum is pierced vertically by two vascular canals; their dorsal orifices are located in the median concavity and their ventral orifices near the middle line. The lateral surfaces likewise are not noticeably depressed.

Two additional lumbar vertebrae (No. 1, Frankfurt) collected by Stromer (1908b, p. 109) in the Mokattam white nummulitic limestone have been referred to this species. They have somewhat lower neural spines and the short transverse processes are abruptly truncated at their extremities.

These lumbar vertebrae conclusively demonstrate the fact that the vertebral column of the larger archaeocetes had already undergone an extensive remodeling at the begin-
ning of the middle Eocene period. This remodeling resulted in the excessive elongation of the centra of the hinder lumbar vertebrae, the enlargement of the metapophyses, the reduction of the postzygapophyses, the loss of articular facets, and the shortening of the transverse processes.

PROTOCETUS


Permanent dental formula: I \(1 \frac{3}{3}\), C \(1 \frac{3}{3}\), Pm \(1 \frac{3}{3}\), M \(1 \frac{3}{3}\); Pm1 has two roots and a laterally compressed conical crown; crowns of hinder upper premolars (Pm3 and Pm4) and of the upper anterior molars (M1 and M2) consist of a large principal cusp, a single large basal cusp on posterior cutting edge, and an enamel-covered postero-internal buttress, possibly the remnant of the postero-internal cusp; hindernoster molar (M3) has vestigial basal cusp on anterior edge of principal cusp; hinder upper premolars (Pm3 and Pm4) and upper molars have three roots; skull elongated; rostrum attenuated; forehead flattened; intertemporal region narrow; sagittal crest high; lambdoidal crests bounding narrow supr-occipital shield prolonged conspicuously backward; temporal fossa large; and no incised pterygoid fossae present.

Vertebral column consists of 7 cervical, ? 12 dorsal, ? 7 lumbar, 1 sacral, and several caudal vertebrae; cervical vertebrae free, centra not compressed antero-posteriorly; axis has peg-like odontoid and relatively long centrum; lower transverse processes of third to fifth cervicals, inclusive, dorso-ventrally flattened and antero-posteriorly widened, but have no vestige of a secondary slender process near base of antero-ventral edge; lower transverse process of sixth cervical greatly elongated; anterior dorsal vertebrae have slender neural spines sloping obliquely backward; hindernoster dorsal vertebrae have broader and nearly vertical neural spines, and no transverse processes; articular facets on postzygapophyses of hinder dorsal and of lumbar vertebrae nearly vertical; lumbar vertebrae have normal centra, not elongated, and neural spines reduced in breadth and height toward hinder end of series; transverse processes of sacral vertebra expanded distally, forming a rather large area for possible attachment to innominate bone; capitulum separated from tuberculum on anterior ribs by a slender neck; and the posterior ribs have a single head.

PROTOCETUS ATAVUS Fraas


*Type locality*—Basal portion of the lower Mokattam series near Cairo, Egypt. In the lowest member of the lower Mokattam series near Cairo large fish bones and the head of an *Arius* were found. Three meters above this basal member is the layer from which *Protoctetus atavus* came and it was associated with remains of fossil crabs and with *Protosiren fraasi*. About 4 meters above this layer is the limestone from which were obtained *Eotheroides aegypticum* and *Tomistoma* sp. (Fraas, 1904a, pp. 200-201).

According to Stromer (Fraas, 1904a, p. 200), the horizon from which this specimen came is equivalent to "Schicht A.Le" of Schweinfurth = "Horizont I a" of Mayer-Eymar = "Basis des Gizehensis-Lagers T1" of Blanckenhorn. The basal stratum of the lower Mokattam of Cairo corresponds with the "Wadi-Rayan series" of Beadnell according to Andrews (1906, p. 235). Lower Lutetian stage, lower middle Eocene.
Type specimen—A nearly complete skull that lacks the extremity of the rostrum; both zygomatic arches are incomplete; and the supraoccipital portion of the lambdoidal crest has been restored on the right side and is incomplete on the left. No. 11084, Württembergische Naturwissenschaftliche Sammlung, Stuttgart; collector, Richard Markgraf; 1903.

Referred specimens—(1) Axis and five cervical vertebrae. No. 11085, Württembergische Naturwissenschaftliche Sammlung, Stuttgart (St. 2, Stromer, 1908b, p. 109).
(2) Eight dorsal, five lumbar, and one sacral vertebrae; and eight rib fragments. No. 11086, Württembergische Naturwissenschaftliche Sammlung, Stuttgart.
(3) Five dorsal vertebrae. No. 11088, Württembergische Naturwissenschaftliche Sammlung, Stuttgart; collector, Richard Markgraf; 1903 (St. 1, Stromer, 1908b, p. 109).
(4) Axis. No. 11089, Württembergische Naturwissenschaftliche Sammlung, Stuttgart (St. 1, Stromer, 1908b, p. 109).
(5) An isolated incisor tooth. No. 1903. II. 22, Paläontologische Sammlung, Alte Akademie, München; purchased from F. Krantz, Bonn a Main, (Mn. 1, Stromer, 1908b, p. 108).
(6) Cranial fragment and a left tympanic bulla. No. 1905. XIIIe. 13, Paläontologische Sammlung, Alte Akademie, München; collector, Richard Markgraf; 1904. (Mn. 2, Stromer, 1908b, pp. 108–109). [This bulla is described as Zeuglodon by Pompeckj, 1922, p. 44.]

SKULL

The skull (pl. 34) of this small archaeocete is less than two feet in length and bears little resemblance to those of Recent cetaceans. Both Fraas and Andrews have pointed out that Protocetus is a highly important link in the history of the Archaeoceti, for here we have a skull that is typically an archaeocete in general form combined with a dentition that is essentially that of a creodont.

The skull may be briefly described as follows: Bones in cranium and rostrum retain normal mammalian relationships; facial region elongated without overlapping of bones; parietals normal in relation to adjacent bones and meet on mid-line to form low sagittal crest that extends forward to hinder edges of frontals; dorsal profile rises gradually behind level of center of orbit; squamosal relatively large, its upper surface convex from before backward; zygomatic process slender, attenuated anteriorly; thin lambdoidal crests bounding supraoccipital shield prolonged conspicuously backward beyond level of occipital condyles; supraoccipital shield strongly concave from side to side, constricted near base and bounded by conspicuously developed lambdoidal crests; exoccipital relatively wide, with sinusous external edge; upper edge of exoccipital in contact with lambdoidal crest of squamosal; foramen magnum large; occipital condyles subpyriform in outline, considerably broader above than below, convex from side to side, and borne on distinct necks; intertemporal constriction narrow; lateral walls of intertemporal constriction are nearly vertical above sphenorbital fissure; forehead flattened; supraorbital processes of frontal broadened, extended laterally beyond level of jugal and arched at extremity; orbit rather small; anterior extremity of jugal mortised into outer face of maxillary as in Dorudon osiris, but no groove for lachrymal duct seems to be present; lachrymal indistinct, presumably wedged in between preorbital end of supraorbital process and the jugal, forming part of anterior wall of orbit, and abutting against hinder border of maxillary; nasals attenuated posteriorly; anterior extremities of nasals constitute posterior border of small dorsal narial

1 It is very difficult to trace the posterior boundaries of the nasals and of the premaxillaries. The nasals seem to extend backward to or slightly behind the level of the oblique fracture in front of the supraorbital processes of the frontals and it is possible that they may have extended 8 to 10 mm. posterior to level of anterior margins of the latter. No trace of the anterior foramen was found, but inasmuch as it is located as a general rule laterally on the rostrum between Pm2 and Pm3, it is quite probable that this foramen is located in the short section that has been restored.
fossa, which is approximately on a level with Pm1; width of dorsal nal fossa (inside measurement) does not exceed 29.5 mm.; extremities of premaxillaries destroyed in front of dorsal nasal fossa; proximal end of maxillary abuts against the supraorbital process of frontal superiorly and inferiorly projects backward below the latter; three molars located on inferior process of maxillary; M1 to M3 set off from palatal surface by a deep excavation; major portion of palatal surface contributed by more or less flattened horizontal plates of maxillaries; bony palate prolonged backward by outgrowths of palatines and pterygoids, forming an enclosed tube for internal choanae; apex of V-shaped elevation on hinder palatal surface located 228 mm. behind level of anterior margin of Pm2; suture between basisphenoid and basioccipital indistinct; ventral surface of basisphenoid bounded laterally in front by thin hamular plates of pterygoids and behind by the low plate-like lateral protuberances of basioccipital; maximum transverse distance between outer surfaces of lateral protuberances of basioccipital estimated to be 63 mm.

The pterygoid fossa for accessory air sinus of middle ear is conspicuously developed in later archaeocetes, especially in Dorudon osiris. If this air sac was developed on the skull of Protocetus atavus, it must have been quite small and located in part on the posterior border of the alisphenoid, and in part on the inner border of the squamosal between the foramen ovale and the level of the extremity of anterior process of periosteal. The curvature of the pterygoid is such that no true pterygoid fossa could possibly have been present. The mandibular branch of the trigeminal nerve leaves the cranium through a notch on the hinder border of the alisphenoid. This notch is bridged across posteriorly by a nodular piece of bone that seems to project from the squamosal. The trigeminal nerve on its outward course then follows a broad groove on the inferior surface of the alisphenoid and reaches the temporal fossa through the notch that is formed by the inferior falciform process of the squamosal and the temporal angle of the alisphenoid. The ventral surface of the attenuated zygomatic process is furnished with a concave oval articular facet, tending toward the peculiar vertical position of true Cetacea, and a thin, short, curved postglenoid process. A broad groove for the external auditory meatus, which originates on postero-internal margin of ventral surface of squamosal, continues its course outward behind the base of the postglenoid process. The narrowest antero-posterior diameter of the groove on the squamosal for the external auditory meatus is 10.6 mm., and the distance from the epi tympanic orifice of the aqueductus Fallopii to external margin of that portion of the squamosal which is grooved for the external auditory meatus is 49.5 mm.; paroccipital process relatively small, with a concavity for reception of stylohyoid, and separated from hinder edge of lateral protuberance of basioccipital by the wide notch for jugular leach; small hypoglossal foramen located on hinder margin of notch for jugular leash; transverse distance between notches for jugular leash, 55 mm.; occipital condyles protuberant; and distance from notch between occipital condyles to posterior margin of hamular process of pterygoid, 112.5 mm.

A cranial fragment belonging to a somewhat larger individual has been described by Stromer (1908b, pp. 108–109). The nasals of this specimen measure about 145 mm. in length and their hinder ends are not separated by a nasal process of the combined frontals. The hinder extremities of the premaxillaries are situated 78 mm. in front of the hinder ends of the nasals. The suture between the frontals and the parietals on the intertemporal constriction is located 98 mm. posterior to hinder ends of nasals. A sharp-edged ridge beginning on the orbital roof is continued backward to the under margin of the large fissura sphenorbitalis, which seems to be situated above the hinder edge of the palatine, and forms the ventral boundary of the groove for the nerves. The dorsal boundary of this groove is formed by a similar parallel ridge which extends backward to level of suture between frontal and parietal, and at the latter point constitutes the dorsal boundary of
the optic foramen. Within the orbit between the anterior ends of the two above-mentioned ridges are four small vascular foramina according to Stromer. At the inner angle of the orbital cavity is a large sphenopalatine foramen, while externally and somewhat above the latter is located the entrance to the infraorbital canal. Stromer also recognizes the entrance to the lachrymal canal in front of the orbit.

For measurements of the skull, see table 62 (p. 246).

TYMPANIC BULLA

The dorsal surface of the involucrum is wrinkled and the ventral surface of the bulla is traversed by a broad obliquely directed groove. The anterior pedicle is rather long, slender, and thin; it has been crushed under the bulla and in its present condition is pressed against the malleus which lies between it and the sigmoid process. The anterior process of the malleus is likewise very slender and its extremity either is fused with the outer lip of the bulla or is lodged in the fissura Glaseri immediately behind the base of the anterior pedicle. The posterior pedicle is rather slender, strongly compressed antero-posteriorly, and consists mainly of a prolongation of the outer lip of the bulla. This pedicle is attached to the basal portion of the posterior process of the periotic.

The left tympanic bulla described by Stromer (1908b, pl. 5, fig. 21) is somewhat larger than those attached to the Stuttgart skull, since it measures 71 mm. in length and 50 mm. in breadth. Pompeckj (1922, p. 44) believes that this bulla belongs to some species of Zeuglodon [=? Dorudon] or perhaps to Eocetus.

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<th>Table 59—Measurements (in millimeters) of the tympanic bulla</th>
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<td>Parameter</td>
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<td>Antero-posterior diameter of tympanic bulla</td>
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<td>Transverse diameter of tympanic bulla</td>
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<td>Maximum vertical diameter of involucreum</td>
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<td>Extremity of sigmoid process to ventral surface of bulla</td>
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<td>Postero-external angle of involucreum to anterior end of involucreum</td>
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<td>Transverse diameter of involucreum posteriorly</td>
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</tbody>
</table>

PERIOTIC

Aside from its smaller size, the periotic (pl. 35) of Protocetus atavus differs from those of all other known archaocetes in the development of a long and rather broad groove which presumably was occupied by the tensor tympani muscle. The anterior process is partially concealed by the overlapping inner edge of the squamosal. The curvature of its outer edge indicates that the anterior process is somewhat foreshortened and that the outer face is decidedly convex. Between the sharp inner edge of the anterior process and the pars cochlearis, a deep groove, which is slightly narrowed anteriorly, extents backward into the epitympanic recess. This groove may have lodged the tensor tympani muscle and, if this interpretation is correct, this muscle had its origin on the posterior border of the alisphenoid and the groove in which it lies, and was inserted on the manubrium of the malleus. Granting that this groove lodged the tensor tympani muscle, then we have in Protocetus atavus a highly important transitional stage in the evolutionary history of the auditory apparatus of whales. In most mammals the mechanism of the inner ear operates in the following manner: When the tensor tympani muscle contracts, the manubrium of the malleus is pulled toward the tympanic cavity, taking up the slack in the triangular ligament, and so rendering the tympanic membrane taut. On contraction, the stapedia muscle draws back the head of the stapes, tilting the anterior end of its footplate toward the tympanic cavity and the posterior end toward the labyrinth, thus rendering tense the annular ligament which encircles the footplate of the stapes. By depressing the footplate of the
stapes into the fenestra ovalis, pressure is applied to the lining membrane of the vestibule and this sets in motion the perilymph which affects the parts of the membranous labyrinth. Sound waves are set up in the ossicular chain and these vibrations affect the cochlea. In later archaeocetes the stalk-like anterior process of the malleus is fused with the outer lip of the tympanic bulla, or at least is rather firmly lodged in the fissura Glaseri which is located on the outer lip of the tympanic bulla in front of the sigmoid process. Corroboratory evidence that this modification of the normal relation of the malleus to the tympanic bulla existed in later archaeocetes is found in the pronounced reduction of the groove for the tensor tympani muscle on the periotics of Dorudon osiris and Basilosaurus cetoides.

The fovea epityubaria (pl. 35, fig. 1), in which the processus tubarius of the tympanic bulla is lodged, is a rather large cup-shaped depression on the internal edge of the squamosal bone. The head of the malleus articulated in a shallow depression, located on the anterior process in front of and slightly external to the epitympanic orifice of the aquaeductus Fallopii and opposite the fovea epityubaria. The maximum diameter of the head of the malleus is 6.5 mm. On the inner rim of the squamosal and opposite the epitympanic orifice of the aquaeductus Fallopii is a small pit, which is interpreted on account of its relative position to be the fossa incudis for the crus breve of the incus. The outer portion of the tympanic surface of the pars cochlearis is irregular in curvature, and is elevated above the remainder of this surface. Crossing the anterior half of this surface in an oblique direction is a rather sharply defined furrow which may indicate the course of the internal carotid artery. The internal or cerebral face of the pars cochlearis is quite rough and somewhat nodular. The epitympanic orifice of the aquaeductus Fallopii is rather minute and the bottom of the channel for the facial nerve is rough and pitted. The area occupied by the stapedial muscle is not distinctly outlined. The fenestra ovalis is concealed by the overhanging outer border of the pars cochlearis; the vestibule is deep and descends obliquely. The fenestra rotunda is about 3 mm. in diameter transversely and is almost triangular in outline. The posterior process of the periotic is wedged between the exoccipital and squamosal, as in Dorudon osiris. This elongated process is expanded distally and projects beyond the exoccipital.

The measurements of the left periotic are as follows: Distance from outer wall of channel for facial nerve to extremity of posterior process, 40 mm.; maximum dorso-ventral diameter of extremity of posterior process, 21.4 mm.; distance from extremity of anterior process to fenestra rotunda, 26 mm.; distance from extremity of anterior process to posterior face of pars cochlearis, 29.5 mm.; maximum transverse diameter of exposed surface of extremity of anterior process, 15.5 mm.; and distance from epitympanic orifice of aquaeductus Fallopii to posterior face of periotic above end of channel for facial nerve, 13 mm.

**PERMANENT DENTITION**

The normal eutherian dentition seems to have been present in Protocetus, that is 3 incisors, 1 canine, 4 premolars, and 3 molars in each upper jaw. The mandible is unknown. In common with the oldest land mammals, there is a marked difference between the anterior grasping teeth and the posterior cutting teeth. In contrast to the archaeocetes of later stages of the Eocene, the cheek teeth of Protocetus do not have step-like cusps on their anterior and posterior cutting edges, and are distinctly secodont.

The three upper incisors were destroyed along with the anterior extremities of the premaxillaries. The isolated incisor tooth described by Stromer (1908, p. 108) has a conical and somewhat laterally compressed crown whose antero-posterior diameter is 17 mm., transverse diameter 10 mm., and height 19 mm. The crown is ornamented with weakly wrinkled enamel and the anterior and hinder edges are angular.
The canine in the right maxillary has a damaged crown. The laterally flattened crown and upper portion of the root of this canine is constricted transversely near the middle, the enamel is ornamented with vertical wrinkles, a sharp vertical carina is present on the anterior edge and a basal cinguloid-like enlargement is present on the outer face.

Neither anterior nor posterior cusps are present at the base of the principal cusp of the two-rooted Pm1. The enamel on the crowns of Pm1 and Pm2 is ornamented with rather coarse plicae, while the hinder cheek teeth have somewhat smoother enamel. The apex of the principal cusp of the two-rooted Pm2 is worn and the enamel surface of the one in the left maxillary measures 15.8+ mm. in depth internally and 18.5+ mm. externally. This elongated premolar does not have a small anterior basal cusp, but does have a low flattened basal posterior cusp. The apex of the principal cusp of Pm3 is likewise abraded, and the enamel surface measures 23.5+ mm. in depth internally and 18.5+ mm. externally. This carnassial tooth has the largest principal cusp of all the cheek teeth and a rather large basal posterior cusp, but apparently possessed no basal anterior cusp. The apex of the principal cusp of the left Pm4 is strongly abraded and the enamel surface that is preserved has a depth of 23+ mm. internally and 14.7+ mm. externally; a large basal posterior cusp and a small cusp located on the basal third of the anterior edge of the principal cusp are also present. The three roots of Pm4 are partially exposed by a fracture extending across the palatal surface of the rostrum and it is obvious that the posterior pair of roots are rather closely approximated. Judging from external indications, Pm3 was likewise three rooted. The five hinder cheek teeth (Pm3 to M3) form a closed series, and the anterior teeth are separated by intervals of varying lengths.

The crown of M1 in the right maxillary is more complete than the one in the left maxillary, but both are imperfect. It is obvious, however, that the crown consists of the principal cusp and a large basal posterior cusp. Although the summit of the principal cusp of M2 is abraded, the enamel surface has a maximum depth in excess of 24.5 mm. internally, while it does not exceed 13.5 mm. externally. This molar has a large basal posterior cusp and a quite small basal exter-anterior cusp. The enamel crown of M3 has a maximum depth of 23 mm. internally and 12.7 mm. externally; the crown consists of a large principal cusp and a vestigial basal anterior cusp. The four hinder cheek teeth have a distinct cinguloid ridge on the external face. Furthermore, the three upper molars and the two hinder premolars have three roots and also an enamel-covered postero-internal buttress which seems to be a remnant of a postero-internal cusp.

For the teeth in the upper jaws, the antero-posterior diameter of the enamel crown at the base is as follows: C—right, 25.5 mm.; Pm1—right, 20.8 mm.; Pm2—right, 33.8 mm., left, 34 mm.; Pm3—right, 36.2 mm., left 34+ mm.; Pm4—right, 25.3 mm., left, 24.8 mm.; M1—left, 22.2 mm.; M2—right, 22.8 mm., left, 17.7 mm.; and M3—right, 14 mm., left, 13 mm.

**Vertebrae**

Assuming that the vertebral column consisted of 7 cervical, 15 dorsal, 13 lumbar, 2 sacral, and 20 caudal vertebrae, and computing the lengths of the centra of the missing vertebrae from the relative lengths of those that have been found, the total length of the skeleton, including the skull, approximated 8 feet or 2.48 meters.

**Cervical Vertebrae**

All of the cervical vertebrae are free. The five hinder cervicals have well-developed pre- and post-zygapophyses. The atlas is unknown. The axis (Fraas, 1904a, pl. 11, figs. 2-5) has a protuberant plug-like odontoid process, convex lateral articular surfaces for articulation with the atlas, the transverse diameter of posterior surface of centrum about equal to vertical diameter, a longitudinal ridge on ventral face of centrum, a high neural spine, and the transverse processes directed obliquely backward. The dimensions of this
axis are as follows: Breadth, 70 mm.; length of centrum + odontoid process, 50 mm.; transverse diameter of hinder end of centrum, 35 mm.; and vertical diameter of hinder end of centrum, 30 mm.

The neural canals of the cervical vertebrae increase in width toward the hinder end of this series. The six posterior cervicals have the transverse processes perforated at the base by a large vertebrastral foramen. The third (Fraas, 1904a, pl. 11, figs. 6–7) and fourth cervical vertebrae have broad lower transverse processes and a rather short centrum. The prezygapophyses of the fifth cervical vertebra (Fraas, 1904a, pl. 11, fig. 8) are widely separated and each is supported by the lateral buttress on the transversely widened pedicle of the neural arch. This lateral buttress is continuous ventrally with the lower transverse process and incloses the vertebrastral canal. The long inferior transverse processes of the sixth cervical (Fraas, 1904a, pl. 11, fig. 9) are directed more downward than outward; the neural canal is wider than high and the neural spine is quite short. The third to the seventh cervical vertebrae, inclusive, have centra that range in length from 18 to 22 mm.; the hinder ends of these centra have transverse and vertical diameters varying from 30 to 32 mm. The greatest transverse diameters of these vertebrae range from 80 to 90 mm. For additional measurements for these vertebrae, see Fraas (1904a, pp. 211, 212).

**Dorsal Vertebrae**

The dorsal series may have consisted of more than 12 vertebrae according to Stromer (1908b, p. 109). Although they are considerably smaller, the anterior dorsal vertebrae (Fraas, 1904a, pl. 12, figs. 1–2) of Protocetus atavus resemble those of Zygorhiza kochii in the general shape of their neural spines, centra, and diapophyses. The absence of transverse processes on the hinder dorsal vertebrae of atavus is a characteristic distinction. The postzygapophyses are prolonged backward to provide a firm articulation with the prezygapophyses of the following vertebrae, and the postzygapophysial facets on the hinder dorsals are nearly vertical in position. The anterior dorsal vertebrae have high slender neural spines which are directed obliquely upward and backward, anterior and posterior demifacets on each side of the centrum for articulation with the capitula, and laterally projecting diapophyses for the tubercula of the corresponding ribs. The dorsals near the middle of the series have a considerably broader and more nearly vertical neural spine, a longer centrum, and large elongated metapophyses. The transitional dorsal identified by Fraas (1904a, pl. 12, fig. 4) as the twelfth in this series possesses the structural peculiarities of the ninth in the dorsal series of Zygorhiza kochii. The one identified as the eleventh dorsal vertebra (Fraas, 1904a, pl. 12, fig. 5) is certainly one of the hinder dorsals.

The centra of the dorsal vertebrae progressively increase in length from the first (25 mm.) to the hindermost in this series (35 mm.). The transverse diameters of the hinder ends of the centra increase from 42 to 55 mm., and the vertical diameters from 25 to 37 mm. The vertical diameters of the neural canals increase from 15 mm. on the fourth dorsal to 25 mm. on the eleventh dorsal, and the transverse diameters from 20 mm. on the seventh dorsal to 27 mm. on the eleventh dorsal. For additional measurements of these vertebrae, see Fraas (1904a, p. 212).

**Lumbar and Sacral Vertebrae**

There are at least seven vertebrae in the lumbar series (Fraas, 1904a, pl. 12, figs. 5–7), and it is quite likely that the complete series consisted of 13 vertebrae. The neural spines of these lumbars are reduced in breadth and height toward the hinder end of this series. The transverse processes of the anterior lumbars slope obliquely outward and downward, while those of the hinder lumbars are bowed strongly downward. The metapophyses are quite slender and the neural canals are broader than high. All of these lumbars have well-
developed pre- and post-zygapophyses, the postzygapophyseal facets being nearly vertical in position. The centra of these seven lumbar vertebrae vary in length from 35 to 45 mm. The transverse diameters of the hinder ends of these centra range from 40 to 53 mm., and the vertical diameters from 35 to 40 mm. The height of the neural canal decreases posteriorly from the first (23 mm.) to the seventh (12 mm.) in the lumbar series, and also diminishes in breadth from 28 to 18 mm. (fifth lumbar). For additional measurements of these vertebrae, see Fraas (1904a, p. 213).

The sacral vertebra (Fraas, 1904a, pl. 12, figs. 8–9) has a small neural canal, and the distal ends of the broad transverse processes are dorso-ventrally thickened. This distal expansion suggests the presence of fairly well-developed innominate bones. Stromer (1908b, p. 109) has shown that what Fraas (1904a, p. 214) took to be the metaphysis is actually the displaced neural spine. The measurements of this sacral vertebra are as follows: Length of centrum, 46 mm.; transverse diameter of centrum, 50 mm.; vertical diameter of centrum, 25 mm.; length of transverse process, 47 mm.; and antero-posterior diameter of distal end of transverse process about 50 mm. For additional measurements of this vertebra, see Fraas (1904a, p. 214).

The caudal vertebrae have not as yet been described.

RIBS

The anterior ribs (Fraas, 1904, pl. 12, figs. 10–12) have slender shafts and are furnished with a sharply defined capitulum and tuberculum, the capitulum being borne on a slender neck. The hinder ribs have a single head.

EXTREMITIES

The pectoral and pelvic elements are unknown.

PROTOCETUS sp.

Locality—No. 145-T-71, Bureau of Economic Geology, University of Texas. On left bank of Two-Mile Creek, from 0 to 100 feet below the first ford above the Two-Mile Church and iron bridge, extending from the southwest fence of Emma and E. J. Houston land (said to belong to a Mr. King) for about 100 feet up to the ford, and downstream from fence of Gary D. Wood's 300-acre tract, and located probably in Emma and E. J. Houston land, J. L. Landrum Survey, southeastern Leon County, Texas.

Above and below the 7-foot zone of glauconitic and fossiliferous marl, in which this vertebra was found, are, respectively, 3 and 4 foot layers containing scattered knobs of red-brown clay ironstone weathered from dense bluish, glauconitic limestone. This marine lentil is in the lower part of the Two-Mile member of the Crockett [= upper Cook Mountain] formation (fide, H. B. Stenzel), which stratigraphically is very nearly the equivalent of the Lisbon formation of the Claiborne group. Upper middle Eocene.

Specimen—An imperfectly preserved dorsal vertebra. Bureau of Economic Geology, University of Texas, Austin, Texas; collector, H. B. Stenzel; 1934.

DORSAL VERTEBRA

The centrum of this vertebra (pl. 15, figs. 4–6) is considerably longer than those of the dorsal vertebrae of Protocetus atavus, although the transverse and vertical diameters of the ends of the centrum and of the neural canal are not markedly different. The preservation of this vertebra is such that precise description is almost impossible. The general configuration of the vertebra, however, and the structures that are preserved indicate that it belongs at the anterior end of the dorsal series, possibly representing the fifth. The demifacet at the antero-superior angle of the centrum for the capitulum of the corresponding rib is triangular in outline and extends over upon the anterior end of the centrum. In
position and shape it resembles the corresponding demifacet on the third dorsal vertebra of Protocetus atavus (Fraas, 1904a, pl. 12, fig. 2). The slender neural spine (antero-superior diameter at base, 25 mm.) originally sloped backward, but has been pushed forward and downward into the neural canal. In view of the imperfect preservation of this vertebra, particularly its processes, the generic allocation must be considered as tentative.

Neural spine broken off about 25 mm. above the base; anterior edge of neural spine is quite thin, but posterior edge is rather wide and transversely flattened near the base; pedicle of neural arch rather wide antero-posteriorly, the minimum diameter (21 mm.) of the right pedicle being less than half the length of the centrum; anterior edge of each pedicle at base almost flush with anterior end of centrum, while hinder edge at base is set back about 10 mm. from hinder end of centrum; both prezygapophyses incomplete; prezygapophysial articular facets slope obliquely downward from external to internal margins, the opposite facets being separated by an interval of at least 15 mm.; postzygapophyses rather narrow transversely (10 mm.), sloping obliquely downward from internal to external margins, the opposite facets being separated by an interval of about 10 mm.; neural canal relatively large, slightly wider than high; both diapophyses destroyed; centrum slightly wider than long; and lateral and ventral surfaces of centrum deeply eroded, obliterating all vestiges of hinder demifacets for ribs.

The measurements of this vertebra are as follows: Length of centrum, 47 mm.; transverse diameter of centrum anteriorly, 52 mm.; vertical diameter of centrum anteriorly, 37 mm.; transverse diameter of centrum posteriorly, 48.5+ mm.; vertical diameter of centrum posteriorly, 41 mm.; transverse diameter of neural canal anteriorly, 28 mm.; and vertical diameter of neural canal anteriorly, 21 mm.

PAPPOCETUS


Dental formula: Di 7/7, De 7/7, Dpm7/7, M7/7; alveolus of Di2 considerably larger than that of Di1 or Di3; Dpm1 has one root; remainder of deciduous premolars (Dpm2 to Dpm4) and the molars (M1 to M3) have two roots; crowns of cheek teeth have a more or less complete circump and the enamel ornamented with fine ridges. Dpm5 has laterally compressed crown, and two or possibly three accessory denticles on posterior cutting edge; Dpm4 has laterally compressed principal cusp and a posterior heel-like cusp; molars (M1 to M3) have a large anterior cusp and a smaller posterior cusp; mandible rather massive, with symphysial region curved upward; symphysis rather strong; axis has blunt odontoid process and rather wide centrum; and skull and remainder of skeleton unknown.

PAPPOCETUS LUGARDI Andrews


Type locality—Hard pyritic clay in a railroad cut on the Port Harcourt railroad at Ameki in the Omobialla District, southern Nigeria, Africa. Associated with this archaeocete in this typical estuarine facies are a leathery turtle (Cosmochelys dolloi Andrews), a crocodile, a large carinate bird (Gigantornis eaglesomei Andrews), a number of fishes (White, 1926) including Cylindracanthus rectus (Agassiz), Odontaspis koerti (Stromer), Galeocerdo latidens Agassiz, and Propisitsi schweinfurthi Dames, as well as a rich fauna of Mollusca (Newton, 1922). Upper Lutetian stage, middle Eocene.

Type specimen—An imperfect left mandible with anterior extremity as well as articular and angular portions missing, but united with a considerable portion of the right mandible, including the hinder portion of the symphysis, is designated as the type specimen by Andrews. Four more or less complete deciduous cheek teeth, in addition to a posterior
molar that has not erupted, are in place in the left mandible and there are two deciduous premolars preserved in the right mandible. No. M-11414, Geological Department, British Museum (Natural History): collector, Sir Frederick Lugard.

Paratype specimen—Three pieces of a left mandible of another individual; on one of these pieces a nearly complete first lower molar is preserved; the third lower molar is in place but has not erupted. No. M-11086, Geological Department, British Museum (Natural History).

MANDIBLES

These mandibles are more massively constructed than those of either Dorudon osiris or Prozeuglodon atrox [= ızis], and the symphysial portion of the jaw is markedly upturned. The symphysial region is very rugose, indicating that the lower jaws were rather firmly united. The mandible of this archaeocete apparently possessed the full eutherian dentition, with 3 incisors, 1 canine, 4 premolars, and 3 molars in each lower jaw, and is especially interesting on account of the carnivore-like characters of the cheek teeth.

<table>
<thead>
<tr>
<th>Table 60—Measurements (in millimeters) of paratype left mandible</th>
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<tbody>
<tr>
<td>Total length of mandible, as preserved (three fragments united at contacts)</td>
</tr>
<tr>
<td>Distance from posterior margin of alveolus for M3 to distal end of mandible</td>
</tr>
<tr>
<td>Greatest antero-posterior diameter of symphysis</td>
</tr>
<tr>
<td>Depth of mandible at level of anterior edge of M2</td>
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<tr>
<td>Depth of mandible at level of anterior edge of M1</td>
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<tr>
<td>Depth of mandible at level of anterior edge of Dpm1</td>
</tr>
<tr>
<td>Antero-posterior diameter of alveolus of Dih</td>
</tr>
<tr>
<td>Antero-posterior diameter of root of Dih</td>
</tr>
<tr>
<td>Antero-posterior diameter of root of Di3</td>
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<tr>
<td>Antero-posterior diameter of root of Dc</td>
</tr>
<tr>
<td>Antero-posterior diameter of alveolus of Dpm2</td>
</tr>
<tr>
<td>Antero-posterior diameter of alveolus of Dpm3, not ascertainable.</td>
</tr>
<tr>
<td>Antero-posterior diameter of crown of M1</td>
</tr>
<tr>
<td>Antero-posterior diameter of crown of M2</td>
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<tr>
<td>Antero-posterior diameter of crown of M3</td>
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<tr>
<td>Transverse diameter of crown of M1, anteriorly</td>
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<tr>
<td>Transverse diameter of crown of M1, posteriorly</td>
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<table>
<thead>
<tr>
<th>Table 61—Measurements (in millimeters) of type mandibles</th>
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<tbody>
<tr>
<td>Left</td>
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<td>-------------------</td>
</tr>
<tr>
<td>Antero-posterior diameter of alveolus of Dpm1</td>
</tr>
<tr>
<td>Antero-posterior diameter of crown of Dpm2</td>
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<tr>
<td>Antero-posterior diameter of crown of Dpm3</td>
</tr>
<tr>
<td>Antero-posterior diameter of crown of Dpm4</td>
</tr>
<tr>
<td>Antero-posterior diameter of crown of M1</td>
</tr>
<tr>
<td>Antero-posterior diameter of crown of M2 not ascertainable; crown not fully erupted, partially hidden</td>
</tr>
<tr>
<td>Maximum antero-posterior diameter of mandible, as preserved</td>
</tr>
</tbody>
</table>

DENTITION

Considering the general uniformity displayed among the Archaeoceti with respect to basic cranial construction, it may be anticipated that the mode of replacement of the deciduous dentition will be less subject to secondary adaptations than those parts that come in more direct contact with factors influencing modification. It is clear in the case of the mandibles of Zygorhiza kochii that the three molars are fully erupted before the deciduous premolars are replaced by the permanent ones. It will be observed on the mandibles of
Pappocetus lugardi (Andrews, 1920, fig. 1) that, although M2 and M3 are not fully erupted, three incisor-like, one canine-like, and four premolar-like teeth as well as M1 constitute the functional dentition. Judging from the conditions found in Z. kochii, it would appear that eight of these teeth represent the deciduous dentition of Pappocetus lugardi.

The relatively large size of the root of the second lower deciduous incisor, which is considerably larger than the others, may constitute one of the diagnostic characters of this genus. There is a short diastema of 30 mm. between the third deciduous incisor and the deciduous canine. The size of the root of the deciduous canine shows that it was slightly larger than the second lower deciduous incisor and like the latter was inclined forward. The roots of the deciduous canines are visible at the anterior broken ends of both of the type mandibles. An isolated tooth, apparently a deciduous canine, has the crown ornamented with vertically striated enamel and possesses a well-defined carina on the anterior cutting edge. Between the deciduous canine and the single-rooted first lower deciduous premolar is an interval of about 45 mm. The second lower deciduous premolar is a two-rooted tooth that has a compressed crown ornamented with vertical knotted ridges, a keel-like postero-internal ridge, no accessory serrations, and a slightly developed cingulum on the inner side. The third lower deciduous premolar is a long laterally compressed, two-rooted tooth; the anterior border and apex of the principal cusp is noticeably worn, and there are two accessory cusps and perhaps a rudimentary basal cusp above the cingulum on the posterior border. The two-rooted fourth lower deciduous premolar is more strongly compressed from side to side than the third lower deciduous premolar, and the crown consists of a large principal anterior cusp and a posterior heel-like cusp above the well-marked cingulum which encircles the base of the crown. Each of the three molars has a large anterior cusp, a smaller posterior cusp, and two roots. The crown of the first lower molar consists of a large anterior principal cusp, whose summit is destroyed, and a smaller posterior cusp, and around the base is a well-marked cingulum. A group of small rounded tubercles extends upward toward the apex on the antero-internal face of the principal cusp of this molar and the remainder of the enamel surface is ornamented with fine ridges which produce a finely creneled effect. The second lower molar is just erupting in the type mandible and in the paratype mandible it is not fully in place. Although incomplete in both mandibles, this tooth resembles the first lower molar and the ornamentation of the enamel crown above the cingulum is rather rough and coarse. The third lower molar, which has not erupted and is only partially exposed in the paratype mandible seems to resemble the first and second lower molars. It has a large basal posterior cusp with a pronounced crest-like cutting edge. The mandibular cheek teeth of Protocetus atavus are unknown, and the lower molars of Prozeuglodon, Dorudon, Zygorhiza, and Basilosaurus are obviously more highly specialized than those of Pappocetus.

CERVICAL VERTEBRA

To this archaeocete Andrews refers an imperfect axis that lacks the upper portion of the neural arch and the lateral processes. The odontoid process is blunter, the lateral articular surfaces for the atlas slope more strongly backward, and the nearly flat posterior surface of the centrum is wider in proportion to depth than the axis of Protocetus atavus. The axes of both of these archaeocetes, however, have centra of the same length and a similar ventral prominence. Conversely the axis of Prozeuglodon atrox has a shorter centrum, the ventral ridge is indicated only by a slight posterior prominence, and the lateral articular surfaces for the atlas do not slope so strongly backward.
Table 62—Measurements (in 

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</thead>
<tbody>
<tr>
<td>1. Anterior end of rostrum (right or left premaxillary) to posterior surface of supraoccipital shield below apex</td>
<td>610 ± 10 r</td>
<td>608 ± 10 r</td>
<td>695 ± 10 r</td>
<td>620 ± 10 r</td>
<td>620 ± 10 r</td>
<td>620 ± 10 r</td>
</tr>
<tr>
<td>2. Anterior end of rostrum (right or left premaxillary) to posterior surface of supraoccipital shield below apex</td>
<td>651 ± 10 r</td>
<td>715 ± 10 r</td>
<td>715 ± 10 r</td>
<td>715 ± 10 r</td>
<td>715 ± 10 r</td>
<td>715 ± 10 r</td>
</tr>
<tr>
<td>3. Transverse diameter across preorbital angles of supraorbital processes of frontals</td>
<td>192 ± 10 r</td>
<td>203 ± 10 r</td>
<td>198 ± 10 r</td>
<td>200 ± 10 r</td>
<td>200 ± 10 r</td>
<td>200 ± 10 r</td>
</tr>
<tr>
<td>4. Transverse diameter across postero-external angles of supraorbital processes of frontals</td>
<td>220 ± 10 r</td>
<td>225 ± 10 r</td>
<td>220 ± 10 r</td>
<td>220 ± 10 r</td>
<td>220 ± 10 r</td>
<td>220 ± 10 r</td>
</tr>
<tr>
<td>5. Greatest zygomatic width</td>
<td>234 ± 10 r</td>
<td>234 ± 10 r</td>
<td>234 ± 10 r</td>
<td>234 ± 10 r</td>
<td>234 ± 10 r</td>
<td>234 ± 10 r</td>
</tr>
<tr>
<td>6. Distance between inner margin of occipital condyle to outer edge of occipital, right or left side</td>
<td>102 r</td>
<td>87.5 r</td>
<td>66.5 r</td>
<td>87.5 r</td>
<td>87.5 r</td>
<td>87.5 r</td>
</tr>
<tr>
<td>7. Distance between outer margins of occipital condyles</td>
<td>103 r</td>
<td>76 r</td>
<td>66.5 r</td>
<td>76 r</td>
<td>76 r</td>
<td>76 r</td>
</tr>
<tr>
<td>8. Greatest or obliquo-vertical diameter of right or left occipital condyle</td>
<td>113 ± 10 r</td>
<td>113 r</td>
<td>113 ± 10 r</td>
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### Incertae Sedis

#### In millimeters of skulls

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<td>713</td>
<td>598</td>
<td>420</td>
<td></td>
<td></td>
<td></td>
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</tbody>
</table>
A REVIEW OF THE ARCHAEOCETI

INCERTAE SEDIS

PONTGENEUS


Cervical vertebrae similar in configuration to those of Basilosaurus cetoides; centra of hinder dorsal vertebrae not noticeably lengthened; centra of lumbar vertebrae of normal proportions, the transverse diameter of the hinder end being slightly less than length of centrum; and centra of anterior caudal vertebrae not disproportionately elongated.

The dental formula, skull, mandibles, fore- and hindlimbs, and pelvis of this large archaeocete are not known.

PONTGENEUS BRACHYSPONDYLU5 (Müller)

1846. Hydrarchos harlani Koch, Kurze Beschreibung des Hydrarchos Harlani (Koch), eines riesennässigen Meerungeheuers und dessen Entdeckung in Alabama in Nordamerika im Frühjahr 1845, Dresden, pp. 1-20, pl. 1 (part).


Type locality—Alabama, presumably in the vicinity of Washington Old Court House. Upper Jackson formation, upper Eocene.

Type specimen—None designated. Müller (1849, p. 26) states that 27 vertebrae in the Koch collection can be referred to this species. Included among these are: (1) 5 dorsal and 8 lumbar vertebrae belonging apparently to one individual, (2) 2 lumbar vertebrae of another individual, and (3) the remainder are caudal vertebrae that appear to belong to several individuals. Five of these vertebrae are tentatively determined as follows: Eleventh dorsal (Müller, 1849, pl. 18, fig. 5), twelfth dorsal (Müller, 1849, pl. 18, fig. 4), second caudal (Müller, 1849, pl. 20, ser. II, No. 8), fourth caudal (Müller, 1849, pl. 20, ser. II, No. 7), and sixth caudal (Müller, 1849, pl. 18, fig. 6), and they are numbered, respectively, M. 68, M. 64, M. 66, M. 67, and M. 65, Geologisch-Paläontologisches Institut und Museum der Universität Berlin; collector, Albert C. Koch; March 1845.

Referred specimens—(1) An incomplete axis and an imperfect third cervical vertebra. From the upper Jackson formation of Alabama. Nos. M. 21, M. 22, Geologisch-Paläontologisches Institut und Museum der Universität Berlin; collector, Albert Koch; 1845 (Dames, 1894, pp. 198–199, pls. 32–33.)

(2) An incomplete fifth cervical vertebra, the type of Pontogeneus priscus Leidy. From the Jackson formation, Ouachita River, Louisiana. No. 13668, Academy of Natural Sciences of Philadelphia.

(3) An incomplete anterior lumbar vertebra. From the upper Jackson formation; precise locality unknown. No. 776, Division of Vertebrate Paleontology, U. S. Nat. Mus.

(4) Five imperfect lumbar and one caudal vertebrae. From the upper Jackson formation, Cocoa, Choctaw County, Alabama; Section 24, Township 11 North, Range 5 West. No. 2211, Division of Vertebrate Paleontology, U. S. Nat. Mus.; collector, Charles Schuchert; November 1894 (Lucas, 1901, p. 619; 1904, p. 437).

VERTEBRÆ

Assuming that the vertebral column consisted of 7 cervical, 15 dorsal, 13 lumbar, 2 sacral, and 21 caudal vertebrae, and computing the lengths of the centra of the missing
vertebrae from the relative lengths of those that have been found, the total length of the skeleton, including the skull, approximated 33 feet or 10 meters.

Inasmuch as there is a rather marked difference in the size of the sexes of some Recent cetaceans, particularly Physeter, Dames (1883, p. 134) suggests that Zeuglodon brachyspondylus may be the female and Zeuglodon macrospondylus [ = Basilosaurus cetoides] the male of the same species of archaeocete. In the case of Physeter, however, the disparity in the lengths of the sexes is not attributable to a lengthening of the centra of a large section of the vertebral column, but rather to a uniform increase in the dimensions of all the vertebrae.

As regards the composition of the vertebral column of Koch's Hydrarchos, Müller (1849, p. 22) states that the neck was constructed of dorsal and lumbar vertebrae of Z. brachyspondylus, the long middle portion of lumbar and caudal vertebrae of Z. macrospondylus, and the terminal portion of lumbar and caudal vertebrae of Z. brachyspondylus. But each of these regions contained vertebrae or series of vertebrae belonging to different individuals.

The axis and the third cervical vertebra referred to this archaeocete by Dames (1894, pp. 197, 199) are not only as large but also quite similar in general conformation to those of Basilosaurus cetoides. Peculiarities that will distinguish these cervical vertebrae from the corresponding ones of B. cetoides are not readily apparent.

The dorsal and lumbar vertebrae referred to this species by Müller (1849) belong for the most part to immature individuals, since one or both of the epiphyses are not ankylosed to the centra of the vertebrae specifically mentioned. The anterior lumbar (No. 776, U. S. N. M.), and the five lumbar (No. 2211, U. S. N. M.) all have the epiphyses firmly ankylosed to the centra and thus belonged to mature individuals. The centra of the dorsal and lumbar vertebrae referred to Pontogeneus brachyspondylus are conspicuously shorter than the corresponding vertebrae of either Basilosaurus cetoides or Prozeuglodon isis.

**Cervical Vertebrae**

The cervical series of this archaeocete is incompletely known. The axis and the third cervical described by Dames (1894, pp. 198, 199) are not only as large but are also quite similar in general conformation to those of Basilosaurus cetoides. One gains the impression from reading Dames' description that these vertebrae are smaller than those of Basilosaurus cetoides. The accompanying table of measurements furnished by Prof. W. O. Dietrich shows, however, that they were not measured accurately by Dames. The dimensions of the fifth cervical, which is the type of Pontogeneus priscus, are intermediate between those of the corresponding cervicals of Basilosaurus cetoides and of Zygorhiza kochii. Considering the rather close resemblance exhibited by the cervical vertebrae that have been referred to this archaeocete to those of Basilosaurus cetoides, it may be anticipated that the remaining cervicals will likewise be quite similar. No cervical vertebrae, that can be allocated with certainty to this archaeocete, have been received by the U. S. National Museum.

**Axis**—An incomplete axis (No. M. 21, Berlin), referred to this archaeocete by Dames (1894, p. 198, pl. 32), lacks the upper portion of the neural arch and the right transverse process. It is characterized by short transverse processes, directed more backward than outward (Dames, 1894, pl. 33, fig. 2), which are quite thin distally, and are perforated at the base by a large vertebrarterial canal (maximum diameter 18 mm.). The large anterior surfaces for articulation with the atlas are similar to those on the axis of Basilosaurus cetoides. The odontoid process is short, broad, and blunt. The hinder face of the centrum is broader than high; from this surface a broad prolongation projects ventrally below the level of the ventral face of the centrum.
Third Cervical—This cervical (No. M. 22, Berlin) was associated with the above mentioned axis. It (Dames, 1894, p. 199, pl. 33, figs. 1a–1c) lacks the left transverse process and most of the neural arch. The lower transverse processes are rather long and thick, apparently connected by a thin isthmus of bone with the thin upper bar which is continuous with lateral buttress on pedicle of neural arch; these processes inclose a very large vertebral arterial foramen (diameter 35 mm.). A short projection arises near base of ventral edge of lower transverse process like on the corresponding cervical of *Basilosaurus cetoides*. The transverse diameter of the anterior end of the centrum (Dames, 1894, pl. 33, fig. 1b) is slightly greater than the vertical diameter; the hinder end of the centrum (Dames, 1894, pl. 33, fig. 1a) is damaged. Both of these surfaces are flat-concave, but the upper and lower borders project more strongly than the lateral borders. Dorsally, the median antero-posterior diameter of the centrum is 35+ mm. The antero-posterior diameter of the basal portion of the left pedicle of the neural arch is about 15 mm.

Fifth cervical—Joseph Leidy (1852, p. 52) proposed the name *Pontognathus priscus* for a fifth cervical vertebra (No. 13668, Academy of Natural Sciences of Philadelphia) “from the Eocene formation of Ouachita, Louisiana.” In describing this vertebra (pl. 36, figs. 1–3) Leidy remarks that it “is perfectly mineralized, and both epiphyses are attached, but portions are broken away, permitting the characteristic tuberculated surface of the body [= centrum] to be seen.” To Leidy this cervical was chiefly “remarkable on account of the relatively deep concavity of its surfaces before and behind.” At first Cope (1868, p. 155) concluded that this name belonged in the synonymy of *Doryodon pygmaeus*. Later, Cope (1868, p. 186; 1869, p. 9) reexamined this cervical vertebra and stated that it belonged to a delphinoid cetacean, apparently on account of the antero-
posterior compression of the centrum. During the same year, Leidy (1869, pp. 430–431) gave the "Washita [=Ouachita] River, Louisiana," as the type locality, and pointed out that this cervical "appears to agree nearly in size, form, and construction with the cervicals described by Müller as those of Zeuglodon brachyspondylus."

This fifth cervical (fig. 82) lacks most of its processes. The anterior face of the centrum is depressed medially and the upper half overhangs the lower half. The anterior epiphysis is incomplete dorsally, on the right side, and ventrally. The hinder face of the centrum is likewise deeply depressed medially and the borders of the hinder epiphysis are irregularly destroyed for a maximum width of 10 mm., exposing the radiating grooves on the posterior face of the centrum. A median longitudinal protuberance on the rugose ventral face of the centrum separates the orifices of the two vascular canals. The lateral surfaces of the centrum are concave. A thin median longitudinal carina, separating the two vascular foramina, is present on the dorsal face of the centrum. The basal portions of the pedicles of the neural arch are compressed antero-posteriorly and expanded transversely. The upper transverse process is reduced to a thin oblique buttress projecting laterally from the external face of the pedicle and apparently is not connected distally with the extremity of the lower transverse process. The lower transverse processes, which were dorso-ventrally flattened near the base, are broken off.

A comparison of the measurements of this cervical with those of the fifth cervical (No. 4675, U. S. N. M.) in the reconstructed skeleton of Basilsaurus cetoides shows that it belonged to a smaller individual. The type cervical of Pontogeneus priscus is also smaller than the cervical figured by Müller (1849, pl. 13, figs. 3–5) which was found in Washington County, Alabama, by Koch in association with a premolar of Basilsaurus cetoides (Müller, 1849, pl. 12, fig. 2).

**Table 63—Measurements (in millimeters) of cervical vertebra**

<table>
<thead>
<tr>
<th></th>
<th>Axial No. M. 21</th>
<th>Cervical No. M. 22</th>
<th>Cervical No. 13669</th>
</tr>
</thead>
<tbody>
<tr>
<td>Antero-posterior diameter of centrum</td>
<td>68</td>
<td>35+</td>
<td>30.5</td>
</tr>
<tr>
<td>Transverse diameter of centrum, anteriorly</td>
<td>88</td>
<td>83</td>
<td>70.5</td>
</tr>
<tr>
<td>Vertical diameter of centrum, anteriorly</td>
<td>89</td>
<td>90</td>
<td>74.8</td>
</tr>
<tr>
<td>Transverse diameter of centrum, posteriorly</td>
<td>73</td>
<td>79</td>
<td>73</td>
</tr>
<tr>
<td>Transverse diameter of neural canal, anteriorly</td>
<td>43±</td>
<td>52</td>
<td>40</td>
</tr>
<tr>
<td>Vertical diameter of neural canal, anteriorly</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Transverse diameter of neural arch at base of pedicles, outside measurement</td>
<td></td>
<td>102+</td>
<td></td>
</tr>
<tr>
<td>Greatest diameter of vertebral canal in transverse process</td>
<td>18</td>
<td>35</td>
<td></td>
</tr>
</tbody>
</table>


*Pontogeneus priscus* Leidy (type).

**Dorsal Vertebrae**

As contrasted with the dorsal vertebrae of Basilsaurus cetoides, the absence of any pronounced lengthening of the centra in the hinder half of this series seems to be the most obvious distinction. The transverse and vertical dimensions of the centra are, however, approximately the same as those of *B. cetoides*. Vertebrae belonging to the anterior half of the dorsal series of this archaeocete have not as yet been described. Until a complete dorsal series belonging to one individual is available, any further elucidation of the peculiarities of the thorax will be subject to question.

According to Müller (1851, p. 243) the large archaeocete with relatively short centra was represented in the Berlin collection by a number of dorsal, lumbar, and caudal vertebrae collected by Koch. As of especial interest, he mentions two hinder dorsal vertebrae
which have transverse processes with rib-facets at their extremities. The length of the centrum is given as 171 mm. and the breadth as 178 mm. Inasmuch as two sets of measurements are given by Müller (1849, pp. 21, 26) for the tenth and twelfth dorsal vertebrae described below, some uncertainty exists as to the vertebrae which are figured in his memoir. The measurements of the twelfth dorsal furnished by Professor Dietrich, with the exception of the neural canal, agree with those given by Müller (1849, p. 26). The tenth dorsal vertebra has not been located.

Tenth Dorsal—The vertebra identified as the tenth in the dorsal series (Müller, 1849, pp. 21, 26, pl. 13, figs. 6–7) belonged to an immature individual, since the epiphyses at both ends of the centrum are missing. The anterior edge of the neural arch is damaged; the metapophyses and the prezygapophyses are destroyed. Pedicles of neural arch rather narrow antero-posteriorly; vestigial diapophysis projects in part from base of pedicle of neural arch and in part from upper lateral face of centrum, and is separated from rudimentary parapophysis, which projects from near center of lateral face of centrum, by a small concavity; postzygapophysial facets nearly horizontal in position and separated by wide notch; hinder ends of postzygapophyses do not project backward to level of hinder end of centrum when allowance is made for missing epiphysis; neural spine incomplete, but stands nearly vertical; and neural canal wider than high. This vertebra, according to Müller (1849, p. 21), constituted the first neck vertebra in Koch's Hydrarchos.

<table>
<thead>
<tr>
<th>Table 64—Measurements (in millimeters) of dorsal vertebrae</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. 10&lt;sup&gt;th&lt;/sup&gt; No. — Berlin</td>
</tr>
<tr>
<td>Antero-posterior diameter of centrum</td>
</tr>
<tr>
<td>Transverse diameter of centrum, anteriorly</td>
</tr>
<tr>
<td>Vertical diameter of centrum, anteriorly</td>
</tr>
<tr>
<td>Transverse diameter of centrum, posteriorly</td>
</tr>
<tr>
<td>Vertical diameter of centrum, posteriorly</td>
</tr>
<tr>
<td>Transverse diameter of neural canal, anteriorly</td>
</tr>
<tr>
<td>Vertical diameter of neural canal, anteriorly</td>
</tr>
<tr>
<td>Transverse diameter of neural arch at base of pedicles, outside measurement</td>
</tr>
</tbody>
</table>

1 Müller, 1849, pl. 13, f. 6–7; pl. 20, ser. II, No. 1.
2 Ibid. pl. 18, fig. 5. 4 Ibid. pl. 18, fig. 4; pl. 20, ser. II, No. 2. 4 Ibid. pl. 18, fig. 1.

Eleventh Dorsal—The vertebra (Müller, 1849, pl. 18, fig. 5), tentatively identified as the eleventh in the dorsal series, has a slightly wider neural canal than the preceding vertebra. This vertebra is likewise incomplete and lacks the neural spine and both metapophyses. The head of the rib articulates, according to Müller (1849, p. 21), in a depression of the lateral face of the centrum. The short postzygapophyses are separated by a wide notch. This vertebra, according to Müller (1849, p. 21), constituted the fourth neck vertebra in Koch’s Hydrarchos.

Twelfth Dorsal—Another imperfect dorsal vertebra (Müller, pp. 21, 26, pl. 18, fig. 4) belonging to a different individual than the one to which the preceding vertebra belonged, and lacks the neural spine, both metapophyses, and both epiphyses. It has a very short transverse process on the lateral face of the centrum. The head of the eleventh rib articulates in a deep pit on the extremity of this process. This vertebra, according to Müller (1849, p. 21), constituted the fifth neck vertebra in Koch’s Hydrarchos.

Fifteenth Dorsal—The vertebra (Müller, 1849, pl. 18, fig. 1), tentatively identified as the hindmost in the dorsal series, lacks the neural spine and the extremity of the right transverse process; the robust metapophyses are damaged; the pedicles of the neural arch are similar to those of an anterior lumbar (No. 776, U. S. N. M.); the postero-basal angle of
the neural spine is conspicuously extended backward, but not to level of hinder end of centrum; and the postzygapophyseal projections are separated by a wide shallow notch.

In the case of Basilosaurus cetoides, normal transverse processes are developed only on the two hindermost dorsal vertebrae. Judging from the development of the transverse processes on the tenth, eleventh, and twelfth dorsal vertebrae referred to this archaeocete, a development of the transverse processes on the two hindermost dorsals similar to those of B. cetoides may be expected. The two hinder dorsal vertebrae of B. cetoides likewise have noticeably wider neural spines than those of the preceding dorsals.

**Lumbar Vertebrae**

Although it has not been possible to assemble a composite set of vertebrae representing the entire lumbar series, there is reason to believe that those available exhibit the essential structural peculiarities of this region. The vertebrae comprising the lumbar region seem to be characterized in part by having centra which are not noticeably elongated. In the case of those examined, the transverse diameter of the hinder end of the centrum is slightly less than the length of the centrum. The neural canals on the anterior lumbars are approximately equal in width and height to those on the corresponding vertebrae of Basilosaurus cetoides; the neural canals of the hinder lumbers, however, are much narrower.

**Third Lumbar**—The anterior lumbar vertebra (No. 776, U. S. N. M.), which may represent the third (pl. 37, figs. 1–2) in the series, lacks both metapophyses, the neural spine is broken off at the base, and the major portion of both transverse processes are missing. It is characterized as follows: Epiphyses firmly attached at both ends of well-preserved centrum, the posterior epiphysis varying from 18 to 21 mm. in thickness; transverse and vertical diameters of anterior and posterior ends of centrum approximately the same; pedicles of neural arch relatively wide antero-posteriorly (minimum diameter of left pedicle, 95 mm.), being equivalent to more than two-fifths of the length of the centrum (223 mm.), rather thick transversely (26 mm.) and set back at base 45 mm. from anterior end of centrum and 65 mm. from hinder end of centrum; neural spine rather wide antero-posteriorly at base (at least 142 mm.); transverse diameter (105 mm.) nearly twice the vertical diameter (54 mm.) of the neural canal anteriorly; a pair of orifices for vascular foramina located near middle of length of dorsal and ventral faces of centrum; foramina on ventral face of centrum separated by a short narrow ridge; ventral face of centrum rather flat from side to side and shallowly concave from end to end; lateral face of centrum slightly concave from end to end; the transverse processes arise from ventral border of lateral face of centrum, and are directed outward, downward, and somewhat forward; these processes are rather thick at base and are set back farther from anterior than from hinder end of centrum. No remnants of the prezygapophyseal facets are preserved on the neural arch at the base of either of the missing metapophyses. The postzygapophysial facets, which are located on the under surface of the damaged postero-basal angle of the neural spine, are horizontal in position, rather broad, and are united posteriorly.

**Ninth Lumbar**—A middle lumbar vertebra (Müller, 1849, p. 26, pl. 20, ser. II, No. 6), tentatively identified as the ninth in the series, lacks the neural spine, the metapophyses are damaged, and the ends of the transverse processes are missing. The postero-basal angle of the neural spine does not project backward to level of hinder end of centrum; the neural canal is wider than high; and the broad transverse processes are set back farther from the anterior than from the hinder end of the centrum. According to Müller (1849, p. 28), the five hinder vertebrae in the neck of Koch's reconstructed Hydrarchos were lumbar vertebrae of this species.

**Posterior Lumbars**—Five posterior lumbar vertebrae (No. 2211, U. S. N. M.), the hinder two of which are tentatively identified as lumbar-sacralis, are very much alike in general configuration. The neural arch, with the exception of the basal portions of its
pedicles, and its processes are entirely destroyed on all of these vertebrae. The transverse processes are sufficiently complete on at least three of these vertebrae to show their essential characteristics.

All of these vertebrae (pl. 37, figs. 3–4) must have had a narrow neural canal, for the interval between the basal portions of the pedicles on the longest of these lumbars is at least 35 mm. less than the corresponding interval on the hinder lumbar vertebra of Basilosaurus cetoides, which has the narrowest neural canal in that series of vertebrae. The pedicles of the neural arch are not set back as far from anterior as from posterior end of centrum; minimum antero-posterior diameter of right pedicle (less than 106 mm.) of the anterior lumbar in this series (possibly the eleventh lumbar) equivalent to about two-fifths of length of centrum (240 mm.); centra contracted medially; lateral face of centrum concave from end to end; ends of centra depressed medially; edges of transverse process at base farther removed from anterior than from posterior end of centrum; transverse processes arise somewhat higher on lateral face of centrum than on the third lumbar, and are directed outward and downward; right transverse process of the penultimate lumbar (? first sacral) attenuated distally and inclined forward; and ventral face of centrum convex from side to side, but depressed in region of vascular foramina. On all five of these centra the ventral orifices of the vascular canals open into a deep fossa, which on the one tentatively identified as the eleventh lumbar measures 26 mm. transversely and 50± mm. longitudinally. The vascular foramina on the dorsal face of the centrum are separated by a short ridge. The hinder most vertebra (? second sacral) in this series lacks most of the centrum anterior to level of anterior edges of neural arches.

Table 65—Measurements (in millimeters) of lumbar vertebra

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Antero-posterior diameter of centrum</td>
<td>223</td>
<td>190.5±</td>
<td>240</td>
<td>241</td>
<td>237</td>
<td>234</td>
<td>208±</td>
</tr>
<tr>
<td>Transverse diameter of centrum, anteriorly</td>
<td>182</td>
<td>155</td>
<td>212</td>
<td>213</td>
<td>208</td>
<td>205</td>
<td>173±</td>
</tr>
<tr>
<td>Vertical diameter of centrum, anteriorly</td>
<td>192</td>
<td>165</td>
<td>212</td>
<td>187±</td>
<td>184</td>
<td>184</td>
<td></td>
</tr>
<tr>
<td>Transverse diameter of centrum, posteriorly</td>
<td>230</td>
<td>214</td>
<td>244</td>
<td>224</td>
<td>224</td>
<td>213</td>
<td>206</td>
</tr>
<tr>
<td>Vertical diameter of centrum, posteriorly</td>
<td>187</td>
<td>200</td>
<td>87.5</td>
<td>87</td>
<td>70±</td>
<td>84</td>
<td></td>
</tr>
<tr>
<td>Least antero-posterior diameter of transverse process near base</td>
<td>...</td>
<td>...</td>
<td>90</td>
<td>87.5</td>
<td>70±</td>
<td>84</td>
<td></td>
</tr>
</tbody>
</table>

1 Müller, 1849, pl. 20, II, No. 6.

Caudal Vertebrae

When contrasted with the caudal series of Basilosaurus cetoides the anterior caudal vertebrae of Pontogeneus brachyspondylus are seen to be characterized chiefly by their relatively short centra, by somewhat narrower neural canals, and by the more posterior location of the transverse processes on the lateral face of the centrum. No hinder caudal vertebrae belonging to this species were available for comparison.

First Caudal—This vertebra (No. 2211, U. S. N. M.) lacks the anterior and posterior epiphyses, the neural arch and its processes, and most of both transverse processes. The circumference of the hinder end of the centrum is eroded. Centrum, viewed from in front, roughly hexagonal in outline; hinder end of centrum seemingly larger than anterior end; neural canal relatively narrow, its estimated width anteriorly being about 62 mm.; pedicles of neural arch located on anterior half of centrum; elongated orifices of vascular canals separated by a narrow ridge on dorsal surface of centrum; greatest antero-posterior diameter (110± mm.) of left transverse process at base approximately the same as that of
the hindermost sacral vertebra (No. 2211, U. S. N. M.), but these processes arise higher on lateral surface of centrum than on the latter; lateral face of centrum shallowly concave above base of transverse process; the deep fossa for ventral orifices of vascular canals located much nearer the anterior (38+ mm.) than the hinder end (120+ mm.) of the centrum, its transverse diameter being 21 mm. and its length 55 to 60 mm.; ventral face of centrum convex from side to side; and hinder end of ventral face of centrum swollen, but having a distinct median sagittal groove located between position of facets for the chevrons.

Second Caudal—One of the imperfectly preserved vertebrae figured by Müller (1849, p. 27, pl. 20, ser. II, No. 8) is tentatively identified as the second in the caudal series, since the antero-posterior diameter of the transverse process at the base corresponds most closely with those on the anterior caudals of Basilosaurus cetoides. The transverse processes are placed in approximately the same position on the lateral face of the centrum as on the first caudal. Orifices on dorsal face of centrum for the vertical vascular canals separated by a short longitudinal ridge; breadth of neural canal reduced; pedicles of neural arch shortened; and lateral face of centrum depressed above base of transverse process.

Fourth Caudal—Another anterior caudal vertebra figured by Müller (1849, p. 27, pl. 20, ser. II, No. 7) lacks one epiphysis, the neural spine, the neural arch, and the ends of the transverse processes. On this caudal the anterior edge of each transverse process is set back at base farther from anterior end of centrum than the hinder edge is from posterior end of centrum. This vertebra, according to Müller (1849, p. 28), was placed by Koch in his reconstruction of Hydrachros as the first of the short hinder vertebrae in the tail.

### Table 66—Measurements (in millimeters) of caudal vertebrae

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Antero-posterior diameter of centrum</td>
<td>210</td>
<td>152.4</td>
<td>140+</td>
<td>155</td>
</tr>
<tr>
<td>Transverse diameter of centrum, anteriorly</td>
<td>189+</td>
<td>177.8</td>
<td>185</td>
<td>192</td>
</tr>
<tr>
<td>Vertical diameter of centrum, anteriorly</td>
<td>179+</td>
<td>190.5</td>
<td>180</td>
<td>192</td>
</tr>
<tr>
<td>Transverse diameter of centrum, posteriorly</td>
<td></td>
<td>190.5</td>
<td>180</td>
<td>192</td>
</tr>
<tr>
<td>Vertical diameter of centrum, posteriorly</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Transverse diameter of neural canal, anteriorly</td>
<td>62±</td>
<td>46.6</td>
<td>55+</td>
<td>55±</td>
</tr>
</tbody>
</table>

1 Müller, 1849, pl. 20, ser. II, No. 8.  
2 Ibid. pl. 20, ser. II, No. 7.  
3 Ibid. pl. 18, fig. 6.

Fifth Caudal—An incomplete vertebra figured by Müller (1849, pl. 18, fig. 7), tentatively identified as the fifth in the caudal series, lacks most of the neural arch, the neural spine, and the ends of both transverse processes. This caudal differs from the fourth caudal in having the point of origin of the hinder edge of the transverse process more closely approximated to the posterior end of the centrum.

Sixth Caudal—Another anterior caudal vertebra (Müller, 1849, p. 22, pl. 18, fig. 6) seems to possess, so far as can be judged from its present condition, the same general characteristics as the sixth in the caudal series of Basilosaurus cetoides. It lacks all of the right transverse process as well as the end of the left transverse process. This narrow dorso-ventrally flattened process is directed outward and downward. At the base the anterior edge of the left transverse process is set rather far back from the anterior end of the centrum, while the point of origin of the hinder edge is almost flush with the posterior end of the centrum. Müller's figure for this caudal shows clearly that the broad notch at the base of the anterior border of each of these processes marks the location of the large blood-vessel, which on succeeding vertebrae passes through a foramen at the base of this process.
ARCHAEOCETE gen. et sp. indet.

Locality—Ocala limestone (upper Jackson formation) on east bank of Flint River, 100 yards south of mouth of Cedar Creek, and nine miles southwest of Cordele, Crisp County, Georgia. Upper Eocene.

Referred specimens—(1) Three anterior lumbar vertebrae. No. 11401, Division of Vertebrate Palæontology, U.S. National Museum; collector, C. Wythe Cooke; October 11, 1925.

(2) Three lumbar vertebrae. No. 11401a, Division of Vertebrate Palæontology, U.S. National Museum; collector, D. A. Harris; 1925.

Fig. 83—Archaecete, gen. et sp. indet. Middle lumbar vertebra, No. 11401, United States National Museum. X 4. a, lateral view; b, posterior view. mp., metaphysis; tr., transverse process. Upper Eocene, Ocala limestone (Jackson formation), Georgia.

LUMBAR VERTEBRAE

It is quite possible that these six vertebrae belong to a young individual of Pontogeneus brachyspondylus. Vertebrae of the type allocated to Pontogeneus brachyspondylus have not as yet been found associated with a cranium. Until we have more detailed information in regard to the skeleton of P. brachyspondylus and to the peculiarities of the elements of the axial column during growth no satisfactory allocation of isolated skeletal parts can be made.

These six vertebrae have unusually short centra. Toward the hinder end of the series the transverse diameters of the centra increase. Four of them have no epiphyses attached to the centrum. On all six of these vertebrae the distinctly flattened lateral surfaces of
the centra slope obliquely from the base of the pedicle of the neural arch to the base of
the transverse process. The transverse processes on all these centra arise below the middle
of the lateral face and almost at the level of the ventral face of the centrum. Toward the
hinder end of the series these processes are progressively inclined more strongly downward.
On all of these centra the antero-basal angle of each pedicle of the neural arch is much
nearer the anterior end of the centrum than the hinder edge is to the posterior end.

The vertebra tentatively identified as the anteriormost one of these six lumbars has a
rather short centrum. The posterior epiphysis of this centrum is missing, both transverse
processes are broken off at their bases, and the neural arch and its processes are entirely
destroyed. The ventral openings of the two dorso-ventral vascular canals are separated
by a very prominent longitudinal ridge. The antero-posterior diameter of the right trans-
verse process at the base is almost equal to the same diameter of the centrum without the
epiphyses.

A vertebra that belongs in the lumbar series near the preceding one is the most com-
plete of the six. The centrum lacks the anterior and posterior epiphyses; the left trans-
verse process and adjacent portion of lateral surface of centrum is completely destroyed;
the right transverse process is broken off near the base; the extremity of the right meta-
pophysis is damaged and the left metapophysis is destroyed; and the anterior border as well

![Fig. 84—Archaeocete, gen. et sp. indet. Ventral view of hinder lumbar vertebra, No.
11401, United States National Museum, × 1. tr., transverse process. Upper
Eocene, Ocala limestone (Jackson formation), Georgia.](image)

as the extremity of the neural spine are missing. This vertebra is characterized as follows:
Pedicles of neural arch (fig. 83a) relatively wide antero-posteriorly (minimum diameter of
right pedicle, 68 mm.), being equivalent to more than half length of centrum (estimated,
when complete, 120 ± mm.); elongated metapophysis projecting upward and outward, and
extending forward considerably beyond level of anterior end of centrum; neural spine
rather wide antero-posteriorly (at least 114 mm. wide at base); and a pair of orifices for
dorso-ventral vascular canals located near middle of dorsal and ventral faces of centrum.
Rather wide prezygapophyseal facets are present, judging from the anterior and hinder
remnants of the one on the right side. The postzygapophyseal facets are located on the
under surface of the postero-basal angle of the neural spine and the latter projects back-
ward beyond level of hinder face of centrum. These nearly horizontal facets are not sepa-
rated posteriorly but diverge anteriorly, and slope upward and backward; they measure
approximately 48 mm. in length and 16 mm. in width (maximum). Transverse diameter
(81 mm.) of the neural canal anteriorly is greater than its vertical diameter (56 mm.).

On the third one of these lumbar vertebrae the left transverse process is broken off
near the base, both epiphyses are missing, and the neural arch is damaged. The neural
spine, both metapophyses as well as the pre- and post-zygapophyses are destroyed. The
neural canal is rather large, its transverse diameter being 80 mm., and its vertical diameter,
58 mm. The least antero-posterior diameter of the left transverse process near the base
is 56 mm. The ventral openings of the two dorso-ventral vascular canals are separated by a prominent longitudinal ridge.

The next lumbar is represented by a portion of the right half of the centrum and the basal portion of the right transverse process. The transverse process arises almost at the level of the ventral face of the centrum, and is directed outward, downward and slightly forward. On the dorsal face the two orifices of the dorso-ventral vascular canals are separated by a prominent ridge.

Another one (fig. 84) of these lumbar vertebrae lacks the anterior epiphysis, the neural arch and its processes, and the upper portion of the centrum between the level of the base of the left transverse process and the right pedicle of the neural arch. The posterior epiphysis is rather thin, the maximum diameter being about 10 mm. The transverse processes arise almost at the level of the ventral face of the centrum, projecting outward and downward, and are dorso-ventrally thickened at the base. The extremity of the malformed right transverse process is twisted backward. The large orifices for the dorso-ventral vascular canals are separated on the ventral face of the centrum by a longitudinal ridge 11 mm. in width.

On the left half of the centrum of the hindermost of these lumbar vertebrae both epiphyses are missing, the whole neural arch is destroyed, and the transverse process is broken off at the base. The transverse process is, however, directed more noticeably downward than on the preceding lumbar.

**Table 67—Measurements (in millimeters) of lumbar vertebra**

<table>
<thead>
<tr>
<th></th>
<th>No. 1 1401a</th>
<th>No. 2 1401</th>
<th>No. 3 1401a</th>
<th>No. 4 1401</th>
<th>No. 5 1401</th>
<th>No. 6 1401a</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>U.S.N.M.</td>
<td>U.S.N.M.</td>
<td>U.S.N.M.</td>
<td>U.S.N.M.</td>
<td>U.S.N.M.</td>
<td>U.S.N.M.</td>
</tr>
<tr>
<td>Antero-posterior diameter of centrum</td>
<td>104*1</td>
<td>103*2</td>
<td>105*2</td>
<td>101*2</td>
<td>112*2</td>
<td>100*2</td>
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<tr>
<td>Vertical diameter of centrum anteriorly</td>
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<td>131</td>
<td>142</td>
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<td>150</td>
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<tr>
<td>Transverse diameter of centrum anteriorly</td>
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<td>...</td>
<td>166</td>
<td>...</td>
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<tr>
<td>Vertical diameter of centrum posteriorly</td>
<td>...</td>
<td>129</td>
<td>146</td>
<td>143</td>
<td>148</td>
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<tr>
<td>Transverse diameter of centrum posteriorly</td>
<td>...</td>
<td>161</td>
<td>103</td>
<td>103</td>
<td>102</td>
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</tr>
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</table>


**ARCHAEOCETE gen. et sp. indet.**

**Locality**—West coast of Vancouver Island, British Columbia, Canada, 1½ miles southeast of Escalante Point, Nootka Sound, on rocks exposed at low tide off shore fronting ranch belonging to G. J. Smith. The laminated sandy and marly conglomerate in which this vertebra was found, according to Prof. M. F. Bancroft, is a member of a well-defined series of beds, which extend inland, and are bounded by a cliff composed of green volcanic rocks of the Vancouver group of formations. These conglomerates are overlain seaward by thin shale and sandstone beds. These beds in the coastal plain of Nootka Sound were heretofore mapped as lower Cretaceous. Molluscs, plant remains, and spheroidal calcareous concretions occur in the conglomerate. Although the six species of gastropods collected at this locality are not sufficiently preserved to be identified with certainty, Dr. Ralph B. Stewart concludes that they may represent an Oligocene fauna, possibly near the Lincoln horizon of western Washington. Late upper Eocene or lower Oligocene.

**Specimen**—An imperfectly preserved anterior lumbar vertebra. No. 8748, Geological Survey, Department of Mines, Ottawa, Canada; collector, Prof. M. F. Bancroft; July 26, 1935.

**LUMBAR VERTEBRA**

The configuration and dimensions of this vertebra correspond most closely to those of lumbar vertebrae (No. 11401, U. S. N. M.) belonging to an undetermined archaeocete that occurs in the upper Eocene Ocala limestone of Georgia. The left side of this vertebra is
fairly well preserved, but both transverse processes are broken off near the base, the right metapophysis is entirely destroyed and the left one is incomplete, and the anterior border of the neural spine is destroyed. The epiphyses are rather thin (10 to 12 mm. in thickness) and are attached to the centrum.

This anterior lumbar vertebra is characterized as follows: Pedicles of neural arch (fig. 85a) relatively wide antero-posteriorly (minimum diameter of left pedicle, 72 mm.), being equivalent to about two-thirds of length of centrum (111 mm.); laterally flattened metapophyses projected upward and slightly outward, and extended forward beyond level of anterior end of centrum; neural spine rather wide antero-posteriorly at base (110 mm.), truncated distally, and compressed laterally; postero-basal angle of neural spine projects backward at least 25 mm. beyond level of hinder end of centrum; no remnants of prezygapophyseal facets preserved; postzygapophysial facets (fig. 85b) widely separated (maximum distance between opposite facets, estimated, 85 mm.); left postzygapophysial facet narrow and curved, and located on outer edge of hinder portion of roof of neural arch; length of left postzygapophysial facet, 25 ± mm. and maximum vertical diameter, 7.5 mm.; transverse diameter (92 mm.) of neural canal anteriorly more than twice its vertical diameter (38.5 mm.); transverse processes quite broad at base, dorso-ventrally flattened and projected outward and obliquely downward; vertical diameter greater than antero-posterior diameter of centrum; a pair of orifices for dorso-ventral vascular canals located near middle
of dorsal surface of centrum; ventral orifices of these canals obliterated; and anterior and posterior faces of centrum shallowly concave. Additional measurements of this vertebra are as follows: Maximum vertical diameter, tip of neural spine to ventral surface of centrum, 315 mm.; transverse diameter of centrum, anteriorly, 166 mm.; vertical diameter of centrum, anteriorly, 131 + mm.; transverse diameter of centrum, posteriorly, 183 mm.; and vertical diameter of centrum, posteriorly, 120 mm.

ARCHAEOCETE gen. et sp. indet.

Locality—In the southeastern part of the town of Jackson, Hinds County, Mississippi, near southwest corner of southwest ¼ of southeast ¼ of Section 10, Township 5 North, Range 1 East, Choctaw Meridian. About 6 feet below the top of Moody's marl member, lower Jackson formation. Upper Eocene.

Specimen—Centrum of a fairly large lumbar vertebra. Private collection of J. Magruder Sullivan, Jackson, Mississippi.

LUMBAR VERTEBRA

The vertebra is damaged to such an extent that it is impossible to furnish a detailed description. Both epiphyses are missing, the outer circumferential layer is eroded near both ends of the centrum, the entire neural arch is destroyed, and both transverse processes are damaged, the right one being broken off near the base and the left one being completely destroyed. The shell of an oyster, Ostrea trigonalis Conrad, is firmly attached to the posterior end of the centrum. This vertebra probably belongs behind the middle of the lumbar series, since the antero-basal edges of the pedicles of the neural arches are somewhat nearer the anterior end of the centrum than the hinder edges are to the posterior end.

This vertebra has a distinctly elongated centrum. Assuming that the thicknesses of the epiphyses that are missing from this centrum are similar to those on the corresponding vertebrae of other archaeocetes, the antero-posterior diameter of this vertebra when complete should have corresponded quite closely to that of lumbers of Pontogeneus brachyspondylus. The transverse and vertical diameters of the anterior end of this centrum are, however, at most only three-fourths of the same diameters of the lumbers of P. brachyspondylus. The rather narrow right transverse process, which projects outward and downward from near the level of the ventral face of the centrum, is located almost at the center. Of the dorsal openings of the two dorso-ventral vascular canals only the left one is present. It is situated near the middle of the dorsal face of the centrum. On the ventral face the opening on the left side is unusually large. There are two small ones on the right side.

The measurements of this vertebra are as follows: Maximum antero-posterior diameter of centrum, without epiphyses, 225 mm.; transverse diameter of centrum anteriorly, 155 + mm.; vertical diameter of centrum anteriorly, 128 + mm.; transverse diameter of neural canal at least, 70 mm.; least antero-posterior diameter of transverse process near base, 60 mm.

ARCHAEOCETE gen. et sp. indet.


Locality—A little gully approximately 21 miles west of College Station and about 5 miles east of Caldwell, on the 275 acres belonging to J. H. Giesenschlag in the southeast corner of the J. Reed Survey, Burleson County, Texas. The bones were found in 1921 by John Navratil lying loosely on the surface about ten feet above the bed of this little gully and may possibly have been derived from a six-inch layer of reddish-brown clay-ironstone. Limonite fills the cavities in the bones as well as the spaces between them, and also forms the matrix in which they are imbedded. The bones are also coated with a thin layer of gypsum.
This bed was originally assigned to the Cook Mountain formation, but more recent field studies (Renich and Stenzel, 1931, p. 98) have shown that it is a marine lentil belonging in the basal part of the Yegua formation.

It has been suggested by Dr. Julia Gardner (1927, p. 250) that the Yegua may represent a period of elevation, initiated by the retreat of the sea, and subsequently with the development of lagoon conditions the marine types were trapped in more or less isolated and partially inclosed bodies of water that became increasingly saline. Yegua formation = upper Claiborne = lower upper Eocene.

**Specimen**—Two imperfectly preserved caudal vertebrae. These were found near 17 vertebrae belonging to an Eocene sirenian and of these 15 were articulated. No. 13856, Division of Vertebrate Paleontology, U. S. National Museum; collectors, John Navratil and Mark Francis; 1921.

![Fig. 86—Archeocete, gen. et sp. indet. Middle caudal vertebra, No. 13856, United States National Museum. X 4. a, lateral view; b, ventral view. Lower upper Eocene, Yegua formation, Texas.](image)

<table>
<thead>
<tr>
<th>Table 68—Measurements (in millimeters) of caudal vertebrae</th>
<th>C. 11</th>
<th>C. 12</th>
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<tbody>
<tr>
<td>Antero-posterior diameter of centrum</td>
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<td>106</td>
</tr>
<tr>
<td>Transverse diameter of centrum, anteriorly</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Vertical diameter of centrum, anteriorly</td>
<td>97.5</td>
<td>93</td>
</tr>
<tr>
<td>Transverse diameter of centrum, posteriorly</td>
<td>118</td>
<td>105</td>
</tr>
<tr>
<td>Vertical diameter of centrum, posteriorly</td>
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<td>Transverse diameter of neural canal, anteriorly</td>
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<tr>
<td>Vertical diameter of neural canal, anteriorly</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Minimum transverse diameter of centrum near middle of its length</td>
<td>89</td>
<td>77</td>
</tr>
</tbody>
</table>

**Caudal Vertebrae**

Eleventh caudal.—The conformation and general appearance of this vertebra indicate that it belongs behind the middle in the caudal series. This vertebra is, however, badly weathered and its processes are for the most part destroyed. The short anterior and posterior portions of the transverse process are separated by a deep but rather narrow notch. On both sides of the centrum the anterior portion of this process is broken off at the base. The essentially complete posterior portion of the transverse process projects at least 25 mm. beyond the level of the right face of the centrum. This projection is unusually robust.
and has a vertical diameter of more than 15 mm. at its extremity. The neural canal is low and apparently rather wide. The right side of the neural arch and both metapophyses are destroyed. The centrum is constricted medially. The posterior face of the centrum is distinctly larger than the anterior face and is hexagonal in outline. The hemapophysial facets are located on rather low protuberances at the hinder end of the ventral surface. The ventral orifice for the dorso-ventral vascular canals is rather minute.

Twelfth caudal—This vertebra (fig. 86a) is imperfectly preserved and is somewhat weathered, but the preservation is better on the left side than on the right. It is characterized by the proportionately low and wide neural canal, by the very low and relatively narrow pedicles of the neural arch, and by the short anterior and posterior portions of the transverse process, which are separated medially by a broad notch. The centrum is rather strongly constricted medially. The anterior and posterior faces of the centrum are hexagonal in outline, and the upper half of the hinder end of the centrum is crushed forward. The hemapophysial facets are located on rather large protuberances at the hinder end of the ventral surface and are separated longitudinally by an interval of at least 20 mm. A small ventral orifice for the dorso-ventral vascular canals is present. Both metapophyses are largely destroyed by erosion.

"ZEUGLODON" cfr. BRACHYSPONDYLUS


Locality—Fayum, Egypt. From a yellow sandstone belonging to the Birket-el-Qurun stage. Lower upper Eocene.

Referred specimens—(1) A posterior dorsal vertebra, probably the twelfth in the series. No. 1904. XII. 135f, Paläontologische Sammlung, Alte Akademie, München; collector, Richard Markgraf; 1904 (Mn. 19, Stromer, 1908b, p. 136, pl. 5, fig. 27).

(2) Two caudal vertebrae. No. 1904. XII. 135f, Paläontologische Sammlung, Alte Akademie, München; collector, Richard Markgraf; 1904 (Mn. 17, Stromer, 1908b, p. 136).

Remarks—The posterior dorsal vertebra (Stromer, 1908b, pl. 5, fig. 27) obviously belonged to an immature individual, since the posterior epiphysis of the centrum is missing and the anterior epiphysis has been shoved upward. According to Stromer, the centrum is approximately 105 mm. long, 144 mm. broad, and 115 mm. high; the neural canal measures 85 mm. transversely and 40 mm. vertically; and the height of the neural spine is 110 mm. The position and configuration of the transverse process of this vertebra corresponds quite closely with the twelfth dorsal of Zygorhiza kochii. The dimensions of the centrum, the relative antero-posterior diameters of pedicle of neural arch and of centrum, and the configuration and position of the transverse process are quite unlike the corresponding dorsal vertebrae of Prozeuglodon isis (Stromer, 1908b, pl. 6, figs. 7, 14) and of Basilosaurus cetoides.

The middle caudal vertebra is described by Stromer (1908b, p. 136) as having a much narrower neural canal than the hindermost of the four caudal vertebrae in the Munich collection (No. 1904. XII. 135) which are referred to Prozeuglodon isis. The metapophyses and distinct facets for the chevrons are present, the lateral and ventral surfaces of the centrum are convex transversely and concave longitudinally, and the reduced transverse process is interrupted in the middle. The centrum is 105 mm. long, 120 mm. broad, and 110 mm. high.

On the hinder caudal vertebra, no processes are developed, and the dimensions of the centrum are given as follows: Length, 50 mm., breadth anteriorly, 85 mm., and height anteriorly, 90 mm.
These vertebrae belonged to an archaeocete of approximately the same size as the species which occurs in the Ocala formation in Georgia (No. 11401, U. S. N. M.). Until more is known in regard to the growth stages of the vertebral column of the larger archaeocetes, the determination of these and similar isolated vertebrae will remain problematical. On the basis of our present knowledge, the vertebrae described by Stromer can not be referred to any of the archaeocetes that have been described from Fayum formations.

"ZEUGLODON" sp.


Type locality—On the northeast end of Seymour Island, near the northeast coast and next to Snow Hill, Weddell Quadrant, West Antarctica. Weathered from a loose sandstone interstratified with conglomerate. Lower Miocene Patagonian marine formation (Wiman, 1905, p. 37).

Type specimen—Two incomplete caudal vertebrae, one tentatively identified as an anterior caudal and the other as a hinder caudal. Nos. 1, 2, Paläontologischen Institut der Universität, Upsala, Sweden; collectors, Otto Nordenskjöld and Joh. Gunnar Andersson; October 30, 1903.

Remarks—Stromer (1908b, p. 147) states that these vertebrae are very similar to the caudal vertebrae of Zeuglodon and so also are the vertebrae from the lower Miocene white sands of Linz, Austria, which are referred to Squalodon ehrlichi [= Patriocetus denggi] Abel, 1913, p. 198] by Brandt (1873a, p. 355, pl. 18, figs. 5b–g, and 6b–g; 1874b, pp. 39–40). The anterior caudal vertebra (Wiman, 1905, pl. 1, figs. 1–2) is not markedly different, except for the greater antero-posterior diameters of pedicle of neural arch and of metapophysis, from the lumbar vertebra of Patriocetus denggi. As regards these two structural details, however, a somewhat closer resemblance seems to exist between this vertebra and some of the anterior caudal vertebrae of Zygorhiza kochii. The vertebrae of Kekenodon onamata and likewise the skeletons of most of the cetaceans that occur in the Patagonian marine formation have not as yet been figured. The inadequacy of the documentary evidence for the structural details of the lumbar and caudal vertebrae of these fossil cetaceans is a formidable obstacle to a precise understanding of the relationships of this form.

"ZEUGLODON" PUSCHII Brandt


Type locality—A fissure in the compact white Jurassic limestone of the quarry belonging to the lime-kiln at Pieklo near Inowlodz, Poland. Age uncertain.

Type specimen—An incomplete vertebra.

Remarks—The vertebra described and figured by Pusch (1837, p. 167, pl. 15, figs. 4a, 4b), on which this species was founded, lacks the neural arch, the neural spine and the major portion of both transverse processes. If one may rely on the scale of reproduction given for the illustrations published by Pusch, the centrum is approximately the same size as that of an anterior lumbar of Zygorhiza kochii. A pair of orifices for the vascular canals, that pierce the centrum in a vertical direction, are located near the middle of the length of the dorsal and ventral surfaces. While Pusch thought that this vertebra belonged to the thoracic series, Brandt identified it as a lumbar vertebra. Brandt (1873a, p. 340) directs attention to the unmistakable resemblance shown by this vertebra to lumbar vertebrae (Brandt, 1873a, p. 355, pl. 18, figs. 5b, c, d, and 6b, c, d) which he allocates to Squalodon
ehrlichii [= Patriocetus denggi] Abel, 1913, p. 197, fig. 13. Abel (1913, p. 206) is in complete agreement with Stromer (1903c, p. 86) that this vertebra is not determinable and concludes therefore that this species should be eliminated from the Archaeoceti.

"ZEUGLODON" VREDENSE Landois


Type locality—"Vreden" in Münster, Westphalia, Germany. Hosius (1893, pp. 68-69), however, declares that the specimen came from the Miocene deposits of the Dutch brickyards, which are located between Zwillbrock in Germany and Eibergen in Holland.

Type specimen—A single tooth received from the Rev. Degener in 1883-84.

Remarks—Since no description of any sort is given by Landois, this name is clearly a nomen nudum. As pointed out by Stromer (1903c, pp. 86-87), Landois merely expresses the conjecture that a new species is represented and in allusion to the presumed locality proposes the name Zeuglodon vredense. Some thirty years before the discovery mentioned by Landois, Roemer (1854, p. 41) stated that a tooth in the collection of the Geological Commission of Netherlands at Leiden, which was found in the vicinity of Eibergen, had been identified by Richard Owen as belonging to a Zeuglodon. Van Deinse (1931, pp. 34-35) mentions other specimens from the vicinity of Eibergen. It is quite likely that most of these specimens are referable to Squalodon antverpiensis Van Beneden.

PONTOBASILEUS TUBERCULATUS Leidy


Type locality—Not definitely known.

Type specimen—A damaged cheek tooth, consisting of one root and corresponding portion of the crown. Cat. No. 11216, Academy of Natural Sciences of Philadelphia.

Remarks—Inasmuch as Leidy stated that the type tooth (pl. 36, figs. 4-5) of Pontobasileus tuberculatus "apparently belonged to an animal of the same order as the Basilosaurus," it is desirable to determine the relationships of this species in so far as it is possible in the light of our present knowledge of the fossil Cetacea. Leidy correctly stated that this tooth when complete had two roots. It is also obvious that the crown was relatively low.

The coarse ornamentation of the black enamel on the crown is unlike that of any known archaeocete, but does resemble quite closely that of some of the squalodonts (Dal Piaz, 1916, fig. 5; Leidy, 1869, pl. 28, figs. 4-7). This ornamentation may be described as tuberculate or denticulate, and extends over all of the portion of the crown which is preserved. Most of the small bluntly pointed tubercles or denticles are arranged in rows which commence at the cingulum and extend in the direction of the apex of the crown. The pseudo-imbricated arrangement of these polished tubercles and the presence of vertical wrinkles on the lateral surface of the very narrow cingulum are probably the most obvious peculiarities of this low-crowned tooth. The basal portion of the crown projects beyond the level of the corresponding face of the root. The basal border of the enamel on the crown is relatively smooth for a distance of 2.5 to 3± mm. above the root. A small oval area (8.5 × 5.5 mm.) of the exceedingly tuberculate enamel has been worn off, exposing the dentine. It is barely possible that a low accessory denticle may have been present in this area. The apex of the crown is missing.

The root is straight, triangular in cross-section, and is attenuated toward the distal end. The thin osseous isthmus connecting this root with the one that is missing extends
downward 10.8 mm. below the base of the enamel crown. The face of the root below the osseous isthmus is rather deeply grooved longitudinally. The opposite faces of the root are somewhat flattened, but have a slight median longitudinal depression.

The proportions and peculiarities of this tooth fragment resemble most closely the low-crowned hinder mandibular molars of *Squalodon*. Although it is considerably larger than the hinder lower molars of most squalodonts, the measurements indicate that it may have belonged to a species related to or possibly identical with *Squalodon tiedemani* (Allen, 1887, pls. 5–6), which was obtained “in dredging phosphatic material from the Wando River, at Charleston,” South Carolina. Leidy states that the type tooth of *Pontobasileus tuberculatus* was found without a label among some *Basilosaurus* remains from Alabama, and remarks: “I suppose it to have been derived from some Eocene or Miocene formation of the Atlantic States.” The general appearance, preservation, and especially the presence of the “remains of two white disks, apparently the basal attachment of barnacles,” are strikingly similar to other teeth obtained from the vicinity of Charleston.

<table>
<thead>
<tr>
<th>Table 69—Measurements (in millimeters) of type tooth</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum length, as preserved..................................</td>
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<tr>
<td>Antero-posterior diameter of crown, as preserved.........</td>
</tr>
<tr>
<td>Transverse diameter of base of crown near middle........</td>
</tr>
<tr>
<td>Transverse diameter of base of crown at hinder end.......</td>
</tr>
<tr>
<td>Antero-posterior diameter of root at level of lower end of isthmus</td>
</tr>
<tr>
<td>Maximum transverse diameter of root below basal border of enamel crown</td>
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</tbody>
</table>
GEOLOGIC AND GEOGRAPHIC DISTRIBUTION OF THE ARCHAEOCETI

The distribution of the known occurrences (fig. 87) of archaeocetes and of various representatives of the shallow-water fauna have been used by Stromer (1906, 1932) and by Andrews (1907) to indicate the location of shore lines of previous land connections between the Old and the New Worlds. Support to this belief that the archaeocetes frequented shallow water is given by Dart (1923, p. 637), who contends that the trigeminal specialization of the archaeocete brain is correlated with a hypertrophy of the tactile sense and that therefore it is highly probable that these animals frequented shallow water. This conclusion does not necessarily follow, for a highly developed tactile sense may be correlated with food getting. There is reason to believe that these animals did not have such keen sight as some of their contemporary land-dwelling allies, for we know that the refractive index of sea-water is not the same as that of air. Therefore sight will be defective unless the eyes are adjusted to function properly when immersed. Reference to the evidence furnished by endocranial casts for the relative loss of sight as contrasted with the obvious development of the trigeminal and olfactory parts is made by Dart (1923, p. 635). Water-dwelling animals with improperly adjusted eyes must depend on a tactile sense to gain information concerning food and enemies.

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KEY TO MAP (FIG. 87)

**Middle Eocene**

1. Lower Mokattam limestone near Cairo, Egypt.
2. Upper Lutetian clay, Amechi, Omobiolla District, southern Nigeria.
3. Crockett formation [= upper Cook Mountain], Two Mile Creek, southern Leon County, Texas.

**Upper Eocene**

5. Santee limestone marl, near junction of Santee Canal with headwaters of Cooper River, Berkeley County, South Carolina.
6. Castle Hayne formation, near Castle Hayne, New Hanover County, North Carolina.
7. Castle Hayne formation, Wadsworth's marl pit, Craven County, North Carolina.
8. Birket-el-Qurn beds near Gar-el-Gehannem, Dimê, and other localities near the lake, and the Qasr-el-Sagha beds, Fayum, Egypt.
9. Ocala limestone (upper Jackson formation), 4 mi. S. of Perry, Houston County, Georgia.
10. Ocala limestone (upper Jackson formation), Flint River, Crisp County, Georgia.
11. Ocala limestone (upper Jackson formation), Ocala, Marion County, Florida.
12. Ocala limestone (upper Jackson formation), Conecuh River, Escambia County, Alabama.
13. Ocala limestone (upper Jackson formation), near Clarksville and Dead Level, Clark County, Alabama.
15. Upper Jackson formation, localities near Fall, Cocoa, Iriney and Melvin, Choctaw County, Alabama.
16. Upper Jackson formation, Clarke County, Mississippi.
17. Moodys marl and Yazoo clay, Jackson formation, near Jackson, Hinds County, Mississippi.
18. Jackson formation, near Ouachita River, Caldwell Parish, Louisiana.
19. Jackson formation, near Montgomery, Grant Parish, Louisiana.
20. Conglomerate, 14 mi. S. E. of Escalante Point, west coast of Vancouver Island, British Columbia.

**Oligocene**

22. Kharkov green glauconitic sands, near Chigirin, Ukraine, U. S. S. R.
23. Kharkov green glauconitic sands, Zmyev and Izyum districts, Ukraine, U. S. S. R.

**Miocene**

25. Ototaran calcareous greensand, localities at Waitaki Valley, Otago, New Zealand.

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Fig. 87—Map showing location of principal localities where archaeocete remains have been found.
The fact that the archaeocetes were present in the seas bordering on northern Africa, England, and the southern United States during the upper Eocene, on Vancouver Island, B. C., and on the Ukraine during the lower Oligocene, and on France and on New Zealand during the lower Miocene introduces some obvious difficulties into the general problem of geographic distribution, if we insist that these archaeocetes were restricted to shallow coastal waters. We have no valid geologic evidence that the Atlantic Ocean and the relations of the opposite continents during early Tertiary time were markedly different then than at present.

Archaeocetes make their first appearance in sediments of middle Eocene age (lower Lutetian stage) in northern Africa. A considerable portion of their evolutionary history seems to have taken place in the seas that covered that area during middle and upper Eocene time. The Eocene deposits in the Fayum basin of Egypt, that have been designated in ascending order as the Wadi Rayan series, the Ravine beds, the Birket-el-Qurun or Operculina-Nummulite beds, and the Qasr-el-Sagha or Carolia beds, comprise some 1300 feet of marine sediments (Andrews, 1906, p. IX). The lower and upper Mokattam limestones of middle and upper Eocene age located near Cairo, Egypt, have a total thickness of ± 750 feet (Blanckenhorn, 1900, table, p. 406). It is in these two series of strata that the greatest variety of successive types of archaeocetes have been found.

Nevertheless, at least one representative of this group (? Protocetus sp., from the Crockett formation of Texas) had reached North America during the middle Eocene. One of the more advanced genera, *Dorudon*, found in Egypt, likewise occurs in the upper Eocene Santee limestone of South Carolina.

We have direct or inferential evidence that these archaeocetes had not migrated northward into the Anglo-Franco-Belgian basin before the upper Eocene Bartonian stage. Notwithstanding many years of search by palaeontologists, no trace of archaeocetes has as yet been recorded from these European marine strata, covering a period of time beginning with the lower Eocene or Paleocene Montian marine sands and ending with the Auversian marine deposits of northwestern France. These Eocene sediments have a total thickness of at least 1500 feet (Boswell, 1929). There is no good reason to suppose, however, that some land barrier held these archaeocetes to the southern Mediterranean shores or that the types found there are the less progressive members of this group.

The archaeocetes evidently did not reach the Indian Ocean during Eocene time. In western India, Eocene sediments (Wadia, 1919, pp. 211, 215–218) having a maximum thickness of more than 11,000 feet are present in the two hill ranges, Khirthar and Laki, on the Baluchistan frontier of Sind Province. These strata represent a time interval that extends from the Paleocene to the upper Eocene (Bartonian stage). They include in ascending order the Ranikot series (2000 ft.), the Laki series (500–800 ft.), and the massive nummulitic limestones that comprise the Khirthar series (3000–9000 ft.). Over 8000 feet of Eocene marine sediments, consisting of the sandstones, limestones and shales that comprise the Bassein group, part of which are at least as old as the Lutetian stage, are found
in the Irawady River basin of Burma (Dalton, 1908, p. 618). If archaeocetes had reached the Indian Ocean during the Eocene, it is quite likely that some record of their presence would have been left in these regions.

Intensive palæontological exploration of the Eocene marine strata on the west coast of the United States has not as yet brought to light a single fragment that can be identified as belonging to an archaeocete. In the Simi Valley district, Ventura County, California, the Eocene sediments (Kew, 1924, pp. 15, 20, 28) comprising the Martinez, Meganos (Santa Susana and Domengene) and Tejon formations have a maximum thickness of at least 8000 feet. In the Santa Ynez Mountains, Santa Barbara County, California, the Eocene section (Kew, 1919, p. 11) is reported to measure about 14,000 feet. Comparable thickness of Eocene strata (Umpqua and Tyee formations) are said to occur in Oregon.

The discovery on Vancouver Island of a lumbar vertebra belonging to a fairly large archaeocete furnishes conclusive proof that at least one representative of this group had arrived in the North Pacific Ocean near the beginning of the lower Oligocene. This archaeocete seems to be related most closely to the undetermined species that occurs in the upper Eocene Ocala limestone of Georgia.

The apparent absence of the Archaeoceti along the gulf coastal plain of North America in formations older than the upper middle Eocene affords, raises the presumption that representatives of this group did not reach this continent at some earlier time. In Alabama (Hopkins, 1918, p. 287), for instance, there are some 1700 feet of Eocene sediments, comprising the Midway, Wilcox, and Claiborne groups, that underlie the Jackson formation.

The absence of archaeocetes from the recorded Eocene faunas of the west coast of the United States, of the northern shores of the Indian Ocean, and of the Anglo-Franco-Belgian basin of Europe (before the Bartonian stage) would not be conclusive in itself; but, coupled with the variety and abundance of archaeocetes in the deposits of northern Africa, it is very strong evidence that they had not as yet invaded these regions.

A number of different types of archaeocetes have been discovered in Africa in marine sedimentary deposits of middle and upper Eocene age. The oldest of these is the somewhat generalized Protocetus atavus, which occurs in a basal stratum of the lower Mokattam limestone near Cairo, Egypt, and according to our present knowledge is a representative of the fauna of the lower Lutetian stage. In the same sequence of deposits in the Mokattam hills near Cairo, but in a stratum belonging to the upper Lutetian stage and overlying the one in which Protocetus occurs, the rather large Eocetus schweinfurthi makes its appearance. The upper Lutetian clay of the Omobiella district of southern Nigeria has furnished mandibles of another generalized archaeocete, Pappocetus lugardi.

In the basin of the Fayum,¹ which is situated on the southern borders of the Libyan Desert, about 60 miles southwest of Cairo, Egypt, Andrews (1906, p. ix) has recorded the occurrence of archaeocete remains of questionable identity in

¹ The archaeocetes, that were mentioned by Stromer (1908b, pp. 107, 152) as having been collected probably in the marine Wadi Rayan (Nummulites giezehensis) beds, were subsequently found to have come from Uadi Rojan on the northern steep cliff of the Fayum basin.
the marine Ravine beds. These beds presumably are referable to the Auversian stage. The lowest escarpment above the lake on the northern slope of the Fayum depression is composed of successive strata, with Ravine beds at the base, and overlying these are the Birket-el-Qurun series and the lower part of the Qasr-el-Sagha beds. From the transition beds of this escarpment, which have been designated as the Birket-el-Qurun series (Operculina-Nummulite beds), the large *Prozeuglodon isis* and the considerably smaller *Dorudon intermedius* have been described. The sandstones and clays comprising the Birket-el-Qurun series are referred to the period of transition between the Lutetian and Bartonian stages, and thus correspond in time to the Auversian stage of the upper Eocene. With this stage, we encounter the first appearance of representatives of two hitherto unknown families (Basilosauridae and Dorudontidae) and their occurrence here signalizes the earliest record of archaeocetes with peculiarly specialized cheek teeth.

About half-way between the northern shore of the lake and the high cliffs (Jebel-el-Qatraní) composed of sands, sandstones, clays, and marls belonging to the lower Oligocene fluvio-marine series and bounding the basin of the Fayum on the north, is a rather high and steep escarpment comprising the higher beds of the Qasr-el-Sagha series. This series of alternating limestones, marls, clays, and sandstones is referred to the Bartonian stage of the upper Eocene (Andrews, 1923, p. 648). From the Qasr-el-Sagha series (Carolina beds), skulls of three small archaeocetes, *Dorudon osiris*, *D. zitteli*, and *D. stromeri*, as well as the endocranial cast of *D. elliotsmithii* whose precise affinities have not as yet been established, have been recognized. The types thus far discovered in northern Africa quite likely present a very incomplete picture of the diversification of the archaeocetes during the middle and upper Eocene. Our knowledge of the factors conditioning the geographic dispersal of the archaeocetes would rapidly widen with the discovery of their remains in the deep-water marine facies of the Lutetian and Auversian stages in southeastern France and northwestern Italy.

Some 60 years ago, a skull of a small species (*Zygohiza wanklynii*) was found in the Barton Cliffs in Hampshire, England, in clay of upper Eocene age. The marine sandy clays comprising the Brockenhurst beds (Boswell, 1929, pp. 422–423) at Roydon, Hampshire, England, have yielded thus far a single caudal vertebra which may have belonged to some small archaeocete (? *Zygohiza juddii*). Documentary evidence for the occurrence of archaeocetes in other deposits of Eocene age in Europe is still lacking.

The Oligocene record of these archaeocetes in Europe is quite meager. In 1873, Brandt described a few imperfectly preserved vertebrae (*Platyophysis paulsonii*) which had been found near Kharkov in Ukraine, USSR. In 1912, Fedorovsky described additional skeletal remains of this archaeocete from a glauconitic green sand belonging to the lower Oligocene “Charkower Stufe” (Lattorfan stage).

*Phococetus vasconum* is known solely from the serrated crown of a cheek tooth which came from the soft calcareous sandstone at Saint-Médard-en-Jalle, about 8 kilometers northeast of Bordeaux, France. Geologists are agreed that this stratum is to be referred to the lower Miocene Burdigalian stage.
As regards the North American continent, we find that the oldest archaeocete remains thus far discovered come from the upper middle Eocene Crockett formation in Texas. The Crockett formation is considered to be nearly equivalent in age to the Lisbon formation, the middle member of the Claiborne group in Mississippi and Alabama, which has been correlated with the Lutetian stage of the Old World Tertiary. A single dorsal vertebra found in southeastern Leon County, Texas, comprises all that is known in regard to this archaeocete. It is tentatively referred to the genus *Protocetus*.

In Burleson County, Texas, in the basal portion of the overlying Yegua formation, two caudal vertebrae belonging to an archaeocete of medium size, were found near 17 sirenian vertebrae, of which 15 were articulated. The Yegua formation is considered to be equivalent in age to the Gosport sand, and the latter is correlated with the Auverrian stage.

There are at least two recorded occurrences of archaeocete remains in the upper Eocene Castle Hayne formation in North Carolina. A lower molar, tentatively referred to *Dorudon serratus*, was collected by Dr. T. W. Vaughan in the New Hanover County rock quarry that is located ½ a mile south of the Castle Hayne railroad station. Emmons (1858, p. 305) reports that "*Zeuglodon*" remains had been found associated with an echinoid (*Cidaris mitchelli*) in North Carolina, presumably at Wadsworth's marl pit in Craven County. The Castle Hayne formation, according to Dr. C. W. Cooke, should occur in this county.

In South Carolina, the upper Eocene green sand belonging to the Santee limestone marl has furnished the small archaeocete *Dorudon serratus*. The Santee limestone marl is overlapped by the Barnwell formation and presumably is slightly older than the latter, although it is referred to the Jackson epoch. A few large bones of an archaeocete were collected in Twiggs County, Georgia, in a yellow sand belonging to lower part of the Barnwell formation (Cooke and Shearer, 1918, p. 43).

The Jackson formation, which consists of calcareous fossiliferous sands and clays of marine origin, outcrops in eastern Texas in the region between the Trinity and Sabine Rivers, and extends eastward across central Louisiana, Mississippi, and into Alabama as far east as the Tombigbee River. In western Mississippi, the Jackson formation consists of a lower member known as Moodys marl and an upper member, the Yazoo clay. In eastern Mississippi the Yazoo clay member attains a maximum thickness of 70 feet but in the western part of that state that member exceeds 500 feet in thickness. Until quite recently it has been thought that archaeocetes did not occur in the lower member. A few years ago, however, Professor Sullivan found an incomplete centrum of a fairly large archaeocete near the top of Moodys marl.

Three types of archaeocetes have been found in the upper Jackson formation, including the Yazoo clay and the Ocala limestone, of the gulf coastal plain. One of these (*Basilosaurus cetoides*) is quite large, another (*Pontogeneus brachyspondylus*) is of medium size, and the third (*Zygophora kochii*) is relatively small. In Alabama the "*Zeuglodon*" horizon (10 to 15 feet) is situated near the base of the upper clay member of the Jackson formation. An abundance of rounded shells
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<td>Lower Miocene</td>
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<td>Calcareous sandstone and green sands, Oamaru series</td>
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<td>Upper Oligocene</td>
<td>Charkower Stufe, green glauconitio sand, Zmiyev Dist., Ukraine</td>
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<td>Upper Jackson formation, including Ocala limestone,</td>
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<td>Qasr-el-Sagha stage (Carolina beds), Fayum, Egypt <em>Dorudon osiris</em></td>
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<td><em>Dorudon stromeri</em></td>
<td>Santee limestone marl, Santee Canal, South Carolina</td>
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<td>Lower Birket-el-Qurun and Ravine stages, Fayum, Egypt *Proseugolodon</td>
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<td>Upper lower Mokattam limestone, near Cairo, Egypt Eocetus scheinfurthi</td>
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<td>Hard pyritous clay, Omobi alla Dist., southern Nigeria *Papposaurus</td>
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<td>Eocene</td>
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<td>Basal lower Mokattam limestone, near Cairo, Egypt <em>Protocetus davus</em></td>
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of small sea-urchins (Schizaster armiger and Macropneustes mortoni), a small scallop (Pecten perplanus), a little oyster (Ostrea falco), and a large nautilus (Atruria alabamensis) occur in the "Zeuglodon" horizon. The yellowish or gray marl, in which skeletal remains of these archaeocetes occur, is often hardened around the bones. From two to four hard ledges, a few inches in thickness and separated by layers of this marl, are also generally present in this horizon.

In Clark County, Alabama, the upper member of the Jackson formation merges laterally into the Ocala limestone (Cooke, 1926, p. 275), and the latter extends eastward into central Florida and southwestern Georgia. Both Basilosaurus cetoides and Zygorhiza kochii have been collected in Clark County. An imperfectly preserved skull of Basilosaurus cetoides was collected near Ocala, Florida, in the light cream-colored Ocala limestone (Cooke, 1915, p. 113). The geographic range of the Jackson archaeocetes has been extended northward into Georgia by the discovery in the Ocala limestone of Basilosaurus cetoides in Houston County and of Zygorhiza kochii in Crisp County. Lumbar vertebrae of quite different proportions from those of Basilosaurus cetoides were found in the Ocala limestone on the east bank of Flint River in Crisp County, Georgia.

The affinity between the archaeocetes of North America and Africa appears to be only that of descent from similar ancestors, and it is quite likely the immediate progenitors of the former are migrants from the Mediterranean seas of the Old World. From evidence available at present, the inference is drawn that the archaeocetes reached the climax of their evolutionary advance toward the close of the Eocene and that the surviving types of the Oligocene and the lower Miocene are descendants of the smaller Eocene forms.

A small species (Kekenodon onamata), whose skeleton may have measured about 23 feet in length, is now known to occur at a number of localities in New Zealand, but apparently always in a calcareous greensand or soft calcareous sandstone. The Kekenodon beds belong in the Oamaru system, which are held to be referable to the Oligocene upper Wairekan stage by McDonald and by Thomson, and to the middle Miocene lower Hutchinson or upper Otataran stage by Park.

The Swedish South-Polar Expedition in 1901–03 under the direction of Professor Nordenskjöld found two caudal vertebrae of a supposed archaeocete on the northeast shore of Seymour Island in West Antarctica. This sandstone and conglomerate is correlated by Wilckens (Wiman, 1905, p. 37) with the Patagonian marine formation. Windhausen (1931) considers that the Patagonian marine formation belongs in the Oligocene epoch, while others place it in the lower Miocene.

MORPHOLOGIC HISTORY OF THE ARCHAEOCETI

The oldest known archaeocetes had already acquired a complicated organ for hearing, they retained a well-developed olfactory apparatus, but their brain structure so far as shown by endocranial casts suggests that their sight was defective. Although these archaeocetes have highly specialized skulls which are quite similar in general appearance and are constructed on the same ground-plan, they tried out occipital shields (fig. 88) of somewhat different contours, but the main path of their evolutionary advance seems to have centered around the remodeling of the
cheek teeth. No instance of telescoping or of overlapping of individual bones in the skull has been observed in any known archaeocete.

The bones comprising the rostrum and braincase of these archaeocetes retain their normal mammalian relationships. The braincase is narrowed anteriorly and elongated, but never shortened antero-posteriorly like in Recent cetaceans, for all have a remarkable elongated intertemporal constriction and large temporal fossae. The parietals are always normal in their relation to other bones and meet on the mid-line to form a sagittal crest. Lambdoidal crests are developed to a varying extent and the exoccipitals are already extended laterally. The high sagittal and lambdoidal crests, and the trenchant cheek teeth are directly correlated with flesh eating. The articular surface on the zygomatic process for the lower jaw tends to assume the peculiar vertical position of Recent cetacea.
All known archaeocete skulls have a flattened forehead and a broadened supraorbital process of the frontal, extended laterally beyond the jugal portion of the zygomatic arch, and arched at the extremity. That laterally expanded supraorbital processes have arisen independently in one or more orders of mammals, and are not wholly an aquatic specialization, is demonstrated by the occurrence of somewhat similar processes on the skull of the upper Eocene hyracoid Geniohyus mirus (Matsumoto, 1926, p. 267, fig. 5). The nasal bones are elongated and, with the possible exception of Protocetus atavus, do not encroach upon the frontals to any marked degree.

The posterior portion of the narial cavity is relatively undisturbed, and turbinal bones and lateral sinuses are present. The opening leading to the nostrils is progressively moved backward, the hinder limit of the dorsal narial fossa being at the level of Pm₁ in Protocetus atavus, and at the level of the interval between Pm₁ and Pm₂ in later archaeocetes. The proximal end of the maxillary abuts against the supraorbital process of the frontal superiorly and inferiorly projects backward below the latter. The premaxillary has an ascending process which does not reach the frontal and anteriorly is conspicuously extended beyond the extremity of the maxillary. The palatines do not extend forward beyond the level of the anterior edge of Pm₄ and the bony palate is prolonged backward by outgrowths of the palatines and pterygoids.

Apparently the mouth was employed mainly as a pair of forceps. The anterior teeth on the long, narrow, beak-shaped rostrum are widely spaced and are arranged in an antero-posterior series. The incisive foramina were eliminated by the linear contact of the premaxillaries along the mid-line of the rostrum. If our interpretation of the archaeocete skull is correct, a somewhat greater use was made of that part of the tooth row which serves for grasping food than of that which serves for grinding or shearing, and consequently the hooked incisors and the canine, as well as the anterior cheek teeth increased in size. The oldest archaeocetes have premolars and molars with non-serrated principal cusps and a reduced postero-internal enamel-covered buttress which seems to be a vestige of the inner portion of the original trigonal crown. The cheek teeth of later archaeocetes have several accessory cusps or denticles on the anterior and posterior cutting edges of the principal cusp. In successive geological stages, the premolars became heavier and acquired higher principal cusps on the crowns, but the molars were weakened, the third upper molar was lost, and the second was somewhat reduced in size. The remnant of the postero-internal cusp disappeared with the third root in the later archaeocetes of the Old and New Worlds. The lower Miocene Kekeno-don onamata of New Zealand constitutes the only known exception to this statement; the cheek teeth of this archaeocete have retained the third root, but the remnant of the postero-internal cusp has been effaced.

There is evidence that the pelvis was progressively reduced during middle and upper Eocene time, since the lower middle Eocene Protocetus atavus probably had innominate bones articulating with the transverse processes of the sacral vertebrae,
while all direct connection between the degenerate pelvis and the sacral vertebrae has been lost in the late upper Eocene *Basilosaurus cetoides*. The remodeling of the forelimbs of some at least of the early upper Eocene archaeocetes had already reached the adaptive stage characteristic so far as known of the later upper Eocene species. Hardly less clear is the evidence that the caudal vertebrae have been altered by the development of a powerful caudal musculature, resulting in the enlargement of the metapophyses, the widening of the transverse processes, and the general increase in the dimensions of the centra of the anterior caudals.

In the *Eocetus-Prozeuglodon-Basilosaurus-Platysphysis* series, the trunk is conspicuously lengthened by the elongation of the centra of the six hinder dorsal vertebrae and of all the lumbar vertebrae. These dorsal and lumbar vertebrae have relatively short and broad neural spines, and short transverse processes disproportionate to the length of the trunk. The aberrantly specialized *Basilosaurus* has the zygapophyses of all the trunk vertebrae, except the eight anterior dorsals, separated by increasing intervals proportional to the length of the centrum.

In the *Protocetus-Dorudon-Zygornhiza* series, the trunk is not conspicuously lengthened by the elongation of the centra of the six hinder dorsal and of all the lumbar vertebrae. These dorsal and lumbar vertebrae have relatively high and rather broad neural spines, and well-developed transverse processes. No noticeable elongation of the centra of either the hinder dorsals or of the lumbars has been observed in any member of the smaller archaeocetes.

**PROTOCETUS**

The oldest geologically of the archaeocetes, which have been discovered in the middle Eocene lower Mokattam limestone near Cairo, Egypt, is a somewhat generalized form. The skull of this archaeocete, *Protocetus atatus* (Fraas, 1904a), is slightly more than two feet in length and, if it has the same vertebral formula as later archaeocetes, the complete skeleton measures about eight feet (2.48 meters) in length. The skull of this small archaeocete bears little resemblance to those of living cetaceans. The characters of the base and back of the skull distinguish it sharply from all contemporary land mammals. In common with the oldest land carnivores and insectivores, there is a marked difference between the anterior grasping teeth and the posterior cutting teeth. In contrast to the archaeocetes of later geological stages, the teeth of *Protocetus* do not bear step-like accessory denticles on the anterior and posterior cutting edges of the principal cusp, and distinct vestiges of the inner portion of the crown are retained.

It is undoubtedly true that many characteristic peculiarities in the skull and skeleton of the immediate precursors have been either masked or effaced in *Protocetus* by adaptive alterations that were tried out by the archaeocete stemstock during the period of transition to life in the water. The forward projection of the elongated premaxillaries beyond the maxillaries on the anteriorly narrowed rostrum, the lateral extension of the antero-posteriorly widened supraorbital processes, the reduction of the area for the insertion of the masseter muscles, the tubular conformation of the intertemporal region, the large temporal fossae transversely
widened by powerful temporal muscles and bounded by a high sagittal crest, by a conspicuously backwardly folded lambooidal crest, and by a posteriorly enlarged zygomatic process, the backward extension of the molar series behind the level of the anterior end of the orbit, the closing in of the postnarial gutter by linear ankylosis of outgrowths from the opposite pterygoid plates, thus carrying the posterior narial opening backward to the basicranial region, the rudimentary condition of the pterygoid fossae, the pushing backward of the glenoid articulation, and the inflated conch-like conformation of the tympanic bulla with its peculiarly developed sigmoid process all indicate the high degree of specialization of Protocetus.

The terminal premaxillary portion of the rostrum and the incisor teeth are missing on the single known skull of Protocetus atavus, but all the remaining teeth in the typical eutherian dentition are present, which indicates that there are eleven teeth in each jaw. The canine is large and the lateral face of its single root is grooved vertically; Pm₁ is much smaller than the canine; Pm₃ has an elongated strongly compressed crown and two roots; but Pm₃ and Pm₄ have three roots. The cheek teeth have antero-posteriorly elongated, laterally compressed, and smooth-edged crowns; with the exception of Pm₁ and Pm₂ all of them are essentially similar in construction. All of the molariform teeth in the closed series (Pm₃ to M₃) still possess the inner root, though in the process of reduction. Pm₃ corresponds to the carnassial of carnivores and M₃ is the smallest of the molariform teeth. In the upper molars the paracone forms a trenchent longitudinal principal cusp, the para-style and metacone are reduced, and the internal protocone is reduced or absent.

In Protocetus the transition to life in the water is certainly far advanced, but not so far that the general construction of the original land form is entirely effaced. The obvious distal thickening of the antero-posteriorly widened transverse processes on the sacral vertebra indicates the retention of a fairly well-developed pelvis, but does not necessarily imply the presence of a functional hindlimb. The strong outward and downward curvature of the transverse processes on the hinder lumbar vertebrae indicates that the ventral muscle mass was relatively weak, although the area for the upper muscle mass was correspondingly enlarged. The conformation of the anterior dorsal vertebrae agrees quite closely with corresponding vertebrae of Zygorhiza kochii, but the hindermost dorsals although possessing unusually large metapophyses lack transverse processes. The nearly vertical position of the facets on the postzygapophyses of the hinder dorsal vertebrae and of the lumbar vertebrae is an additional characteristic peculiarity of the vertebral column. The cervical vertebrae of Protocetus likewise exhibit a remarkable resemblance to those of upper Eocene archaeocetes. In Dorudon and Zygorhiza, for instance, the construction of the atlas is quite similar to that of Protocetus, inconsequential alterations in the inferior transverse processes of the third and fifth cervicals have been made, but the sixth cervical with its elongated ventrally directed inferior transverse processes exhibits very little if any remodeling.

Since, however, such parts of the skeleton as are known for the lower middle Eocene Protocetus seem to indicate that it is well adapted for a pelagic life, it is by
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no means certain that its immediate predecessors were descendants of any Tertiary land mammal. Such a rapid remodeling of the body during early Eocene is inconceivable, even though a complete change in the mechanical conditions of life required corresponding structural changes for an effective adaptation. The fact that all of the upper Eocene archaeocetes, which are known from more adequate skeletal remains, are so well adapted for a marine life indicates that their geological history extends back into the Mesozoic era.

Let us consider for a moment some of the possible reasons which induced the forebears of the Archaeoceti to take to the water. It is fairly certain that at the close of the Age of Reptiles all the groups of the great marine reptiles, with the exception of the crocodiles, had for some inexplicable reason become extinct (Andrews, 1908, p. 211) so that with the exception of the fishes and the crocodiles no competitive vertebrates frequented the Eocene seas. In consequence of these conditions, if any terrestrial or swamp-dwelling form adopted a pelagic life, freedom from competition and possibly from enemies would offer exceedingly favorable conditions for its rapid spread and multiplication. Whether or not its progeny found a safe refuge in the water from more active predatory types or an abundance of readily procured food in shallow water along the shores, food-getting no doubt played a prominent rôle during the initial stages of their adaptation to an aquatic life.

Assuming then that the archaeocetes are offshoots of some terrestrial predatory type, the next question is, do we find any evidence for such an ancestry in the dentition of the oldest known species? This may be answered in the affirmative, for cheek teeth in the upper jaw of the middle Eocene Protocetus have a trigonal crown and three roots. Predatory land mammals twist or tear off the flesh of their prey piece by piece, and trigonal teeth seem to fit best the requirements for the chewing of flesh. On land as pointed out by Döderlein (1921, p. 54) the prey of a predatory mammal, if of sufficient size, will drag while being carried to some convenient spot either to be devoured at leisure or hidden for a subsequent meal. In water, the natural buoyancy of the medium would tend to support the captured prey to some extent, but the prey could not be hidden for future consumption. Hence new prey must necessarily be procured for each meal. In water a flesh eater with trigonal teeth would no doubt feed upon fish or prey which did not possess some sort of an effective protective covering, such as a hard shell or spiny armature. A mammal with trigonal cheek teeth dwelling in water necessarily must feed upon prey which is small enough to be held in the mouth while it is being chewed. The trigonal type of cheek tooth served its purpose, while the animal was relatively small, for it is well adapted for twisting and chewing flesh. When the animal attained a larger size, the food requirements increased in proportion. Feeding periods would be lengthened, if the animal persisted in feeding upon such small prey, and ultimately it would reach the limit of its endurance unless corresponding changes in the bodily metabolism were brought about. Since every animal is a physiological unit, it therefore follows that any impairment of an essential structure will affect to some degree, temporarily at least, the metabolism of the whole body. Mechanically necessitated structural changes are thus closely
tied up with physiological requirements of the body. Thus the acquisition of high-crowned cheek teeth with serrated cutting edges by the large-bodied warm-blooded archaeocetes of the upper Eocene seems to be directly correlated with some change in food habits. This series of large shearing cheek teeth in the upper and lower jaws enabled the animal to tear or cut its prey into morsels small enough to be swallowed and consequently much larger prey could be sought.

Fraas (1904a, p. 210) likewise postulates on adaptive transformation of the dentition of Protocetus to that characteristic of later Archaeoceti, during which some of the teeth lost most of their function of crunching and tearing tough meat, and were remodeled for the grasping and holding of prey, since that function had been lost by the remodeled forelimbs. The anterior teeth became better fitted for grappling, and the development of serrated cutting-edges on the hinder cheek teeth increased the shearing effectiveness of that series.

Fraas has suggested Protocetus atavus as the probable ancestor of all later archaeocetes, but this species does not entirely meet the required conditions for a progenitor of the larger archaeocetes. Protocetus does seem to stand directly ancestral to Dorudon and Zygorhiza in all details of its cranial construction, but the latter exhibit a considerable degree of progress in skull, dentition, and skeleton.

PAPPOCETUS

It is not unlikely that further exploration in the upper Lutetian clay of the Omobiala District of southern Nigeria will eventually result in the acquisition of additional skeletal remains of Pappocetus lugardi (Andrews, 1920). Imperfect mandibles belonging to two individuals of this middle Eocene archaeocete reveal that the lower ramus is more massively constructed than that of Dorudon osiris and unlike the latter the ventral border beneath the hinder end of M2 turns upward for a short distance, forming a step-like notch on the inferior profile when the mandible is viewed from the side. One of the most obvious peculiarities of Pappocetus is the marked upturning of the anterior end of the mandible, the upward bent portion corresponding to the region of the symphysis. It is quite possible that this anomalous peculiarity is fortuitous and the result of crushing.

Both mandibles belonged to immature individuals, for the hindermost molars are not cut in either specimen. The skull to which they belonged was considerably larger than that of Protocetus atavus, which occurs in deposits belonging to the lower Lutetian stage, and was at least as large as those of large individuals of the upper Eocene Dorudon osiris. The cheek teeth in these mandibles are especially interesting on account of their carnivore-like characters. The hinder deciduous premolars and all of the molars have two roots and possess a well-defined cingulum, but lack distinct vestiges of the inner portion of the crown. The presence of three distinct accessory cusps on the hinder cutting edge of Dpm3 seems to foreshadow the serrated crown of later archaeocetes. The crowns of the remaining cheek teeth are wholly unlike those of any known archaeocete. Each of the three molars has a large anterior principal cusp and a smaller posterior cusp. The lateral compression of the molar crown has not as yet effected the construction of a conspicuously higher principal cusp, the corresponding reduction of the posterior cusp,
and the development of a serrated hinder cutting edge. In contrast to archaeocetes from later geological horizons, the second lower incisor judging from the alveolus is relatively much larger.

The conclusion seems therefore warranted, subject to the limitation that mandibles are alone available for consideration, that the cheek teeth represent a slightly more advanced stage of specialization than those of the lower middle Eocene Protocetus.

EOCETUS

It is obvious that the cheek teeth of Protocetus atavus represent one of the end stages in the reduction of the inner portion of the trigonal crown. It is quite probable also that Protocetus is a middle Eocene representative of only one of several lines of descent in the Archaeoceti. The occurrence of a considerably larger archaeocete in the same geological series in the Mokattam hills near Cairo, Egypt, but in a horizon overlying the one in which Protocetus was found, lends some support to the view that at least two lines of descent existed on the north coast of Africa during middle Eocene time. To the last-mentioned archaeocete, Fraas (1904a) gave the name Eocetus schweinfurthi.

As compared to Protocetus atavus, the skull of Eocetus schweinfurthi is extraordinarily large. This skull is at least 120 mm. longer than the largest available skull of Dorudon osiris and about 250 mm. shorter than the best-preserved skull of Prozeuglodon isis. In general construction, the skull of Eocetus schweinfurthi corresponds quite closely with skulls of the larger archaeocetes from the succeeding horizons of the middle and upper Eocene. This skull has a high supraoccipital shield bounded by prominent lambdoidal crests, a remarkably high sagittal crest, and greatly enlarged temporal fossae, and the lateral extension and widening of the supraorbital processes of the frontals has reached the stage characteristic of all later archaeocetes. The skull of Eocetus schweinfurthi approaches that of Prozeuglodon isis in the position of the dorsal narial fossa, although this fossa is abruptly closed anteriorly. The molariform cheek teeth exhibit a remarkable resemblance to those of Protocetus and M3 apparently possesses the inner (third) root. The principal cusp of each cheek tooth is relatively higher than in Protocetus and has not as yet acquired steplike cusps on the anterior and posterior cutting edges. The development of these accessory denticles is, however, foreshadowed in the presence of a crenelated carina on the cutting edges of the molar crown. The inner portion of the crown of the hinder premolars and of the molars has been lost or at least is reduced to a vestige.

The lumbar vertebrae (Stromer, 1903c, pp. 83–85) found in the same horizon as this skull and likewise referred to Eocetus demonstrate conclusively that the vertebral column of the larger archaeocetes had already undergone extensive remodeling near the beginning of the middle Eocene period. This remodeling resulted in the enlargement and excessive elongation of the centra of the hinder lumbar vertebrae, the enlargement of the metapophyses, the reduction of the postzygapophyses, the recession of the prezygapophysial facets, and the widening of the transverse processes.

Eocetus is considered by Fraas (1904a, p. 219) to represent a stage intermediate between Protocetus and Zeuglodon [= Prozeuglodon + Dorudon]. As regards
the progressive specialization of the dentition, *Eocetus* may well represent a stage intermediate between the *Protocetus* type of cheek tooth and that of an immature individual of *Prozeuglodon isis* [= *Prozeuglodon atrox*]. But the most conclusive proof that *Eocetus* is not directly related to the smaller archaeocetes of the upper Eocene is found in the lumbar vertebrae, which are wholly unlike in construction those of either *Dorudon* or *Zygorrhiza*. The subsequent remodeling and the elongation of the centra of the *Eocetus* type of vertebra might result eventually in the development of the excessively elongated lumbars possessed by *Prozeuglodon isis* and *Basilosaurus cetoides*.

**PROZEUZGLODON**

Some of the subsequent stages in the progressive specialization and perfection of the cheek teeth are found in archaeocetes from the succeeding geological horizons of the upper Eocene. At the beginning of the upper Eocene, much larger archaeocetes with a more specialized type of cheek teeth make their appearance in the Birket-el-Qurn stage of the Fayum. The largest of these is *Prozeuglodon isis* (Andrews, 1904), whose skull alone measured nearly four feet in length. The dorsal narial fossa on the skull of this species is in approximately the same relative position as on the skull of *Protocetus atavus*, its hinder limit being marked by the anterior ends of the nasal bones which terminate at the level of the hinder edge of the crown of Pm1, while in *Protocetus* the anterior ends of the nasals are at the level of the center of the crown of Pm1. Among the structural peculiarities of the skull of *Prozeuglodon isis* not clearly shown on the skull of *Protocetus atavus* are the presence of an elongated compressed antorbital foramen in each maxillary, a distinct lachrymal bone and lachrymal duct, as well as an accentuation of the lateral descending processes on the basioccipital. The pterygoid fossa for the accessory air sinus of the middle ear are developed, however, in the typical cetaceous condition. The mandible has the elongated form of most Recent odontocetes, with a symphysis extending backward to level of middle of Pm2, a relatively large coronoid process, and the strange gaping hinder entrance to the alveolar canal; the condyle, furthermore, is placed low and faces backward.

A skeleton of *Prozeuglodon isis*, including a considerable portion of the vertebral column, the ribs, the sternum, and the forelimb with the exception of the manus, was found in 1906. One important alteration in the axial skeleton is that the sacral or sacrals are not differentiated from the hinder lumbars by having the transverse processes distinctly modified for attachment to the pelvis. Judging from the fact that the largest elongated lumbar vertebrae of this species measure 12 inches (310 mm.) in length, one may conclude that the complete skeleton measured more than 40 feet in length. The sternum consists of several sections, the anterior one being unusually large and heavy. It is interesting to note that the scapula is essentially whale-like, and that its conformation is precisely like that which might be expected if it represents a stage in the series through which those of Recent cetaceans have passed. The supraspinous fossa is smaller than is
the case in the creodonts, but is much larger than in any Recent whale. There is a fossa for a strong teres muscle on the glenoid border of the scapula, the acromion is wide and greatly elongated, and the slender coracid process is quite prominent. The humerus, as contrasted with those of creodonts, has not been markedly altered, since it has distinctly separated greater and lesser tuberosities and a well-developed trochea, but the prominent deltoid crest extends much farther distally. The radius and ulna have correspondingly well-developed surfaces for articulation with the humerus and the ulna has a rather large olecranon, all of which contribute to the formation of a hinge-like elbow joint; the distal ends of the radius and ulna have facets for articulation with the carpal bones.

The stage in the remodeling of the cheek teeth represented by Prozeuglodon isis is far in advance of that of either Eocetus or Protocetus. As compared with Eocetus, Pm1 has become single-rooted like the incisors and the canine. With the exception of Pm1, all of the upper premolars and molars have acquired distinct accessory cusps on the anterior and posterior cutting edges of the crown. The cheek teeth of the adults have not more than two roots and the postero-internal cusp has entirely disappeared. The hindermost molar, M3, which is small in Protocetus, is absent in Prozeuglodon isis. Eleven cheek teeth are present in each mandible. The incisors, the canine, and Pm1 are more or less alike in general appearance and have a simple conical laterally compressed crown; Pm2, Pm3 and Pm4 have a compressed crown which is serrated on the anterior and posterior cutting edges; M1, M2 and M3 also have a laterally compressed crown, the anterior edge being grooved vertically and the hinder edge strongly serrated. The tooth succession is vertical like in terrestrial carnivores and the deciduous dentition is not replaced until the animal attains almost adult size.

Two skulls and three isolated cervical vertebrae, which were found in the lower Birket-el-Qurun deposits west of the lake in the Fayum, formed the basis for Prozeuglodon atrox (Andrews, 1906, p. 243). Stromer (1908b, p. 128) was undoubtedly correct in concluding that these skulls belonged to immature individuals of the previously described Prozeuglodon isis. The deciduous dentition present in these skulls is of especial interest because some of the cheek teeth still possess remnants of the Eocetus-Protocetus crown. The serrated crowns of the two hinder upper premolars and the first upper molar have an enamel covered postero-internal buttress supported by a third root, and this buttress is apparently a remnant of the postero-internal cusp.

The cheek teeth of Prozeuglodon have been markedly remodeled by lateral compression and antero-posterior elongation of the crown. The molars in the upper jaw as well as the three hinder premolars in the upper and lower jaws have acquired a series of accessory denticles on their sharp cutting edges. Thus the original trigonal crown of the cheek teeth of the older archaeocetes has been successively remodeled by lateral compression, by the complete reduction of the inner portion of the crown, and by the development of a strongly serrated high principal cusp admirably adapted for shearing.
BASILOSAUROID

The aberrantly specialized *Basilosaurus cetoides*, which so far as known is restricted to the upper Eocene Jackson formation (Yazoo clay and Ocala limestone) of southern United States, attained a length of 55 to 65 feet and the skull did not constitute more than one-thirteenth of the total length of the animal.

The complete cervical series of the larger archaeocetes is known for the first time in *Basilosaurus cetoides* and, although comparison of these vertebrae with those of the earlier types shows that little remodeling has taken place in the former, the peculiar construction of the whole neck is nevertheless quite interesting. The five anterior cervical vertebrae are curiously interlocked, for besides the normal articulating pre- and post-zygapophysial facets, the atlas has a robust backward projecting hypapophysis, the neural spine of the axis overhangs in front the atlas, and behind the neural spines of the third and fourth cervicals. The transverse processes of the third, fourth, and fifth cervicals are lengthened and have a slender ventral projection which is directed obliquely forward.

The thorax is relatively slender in proportion to the length of the entire skeleton. From the first to the eighth in the dorsal series the progressive lengthening of the centrum is gradual, but beginning with the ninth and again with the eleventh dorsal the length of the centrum is abruptly increased, resulting in a condition unique among mammals. The diapophyses are quite short on the anteriormost dorsals, but they increase in length toward the middle of the anterior half of this series. The ninth dorsal is the transitional vertebra. On the tenth and eleventh dorsal vertebrae no obvious transverse processes are developed. The heads of the corresponding ribs articulate in circular depressions on the lateral surfaces of the ninth and tenth centra; but on the centrum of the twelfth dorsal rudimentary nodular-like transverse processes are present. The two hindermost dorsal vertebrae have acquired strong transverse processes on a line with and similar in conformation to those of the lumbar vertebrae.

Cope (Lucas, 1895, p. 746) believed that the regular articular end of the first sternial segment of *Basilosaurus* indicated that the animal was in the habit of rearing the front part of the body out of the water, and that this assumption was supported to some extent by the articular relations of the dorsal vertebrae. The relations of the articular facets are such as to permit movement from side to side, as well as up and down, and this in turn indicates the presence of rather thick intervertebral cartilages. Flexibility in the dorsal series of vertebrae, associated with a relatively short sternum, has also been interpreted as an adaptive alteration for resisting the temporary effects of compression on the thorax when diving. The ribs have been greatly strengthened and have acquired a club-like distal enlargement. The marrow cavity of the rib has been reduced, resulting in a condition known as pachyostosis. Nopcsa (1923; 1926, p. 640) suggests that pachyostosis is caused by a deficiency in the air supply. If this interpretation is correct, we may then assume that the respiratory mechanism of these archaeocetes was not as yet adequately adjusted for prolonged submergence.
This large archaeocete has an elongated trunk and tail, a relatively short neck, thoracic and lumbar vertebrae with low neural spines and short transverse processes disproportionate to the length of the skeleton, and zygapophyses of all the trunk vertebrae, with the exception of the first eight dorsals, separated by increasing intervals proportional to length of centrum. The centra of the hinder dorsal, the lumbar, and the sacral vertebrae are greatly elongated, although the neural arches and the neural spines have remained relatively short. This specialization is unique among mammals, for the greater part of the vertebral column is articulated only by the centra, the opposing zygapophyses being separated by too wide an interval to function in a normal manner. The interval separating the hinder basal angle of the neural spine from the end of the metapophysis of the following vertebra equals about half the length of the centrum. In the case of the Recent Globicephala melaena, which has the metapophyses reduced to vestiges on the seven anterior lumbar vertebrae and missing entirely on the remainder of the lumbar and the caudals, this interval is equivalent to about half the antero-posterior diameter of the neural spine in the case of the anterior lumbar. Posteriorly the interval progressively increases so that between the third and fourth caudals it is equal to width of the neural spine. The extremities of the transverse processes of the two sacral vertebrae of Basilosaurus are distinctly roughened, indicating that some sort of a ligamentary connection was retained with the degenerated pelvis. The existence of a tiny femur discloses the functionless condition of the hindlimb. One of the most unusual specializations in Basilosaurus is the thickening of the laminated outer circumferential layer on the centra of lumbar and of caudal vertebrae. In some instances this layer is more than an inch in depth.

The tail of Basilosaurus cetoides constitutes one-third of the total length of the skeleton. The chevrons are not very large and they never rival the neural arches in size. The anteriormost caudal vertebrae have assumed the general appearance of the sacral and lumbar vertebrae. On the anterior half of the tail, the centra have been elongated, heavy flattened transverse processes and enormous metapophyses have been developed, the neural arch has been lowered, the laterally compressed neural spines have been shortened, and all trace of articulating zygapophyses has been lost. Since the transverse processes of the caudal vertebrae of Basilosaurus cetoides are directed obliquely downward and outward, there is reason to believe that the inferior muscle mass of the tail was weaker than the upper mass. The caudal muscles, which have their origin in part on sacral and caudal vertebrae, in conjunction with the back muscles required an increased area along the vertebral column for attachment and this has been effected by an enlargement of the centra of these vertebrae. The hindermost eight caudal vertebrae are atrophied as though they had been embedded in a caudal fin.

Howell (1930, p. 198) concluded that these structural details indicated “that the spinal musculature was not developed to a point where it could handle a caudal fluke of a Recent cetacean type,” and that these details permitted great mobility
to allow for the serpentine motions of the tail; furthermore that the propulsive mechanism must have been in the nature of a pair of symmetrical and continuous lateral fin-folds extending in a fore-and-aft direction along most of the length of the tail.

Without attempting to follow out in detail all the implications of Howell’s assumption, it may suffice to call attention to a few pertinent structural details of the axial skeleton. As will be noticed from an examination of the caudal series of *Basilosaurus cetoides*, the eight hindermost caudals are in form and degree of atrophy like the corresponding vertebrae embedded in the caudal flukes of Recent Cetacea. As regards the length ratios of the several regions of the axial skeleton, the percentages given in the following table show that *Basilosaurus cetoides* and *Sibbaldus musculus* are not conspicuously unlike. The relative length of the lumbar region of one of the Recent dolphins (*Lagenorhynchus acutus*) exceeds that of *Basilosaurus*. All of the skeletons measured are exhibited in the United States National Museum. The probable error in restoring the amount of intervertebral substance in the mounted skeletons of the fossil and Recent cetaceans is assumed to be approximately the same in each case. Therefore, for the purpose of the following comparisons the extent of the error may be disregarded.

It is obvious that the available area for origin of the caudal muscles on the *Basilosaurus* skeleton is relatively much smaller than it is on skeletons of Recent Cetacea. As an index to the size of the area for origin of the caudal muscles, the ratios of the maximum vertical and of the transverse diameter of the anteriormost caudal vertebra to the total length of the caudal series were computed for *Basilosaurus cetoides* and *Sibbaldus musculus*. In the case of *Basilosaurus* the maximum vertical diameter, tip of neural spine to ventral face of centrum, of the anteriormost caudal equals approximately 6 per cent and the maximum distance between the extremities of the transverse processes equals about 8.7 per cent of the total length of the caudal series of vertebrae. The corresponding percentages for *Sibbaldus*
musculus are, respectively, 15.6 and 13.85. As regards the anteriormost lumbar vertebra of Basilosaurus, the maximum vertical diameter, tip of neural spine to ventral face of centrum, equals about 3.3 per cent, and the maximum distance between the extremities of the transverse processes equals about 3.7 per cent of the total length of the combined lumbar-caudal series of vertebrae. The corresponding percentages for Sibbaldus musculus are, respectively, 8.13 and 11.3.

These estimates show that the caudal musculature of Basilosaurus was necessarily less powerful than that of Sibbaldus. Nevertheless there is no valid reason for assuming that these muscle masses were not strong enough to manipulate caudal flukes much smaller than those of Sibbaldus.

The body of Basilosaurus was relatively much more slender and the head conspicuously smaller than in Sibbaldus. Consequently a less powerful propelling mechanism would suffice. In the case of Basilosaurus the maximum vertical diameter of the thorax, extremity of neural spine of fifth dorsal vertebra to ventral face of mesosternum, equals about 6.7 per cent of the total length of the entire skeleton. For Sibbaldus, the maximum vertical diameter of the thorax at level of the fourth dorsal vertebra equals about 13 per cent of the total length of the entire skeleton. The external and skeletal measurements of a blue whale of approximately the same length as the Basilosaurus skeleton show that the bulk of the whale's entire body in cubic feet is at least five or six times as great as that of the basilosaur.

It is quite likely that the skeletal ratios computed by Fraas (1904a, p. 215) are inaccurate. His conclusions are based on an erroneous assumption that the several regions of the vertebral column comprised fewer vertebrae than have been shown to exist in these regions in the Basilosaurus cetoides skeleton and in the similarly constructed Zygorhiza kochii skeleton.

Assuming that the vertebral column of Protocetus atavus consisted of 7 cervicals, 15 dorsals, 13 lumbars, 2 sacrals, and 20 to 22 caudals as in Basilosaurus cetoides and Zygorhiza kochii, and computing in the case of Protocetus the lengths of the centra of the missing vertebrae from the relative lengths of those that are known, we find that the ratio of length of thorax to entire skeleton is approximately the same (19 ± per cent) in these three archaeocetes. We observe also a progressive decrease in the relative length of the head to that of the entire skeleton, since it comprises 24 per cent in Protocetus, 16.8 per cent in Zygorhiza, and 7.4 per cent in Basilosaurus. Similar ratios are revealed by the cervical series. These do not necessarily indicate any pronounced shortening of the neck itself although there is some evidence of an antero-posterior compression of the centra, the neck comprising approximately 8 per cent of the entire skeleton in Protocetus, 5 per cent in Zygorhiza, and 2.4 per cent in Basilosaurus. The lumbar-sacral series constitutes approximately 24+ per cent of the entire skeleton in Protocetus and Zygorhiza in contrast to 36.6 per cent in Basilosaurus. The tail, however, was probably relatively shorter in Protocetus than in either Zygorhiza or Basilosaurus, since the computed length of the caudal series does not exceed 24 per cent of the total length of the skeleton, while it is 34 per cent in both of the latter.
DORUDON AND ZYGORHIZA

Among the upper Eocene representatives of the smaller archaeocetes of the Old and the New Worlds, two genera (Dorudon and Zygorhiza), each represented by two or more species, are known rather completely as to the skeleton. One of the smaller archaeocetes, Dorudon intermedius, occurs in the Birket-el-Quru deposits of Egypt along with Prozeuglodon isis. It has a skull approximately 31 inches (795 mm.) in length, and its entire skeleton was probably not more than 16 feet long. In the overlying beds, which belong to the Qasr-el-Sagha stage of Egypt and which are correlated with the Bartonian stage of England, skulls of three types of small archaeocetes (Dorudon osiris, D. stromeri, and D. zitteli) have been recognized. The largest of these is Dorudon osiris and for this species skulls ranging from 29 inches (751 mm.) to 33 inches (838 mm.) in length have been described. These smaller archaeocetes exhibit progress in several directions in the remodeling of the hinder surface of the skull.

In the case of Dorudon intermedius of the Birket-el-Quru stage, the high occipital shield is imperceptibly constricted near the middle, the ratio of maximum width to height above foramen magnum being approximately 62 : 100, the lateral portions of the lambdoidal crests are less strongly folded backward than in D. osiris, the occipital condyles and the foramen magnum are fairly large, and the braincase is moderately vaulted.

As regards Dorudon stromeri of the Qasr-el-Sagha stage, the broad nearly vertical occipital shield is not constricted near the middle (its width being approximately equal to its height above foramen magnum), the lateral portions of the lambdoidal crests are not sharply folded backward, the occipital condyles and the foramen magnum are relatively large, and the braincase is vaulted.

In the more specialized Dorudon osiris of the Qasr-el-Sagha stage, the high occipital shield is conspicuously pinched-in near the middle, the ratio of minimum width to height above foramen magnum being approximately 44:100, the lateral portions of the lambdoidal crests are sharply folded backward, the occipital condyles and the foramen magnum are considerably smaller, the sagittal crest is higher, and relatively little evidence of vaulting of the braincase persists.

According to Andrews (1923, p. 651), the remodeling of the archaeocete skull during upper Eocene time culminated in the Dorudon osiris type of occiput and the following correlated alterations in the cranium: (1) A pronounced narrowing of the occipital surface above the foramen magnum, resulting mainly from the backward folding of the prominent lambdoidal crests and an increase in the height of the sagittal crest, these modifications bringing about an increase of surface for the attachment of jaw muscles; (2) a reduction in the size of the occipital condyles and the foramen magnum; (3) a decreasing convexity of the lateral cranial walls accompanying the depression of the upper portion of the brain; and (4) an increase in the length and slenderness of the rostrum. The stage in the recession of the dorsal narial opening is identical in Dorudon intermedius, D. stromeri, and D. osiris.
The small archaeocete, *Zygorhiza kochii*, that occurs in the upper Jackson formation of North America has a skull nearly 33 inches (830 mm.) in length and a skeleton about 16 feet (4.93 meters) in total length. The upper cheek teeth, while similar to those of *Dorudon*, are characterized by the presence of a conspicuous epiplerated cingulum. In most details, the conformation of the skull is quite similar to that of *Dorudon*, but the conformation of the occipital shield has not been duplicated among any of the recognized species of that genus.

As regards both *Dorudon* and *Zygorhiza*, the skull is elongated in both facial and cranial regions, the rostrum is slender, the cranium is rather wide posteriorly and more or less vaulted, no air cells are present in the bones inclosing the cranial cavity, and the basi-cranial axis is horizontal, not bent upward as in the Recent members of the Odontoceti. The endocranial casts show that the olfactory peduncle is extraordinarily long and slender, the cerebrum is narrow, and the cerebellum is very short and broad. The narial passages are elevated anteriorly, the narial muscles are obviously well developed, and the lateral maxillary sinuses are located in front of and not beneath the forehead. The lacrimal is located anterior to the orbit and the large open lacrimal duct is completely outside of the orbit. The inferior process of the maxillary bearing the molars is separated from the palatal surface by the deep fosae which lodge the crowns of the lower molars. On the anterior end of the rostrum the pits for the reception of the apices of the lower single-rooted teeth are located on the outer side of the grasping teeth, while the pits for the lower cheek teeth are on the inside of the upper serrated shearing teeth, showing that the upper and lower tooth series cross over when the jaws are closed. The milk teeth are shed at a relatively late growth stage. The dentition is heterodont. **I** to **Pm2** are separated by a diastema, and **Pm3** to **M2** form a closed series. The cheek teeth have high crowns, the principal cusp being serrated on its anterior and posterior cutting edges except in the case of the lower molars; these are serrated only on the hinder cutting edge. All of the teeth have the usual dentine, cement and enamel. As regards the transformation of the cheek teeth, *Dorudon osiris* is far advanced, for **Pm1** has become a true rake-tooth, **Pm2** to **Pm4** have robust principal cusps, but on the molars this cusp has been shifted farther forward, while **M3** has been suppressed. The mandible is elongated, the symphysis is not firmly ankylosed, and the coronoid process is rather large.

The relationship of *Dorudon* and *Zygorhiza* to *Basilosaurus* appears to be a remote one, despite a remarkable similarity in the construction of the skull and the dentition, since the thoracic and lumbar regions of these smaller archaeocetes have not been altered by a lengthening of the centra of these vertebrae. These relatively short-bodied archaeocetes have a stout neck. Their thoracic and lumbar vertebrae have high neural spines and well-developed transverse processes.

As regards the neck, the atlas has a large hypophyseal process and has nearly vertical laterally projecting transverse processes pierced antero-posteriorly at the base by small arterial canals; the axis possesses a well-developed conical odontoid process and its transverse processes are pierced at the base by a foramen; the third
to sixth cervicals, inclusive, have large vertebral arterial foramina at the base of the transverse processes; the sixth cervical has unusually long ventrally directed transverse processes. On the seventh cervical the robust laterally projecting lower transverse processes persist and the upper transverse processes are reduced to a lateral buttress on the pedicle of the neural arch. The first rib articulates in part with a postero-superior facet on the lateral surface of the centrum of the seventh cervical vertebra.

The dorsal series consists of fifteen vertebrae. As contrasted with Protoctetus atavus, the most radical alteration that has been effected in the construction of the thorax of the smaller upper Eocene archaeocetes seems to have been the development of transverse processes on the six hinder dorsal vertebrae and presumably also a corresponding increase in the number of ribs. The posterior dorsals possess fairly long transverse processes which bore single-headed ribs on their extremities. The neural spines of the dorsal vertebrae differ noticeably among themselves as to their slant, those on the anterior dorsals sloping strongly backward, those on the hindermost dorsals being almost upright. The ninth dorsal vertebra is the transitional vertebra, for the diapophysis is reduced to a vestige on the lateral face of the pedicle of the neural arch, while the parapophysis is still rudimentary.

All of these small archaeocetes have lumbar vertebrae with centra of normal dimensions, but the zygapophyses of successive vertebrae on the hinder half of this series apparently do not articulate. While the centra are not in any direction strikingly altered in form as compared to those of Protoctetus atavus, the transverse processes of the hinder lumbar and sacral vertebrae have lost their outward and downward curvature and have become almost straight, the metapophyses have been elongated, but the neural arches have undergone relatively little change either in construction or in position. The sacral vertebrae are not differentiated from the lumbar vertebrae by having transverse processes modified for the attachment of the pelvis.

The shifting of the articular facets on the postzygapophyses from the nearly vertical position found on the hinder dorsals and lumbar vertebrae of Protoctetus to the more or less horizontal position of the same facets on the corresponding vertebrae of Zygorhiza and Basilosaurus is no doubt another aquatic specialization, since the last-mentioned condition characterizes most Recent cetaceans.

The caudal vertebrae are rather robust, although the centra of the anterior ones are not conspicuously elongated. In front of the middle of the caudal series the transverse processes of some of the vertebrae are perforated at the base by a foramen. The metapophyses are elongated on the anterior caudals, but are progressively reduced from the first to the fourteenth in this series. The neural spine rapidly diminishes in height from the first to the fifth caudal and is missing entirely on the seventh caudal.

These smaller archaeocetes must have had a propelling mechanism of considerable strength, for among living cetaceans the most active swimmers have a
vertebral column of this type. The conclusion can be drawn that these short-bodied archaeocetes propelled themselves by upward and downward strokes of the caudal flukes, after the manner of living whales. They were undoubtedly powerful swimmers, capable of diving or turning at will, and were equipped with a dentition admirably fitted for seizing and holding their prey.

Adaptation to life in the water brought about many changes in the bodily organization of archaeocetes. Certain organs were remodeled to conform to the new use to which they were put, while others were lost. Efficient organs for propulsion were required to facilitate movement in water. Hence the motive power was transferred from the limbs, which ordinarily serve as ambulatory organs for land mammals, to powerful caudal flukes at the hinder end of the body which became the propelling mechanism, the hindlimbs became vestigial, and the forelimbs were changed into steering and balancing organs.

The elimination of all structures which offered resistance to the water became necessary. Since there are definite stream-line requirements for progression in water, both as regards form and propelling mechanism, it is of interest to note that the archaeocetes had already by the middle Eocene acquired a torpedo-shaped body. An excellent illustration of convergence in external body form brought about by mechanical requirements of an aquatic life is found in the torpedo-shaped bodies of pelagic vertebrates (Abel, 1924, pp. 94–102). The body may resemble either an elongated torpedo or a short stout torpedo. The typical short torpedo shape is met with in fishes, ichthyosaurs, dolphins and presumably also in the short bodied archaeocetes. The gigantic *Basilosaurus* and some of the more primitive ichthyosaurs, such as *Cymbospondylus* (Abel, 1924, p. 16), have the elongated torpedo type of body.

It is readily apparent that any mammal during the initial stages of its adaptation to life in the water must experience some difficulty in moving in a medium as dense as water. The limbs no longer support the weight of the body, since it is buoyed up to some extent by the water, but must be employed for propelling the animal to the surface of the water and for effecting a forward thrust of the body. Whatever mechanical device is employed to propel the body through the water, during motion the head is subjected to adverse pressure of the relatively stationary water which is piled or pushed up in front as the animal progresses forward, and this pressure increases with the speed of the animal. This necessitates some sort of a "cut-water," if progression is attempted for any appreciable length of time and at a fairly rapid pace. In most cetaceans, a slender or pointed rostrum is developed to facilitate passage through the water, though in some of the larger forms it may be lost or masked by other external stream-line alterations. The manner in which movement through the water is effected is more or less the same in all living cetaceans, that is by up and down movements of the transverse tail fin, the forelimbs being employed mainly for steering and balancing.

Any animal which employs its tail for propulsion must have an anterior steering mechanism. The archaeocete neck is relatively so short that it, in conjunc-
tion with the head, would constitute an inefficient mechanism for such a purpose. Thus a separate mechanism for steering is required and the most available structure is the forelimb. This has been remodeled to conform to the use to which it is put, that of balancing and steering. Therefore a ball and socket articulation between the humerus and the shoulder blade has been retained. These archaeocetes have a forelimb that retains many of the characters of land mammals. On comparison it will be observed that the forelimb of one of the small archaeocetes (*Zygorrhiza kochti*) has a limb which in many of its details exhibits a remarkable resemblance to that of the fur seal. Judging from its peculiarities, however, one might infer that structurally it had passed beyond the adaptive stage present in the forelimb of the fur seal (*Callorhinus alaskanus*). The shoulder blade has already acquired many of the peculiarities of Recent cetaceans, while the humerus has held more closely to the conventional form, retaining a prominent deltoid crest, greater and lesser tuberosities, and a typical hinge-like but non-rotary elbow joint. The elbow joint of all known archaeocetes is capable of flexion and extension, but nevertheless its conformation leads one to believe that pronation and supination was greatly reduced. The position as well as the prominence of the lesser tuberosity and the great length of the deltoid crest of the humerus are unquestionably correlated with the functional use of the subscapularis and deltoid muscles, and may indicate that the flipper was normally flexed and presumably held close to the body. The slender ulna retains a distinct olecranon process, and the bent radius is slightly widened distally.

The wrist bones of these archaeocetes are noticeably flattened. Since the dorsal and plantar faces of these carpals are quite rugose, there is reason to believe that the lower portion of the forelimb had lost its synovial character and had become more or less fibrous. The restriction of flexibility of the wrist prevented it from being bent backward when the flipper was elevated. In Recent cetaceans the flipper has been additionally strengthened by fibrous joints.

The elongation of the segments of each finger and the regressive condition of the ball-and-socket contacts between the several phalanges, taken in conjunction with the flattening of the carpus, all indicate that by late upper Eocene time the forelimb of these archaeocetes had passed beyond the stage of development now found in the Otariidae, although the flipper may have been somewhat similar in shape. The fibrous intersosseous tissue in conjunction with the type of articular joint retained by *Zygorrhiza* would give considerable elasticity to the flipper, but would tend to prevent it from being utilized for progression on land or for holding food that is being eaten. In the case of the sea-lion, the retention of certain terrestrial structural features in the forelimb seems to be intimately related to the degree of connection they have retained with the land, for the young of all Otariidae are born on land.

The hindlimbs of all these archaeocetes, with the exception of the gigantic *Basilosaurus*, are unknown, and in *Basilosaurus* they are reduced to a vestigial condition.
On the whole, the skeletons of these Eocene archaeocetes were very highly modified to facilitate passage through the water, and the changes noted appear to be directly related to a change in the mechanical conditions of life.

**PLATYOSPHYS**

The several known types of archaeocetes show to what extent the skeleton may be susceptible to alterations that affect the relative length-ratios of the different regions of the axial skeleton, and particularly that in certain types the vertebrae in large sections of the spinal column tend to depart widely from the generalized construction while in others the vertebrae comprising these same sections have retained their original peculiarities more or less intact. It is therefore possible to draw rather definite conclusions respecting the general build of an archaeocete from the peculiarities of isolated vertebrae from the trunk and caudal regions. In the case of the large archaeocete that occurs in the green glauconitic sand in Ukraine, U. S. S. R., belonging to the lower Oligocene Kharkov stage, the skeleton is known at present solely from isolated lumbar, sacral, and caudal vertebrae. Although *Platysphysis paulsonii* has large lumbar vertebrae with elongated centra, the largest of which measured 11 inches in length, articulating zygapophyses have been retained and the transverse processes have been noticeably broadened. On the fifth lumbar (Fedorovsky, 1912, pl. 2, figs. 6–8) the greatly enlarged metapophyses project forward beyond the level of the anterior end of the centrum, while the postzygapophysial facets are located on the under surfaces of two slightly diverging processes that project backward from the base of the neural spine almost to the level of the hinder face of the centrum. The sacral vertebra possesses both pre- and post-zygapophyses and the metapophyses are quite wide. The centra of the anterior caudal vertebrae attain a length of at least 8 inches and the chevrons are rather large. These vertebrae conclusively demonstrate that the lumbar-sacral region was lengthened by the elongation of the centra, that added strength was given to the trunk region by the retention of interlocking zygapophyses, and that the spinal column as a whole was rather solidly built.

The origin of *Platysphysis paulsonii* seems to be far removed from *Basilosaurus cetoides* and the several points of resemblance in the construction of the processes on the vertebrae are merely characteristic heritages from a common ancestral stock. In the case of the gigantic *Basilosaurus cetoides* the trunk region exhibits such a pronounced specialization in a definite direction, that it is entirely beyond the bounds of possibility that its descendants could have possessed lumbar vertebrae which on the one hand retained their large proportions and on the other reverted to the original construction of the older precursors of the archaeocete stock. The type of specialization observed in the vertebrae comprising the trunk region of *Platysphysis paulsonii* renders entirely improbable any direct descent from *Basilosaurus*, but does represent precisely what might be expected to result from a remodeling of vertebrae similar to those possessed by the middle Eocene *Eocetus schweinfurthi* (Stromer, 1903c, p. 84, fig. 1).
KEKENODON

So far as known the archaeocetes did not reach the seas bordering New Zealand until Mid-Tertiary time. With the arrival of *Kekenodon onamata*, the last surviving remnant of an earlier dispersal from the north so far as our present knowledge goes, the archaeocete stock seems to have made a final but futile effort to compete with an increasing variety of more highly specialized predaceous porpoises belonging in or at least related to the family Squalodontidae. The horizon in the calcareous greensand and calcareous sandstone in which *Kekenodon* occurs is limited in vertical extent, and according to Park always occurs at the base of the Waitaki or Ngapara stone. The age of the *Kekenodon* horizon is here considered to be lower Miocene.

The New Zealand archaeocete is of especial interest since some of the cheek teeth still possess the inner root, although the inner portion of the crown has been entirely effaced. The serrate-edged cheek teeth of *Kekenodon onamata* have laterally compressed crowns ornamented with vertical striae, accessory denticles on anterior and posterior cutting edges, and the cingulum either weak or absent. Although the crowns of the cheek teeth are not strikingly altered as compared with those of the upper Eocene genus *Dorudon*, the roots are massive, three or four times as long as the crown. The teeth identified as Pm3 and Pm4 have three roots. The roots of all the cheek teeth are united for a considerable portion of their length and are usually closely approximated at their extremities. The canines are large, almost 6 inches in length, and the medially dilated root curves backward; the sharp-pointed conical crown 1\(\frac{1}{2}\) inches in length is covered with polished enamel which is fluted. The roots of the incisor teeth are gradually enlarged below the neck to about the middle of their length and are attenuated toward the extremity.

Hector (1881) states that the form of the skull can not be determined from the fragments which were found, but that they do "indicate a massive solid jaw, one portion showing the posterior part of the ramus as having a depth of 6 or 7 inches."

No direct line of ancestry for *Kekenodon* has been traced either in the New Zealand Tertiary or elsewhere in the southern hemisphere. The construction of the cheek teeth indicates that the progenitors of *Kekenodon* must have wandered at a relatively early period from the assumed birthplace of the archaeocete stock in the Mediterranean seas toward the south where *Kekenodon* became the surviving representative of an at one time dominant marine group. In order to explain the presence of three-rooted cheek teeth in a Miocene archaeocete it appears necessary to look to some other factor than the mechanical requirements of food-getting and food-mastication. That all of the archaeocetes were predaceous animals is of course evident from their teeth, the anterior ones being adapted for the seizure and retention of slippery prey, and the cheek teeth for shearing. The persistence of the third root on some of the cheek teeth of *Kekenodon* may perhaps best be accounted for by considering the fact that the jaws seem to have been rather massive and thus the roots would be subjected to relatively little crowding.
From an attentive examination of all these archaeocetes, some of which attained partial and others almost complete success as air-breathing water animals, we observe that they had already acquired the fundamental adaptive alterations which were subsequently perfected to varying degrees and in different directions by later Tertiary odontocetes and mysticetes. Under progressively changed conditions and with concomitantly changed habits, the bodies of these archaeocetes were remodeled to such an extent that most of the original morphological details were almost completely effaced.

GENETIC RELATIONS OF THE ARCHAEOCETI

In the following review of arguments presented by paleontologists, comparative anatomists, and embryologists to elucidate the genetic relationships of the Archaeoceti, the Mysticeti, and the Odontoceti, it will be observed that the inconclusiveness of the evidence, on which most of these conflicting views and opinions are based, is attributable in part to the difficulty of distinguishing between homoplasic resemblances to distantly related forms and resemblances which are seemingly common heritages from a more primitive ancestral stock. It becomes increasingly apparent that the genetic significance of homological resemblances and divergences can rarely be appraised with confidence until the general adaptive trend and possible change of function of each organ (Kükenthal, 1922, p. 75) is fully understood and critically analyzed. The distinctions between plastic and implosaic organs are less trenchant in animals like cetaceans which have been subjected to profound physiological, anatomical, and osteological adjustments for habitual life in sea-water. Anatomists and palaeontologists alike have seized upon isolated resemblances of single structures in visceral organs, reproductive tract, brain, and dentition as conclusive proof of the adequacy of the assembled evidence brought forth in support of some particular derivation, notwithstanding the obvious fact that the viscera, particularly the digestive tract, have been altered for the assimilation of a specific kind of food mixed with quantities of sea-water, the reproductive tract has been adjusted for aquatic parturition, the brain has been reshaped in conformity with progressive remodeling of the cranial walls, and the dentition has been remodeled for a specialized kind of food gathering. Alterations of different degrees and in different directions have been effected in all parts of the skeleton, and in Recent cetaceans comparatively little of the original construction has been retained. The progressive loss of generalized characters has been made manifest in the several lines of cetacean descent, though representative types to illustrate all of the successive stages in this evolutionary advance are as yet wholly inadequate for conclusive proof. Documentary evidence illustrating the ascending stages of specialization in each of the several lines of cetacean descent is likewise inadequate.

RESEMBLANCES OF THE ARCHAEOCETI TO THE MARINE REPTILIA

The same general influences which led to mechanically necessitated alterations in the skeleton in isolated groups of marine reptiles, as for instance the ichthyo-
saurs, thalattosaurs, mosasaurs, and dolichosaurs, were again manifested in the remodeling of the archaeocete skeleton. In all these types of marine animals, there is a tendency to remodel the primitive land type of skeleton into a torpedo-shaped body.

Considering the unusually large size and imperfect preservation of the vertebrae studied by Harlan (1834, pp. 402-403), it is not surprising that the presence of a pair of vascular foramina on the dorsal and ventral faces of the centrum misled him into believing that this hitherto unknown animal represented the king of the saurians. Koch (1845b) ignored the published conclusions of Owen (1839) in regard to the mammalian nature of Basilosaurus. It seems incredible today that the absurdities in Koch's attempted reconstruction of a typical reptile skull for Hydrarchos [= Basilosaurus], in which were combined heterogeneous cranial fragments belonging to two genera, should have escaped the notice of some of the contemporary naturalists. Carus (1847, p. 6, pl. 4, fig. 11), who was granted permission to examine this reconstructed skull in his laboratory, likewise undertook a schematic restoration of a reptile-like skull, though it may be said to his credit that he perceived the cranial fragments represented two species rather than two individuals differing in age. Wyman (1845), however, after examining the 114-foot long skeleton of Hydrarchos sillimani exhibited by Koch in New York, published some rather critical comments on the head, the vertebral column, the ribs, and the forelimbs. To those who have any acquaintance with osteology, states Wyman, it is evident that these remains "never belonged to one and the same individual," and the "anatomical characters of the teeth indicate that they are not those of a reptile, but of a warm-blooded mammal." Müller (1849) recognized the cetacean affinities of this animal and specifically called attention to the mixture of skeletal elements, belonging to several different individuals, in Koch's reconstructed skeleton.

The hypothesis that the Cetacea are direct descendants of the hydrosaurs and the pythomorphs rests largely upon the analogy that is offered by resemblances in the general structure of the cetacean forelimbs to those of marine reptiles and to a lesser extent upon the presence of numerous teeth in the jaws of representatives of both groups. Paquier (1894, p. 18) has discussed the importance of these fancied resemblances and directed attention to the fact that the oldest ichthyosaurs, especially the Triassic Mixosaurus (Baur, 1887) as well as Cymbospondylus, Merrymia, and Delphinosaurus (Merriam, 1908, p. 64), have slightly modified and very strong limbs, and that the remodeling and shortening of these structures becomes more pronounced with the passage of geologic time. One of the most singular modifications is found in the upper Jurassic Ophthalmosaurus icenicus (Andrews, 1910, p. 61, fig. 42) and also in Baplanodon marshi (Gilmore, 1905, fig. 23) in which the reduced humerus is followed apparently by three epipodials instead of the usual radius and ulna, and the transformation of the forelimb has reached a stage so advanced that it is difficult to distinguish the lower limb elements from the metapodials. This reduction of the limbs, according to Paquier, in conjunction with
modifications in the dentition, indicate a remodeling that parallels that of the Cetaceae, and hence the resemblances observed between the Cetaceae and the Ichthyosauria are to be explained by the phenomenon of convergence. Paquier concludes, however, that the adaptive changes observed in these marine reptiles indicate a rectograde rather than a progressive development.

Ignoring the manifold and fundamental structural differences in the skull, mandible, and vertebral column, as well as the pectoral and pelvic girdles, that separate marine reptiles from placental mammals, Steinmann (1907, pp. 468, 512–514; 1908, pp. 233–255) advocates the derivation of the Physeteridae (and Archaeoceti) from the Pleisosauria, the Delphinidae (and Squalodontidae) from the Ichthyosauria, and the Mysticeti from the Thalattosauria (including Pythonomorpha etc.). It is admitted by Steinmann that there exist important differences in the skulls of reptiles and mammals, and that the following alterations became necessary: (1) elimination of quadrate from jaw articulation, (2) ankylosis of bones in mandible, (3) shortening of the jaws and (4) formation of a double occipital condyle. The trivial phylogenetic importance of the characters cited by Steinmann to demonstrate the close relationship of the Plesiosauria to the Physeteridae (and Archaeoceti) is shown by the following summary of his tabular comparison (1908, p. 237): Body length, 5 to 15 meters in Plesiosauria and 8 to 18 (23) meters in Physeteridae (and Archaeoceti); teeth abundant in Plesiosauria and more or less unequal, but seldom abundant and often unequal and dwarfed in Physeteridae (and Archaeoceti); profile of occiput sloping steeply in both; as well as the oblique nasal passages; the compressed mandible; long or short symphysis; cervical ribs often two-headed; wrist bones not or hardly reduced; normal number of fingers; and supernumerary phalanges.

Since archaeocetes of immense size already specialized like the Cetaceae as regards propulsion had made their appearance by middle Eocene time, Steinmann concluded that the interval represented by the Cretaceous would hardly suffice to transform the body of a small land mammal into that of a giant marine whale. Influenced by this conclusion, he attempts to show that cheek teeth with roots and with laterally flattened 3-angled crowns, which are serrated on anterior and posterior cutting edges, are reptile-like characters. As regards the rooted teeth of ceratopsids, Hatcher (1907, p. 44, fig. 43) has shown that their peculiar conformation is correlated with the replacement of teeth from the dental magazine. The resemblance of the serrate-edged crowns of cheek teeth of archaeocetes to those of Iguanodon, Scelidosaurus, Palaeoscincus, Stegosaurus, etc., is rather far fetched.

The dentition, the form of the skull (particularly the laterally extended supraorbital processes of the frontals which project over the straight jugals), the position of the narial passages (choanae already pushed far backward although recession of outer narial opening is not equally marked), the absence of incisive foramina, and the presence of a mandibular symphysis all argue against the derivation of the archaeocetes from creodons or similar primitive mammals according
to Steinmann. Inasmuch as these characters are discussed at some length under resemblances to several orders of mammals, no refutation of this statement is necessary here.

Steinmann objects to the assumption that the rostrum has been elongated and the number of teeth increased in cetaceans, and states that since the hinder cheek teeth are crowded together, they are in the process of reduction and that the position of these molars on the rising anterior edge of the coronoid process is an indication of shortening of the archaeocete mandible. This structural condition according to Steinmann shows that the archaeocetes were derived from some type with a longer rostrum and more numerous teeth, and that a *Plesiosaurus* comes the closest to fulfilling the requirements necessitated by his interpretation. Steinmann (1908, pp. 235, 240–241) asserts that a close agreement exists in the ear bones of whales and marine reptiles. Dollo (1907), however, explicitly states that the resemblances observed between the tympanic bulla of whales and the quadrate of *Ichthyosaurus* and the mosasaur *Plioplatecarpus* are clearly a case of convergence.

In view of the prior exhaustive investigations of Weber (1904, p. 552) and Kükenthal on the embryology and comparative anatomy of the Cetacea as well as the palæontological studies of Müller, Abel, and Fraas, it is entirely incomprenensible to Stromer (1908b, pp. 169–171) how Steinmann could have misinterpreted such superficial convergence phenomena. Steinmann, as Stromer points out, entirely ignores the presence in the Archaeoceti of the typical eutherian dental formula, nasal musculature of the land mammal type, the structure of the auditory apparatus, the two well-developed occipital condyles, the lengthened upper portion of the forearm and the obvious elbow joint, as well as the construction of the cervical and dorsal vertebrae of *Protocetus*.

**RESEMBLANCES OF THE ARCHAEOCETI TO THE PROMAMMALIA**

Before taking up in detail the thesis elaborated by Albrecht (1886) that the Cetacea, although standing apart from all other mammals, are derived directly from the hypothetical Promammalia, the ancestors of the entire mammalian series, it is necessary to call attention to his explicit statement that the archaeocetes are not only true cetaceans, but also that they have no close connection either with the pinnipeds, with the ungulates, or with any other order of mammals. Briefly stated, Albrecht sought to prove two things, the first of which is that the Cetacea represent a wholly independent side branch of mammals descended from the Promammalia, and the second that of all Recent mammals the Cetacea stand the nearest to the first mammals that made their appearance on this earth. The second conclusion was first suggested by Brandt (1873a, p. 4). Albrecht, moreover, went a step farther in asserting that these problematical Promammalia were cetoid water animals and that inasmuch as they were aquatic it was therefore obvious that the Cetacea had never at any time left the water to dwell on land.

Albrecht relied principally on skeletal and dental characters for evidence to support his argument. As proof for his assertion that the cetacean forelimb re-
tained heritages from a primitive fin-like appendage and that hyperphalangism was not a secondary condition, Albrecht stated that no mammal with the exception of some Cetacea possess (1) more than two phalanges on the thumb, (2) more than three phalanges on the fourth finger, and (3) proximal as well as distal epiphyses on the carpal bones. Albrecht is likewise impressed by the division of the unciniform (hamatum) into carpale IV and carpale V as reported by Bardeleben (1885, p. 87) in a specimen of Ziphius [=Hyperoodon], the presence in flippers of Tursiops tursio of an ossified element on the radial border of the manus, representing the last remnant of a digitus sephularis, and also of a bone in front of the trapezoid (multangulum minus) between the base of metacarpal II and metacarpal III. He also believed that the cetacean dorsal fin was derived from the ichthyopsidian back fin in which the dermato- and interneuralia were not as yet ossified. The vertebrae of the Cetacea, according to Albrecht, retained a peculiar type of zygaphophysial articulation which was a direct heritage from the fishes. Furthermore, he was convinced that the Cetacea never possessed a pelvic girdle or at least the innominate bones were never directly connected with the sacral vertebrae. He also attempted to homologize certain cranial elements, particularly the vomer, the alisphenoid, and the squamosal, with bones in the skulls of fishes and other non-mammals. Albrecht laid especial emphasis on the absence of sebaceous and sweat glands, of smooth muscles on the head, and of ear muscles as an indication of the primitiveness of the Cetacea. Finally, the hairs that occur around the mouth were held to represent the initial stage in hair development.

In the odontocetes, the homodont character of the dentition, the presence of teeth with a single root, the equal spacing of the teeth in the jaws, as well as the unusually large number of teeth are regarded by Albrecht as an indication of primitiveness. The fact that the hinder teeth have differentiated as molars in Zeuglodon, in Squalodon, and in the toothed precursors of the Mysticeti is no proof according to Albrecht that the isodont Cetacea were derived from anisodont progenitors.

Albrecht likewise accepts Howes’s interpretation (1879, p. 471, pl. 29, figs. 8–10) of the cartilaginous nodule on the inner edge of each thyrohyal of Phocaena phocoena as remnants of the second branchial arch.

Among the skeletal characteristics cited by Albrecht as peculiar to the Cetacea are (1) the independent ossification of the transverse processes of the thoracic vertebrae, (2) the position of the cribriform plate on the skull, (3) the absence of the exethmoid in the construction of the turbinate complex, (4) the unperforated condition of the alisphenoid, (5) the exclusion of the squamosal from the construction of the internal cranial surface, (6) the ankylosis of the mandibular symphysis in most cetaceans, (7) the presence of a distinct supra-angulare on a mandible of Balaenoptera sibbaldii Gray [= Sibbaldus musculus], (8) the regular arrangement of infraorbital and mental foramina, (9) the cochlea making one and a half turns, and (10) the malleus connected with the tympanic membrane solely by a ligament.
Weber (1887) rejects in its entirety the hypothesis advanced by Albrecht. In his critical analysis of the evidence presented by Albrecht, Weber has shown conclusively that cetaceans are eutherian mammals and that their morphological peculiarities in no way point toward derivation from any problematical Promamalia. He observes that Albrecht treated the Cetacea as if they were all fossils by basing his arguments on an interpretation of the skeleton and, with the exception of ear and skin structures, by ignoring entirely the evidence revealed by the soft parts.

As regards the manus, Weber directs attention to the fact that only in *Globicephala* does the thumb possess more than two phalanges and that most cetaceans either have no thumb or else a vestigial one. Furthermore, the thumb is the first digit to be lost by reduction. Ryder (1885) and Weber (1887, p. 48) argue that hyperphalangism is not a primitive condition. According to their interpretation the extra terminal digital segments are ontogenetically as well as phylogenetically of later origin than the proximal ones, the additional phalanges originating in the secondary segmentation and ossification of the strand of cartilage attached to the ungual phalanx (see also, Symington, 1906). By others, the reduplication of the bones in the fingers has been explained as the result of either the independent ossification of intercalary synsdesmoses (Howes and Davies, 1889), or the retarded ossification of the shaft and the accelerated ossification of the separated phalangeal epiphyses (Kükenthal, 1893, pp. 307–312). The arguments for and against these theories to account for hyperphalangism have been summarized by Howell (1930, pp. 260–267).

The supposed occurrence of proximal and distal epiphyses on the carpal bones rests on an erroneous interpretation of a statement made by Flower (1885, p. 302) that in *Physeter* “many of the carpal bones, in addition to the usual central nucleus, have epiphysial ossifications developed in the periphery of the cartilage, which ultimately unite with the central piece of bone.”

The presence of five distal carpals in *Hyperoodon rostratus* (Turner, 1885, fig. E) as well as an os centrale in *Mesoplodon bidens* (Turner, 1885, fig. C) and in *Globicephala melaena* (Turner, 1885, p. 186) escaped the notice of Albrecht. As regards the presumed remnant of a digitus scaphularis, Kunze (1912, pp. 603–604) decided that this structure in *Tursiops* and *Phocaena* was the prepollex.

The investigations of Ryder (1887, pp. 429, 436, 482) and of Weber have shown that the cetacean dorsal fin is formed from connective and adipose tissue. This fin is rudimentary in the humpback but quite conspicuous in the finback. Among the odontocetes, the dorsal fin reaches its highest development in the killer (*Orcinus orca*) while in the North Pacific porpoise (*Lissodelphis borealis*) it is not developed.

Aside from the fact that the pelvic bones of *Basilosaurus cetoides* were not known at the time of this controversy, it suffices to remark that Albrecht as noted by Weber ignored the existence in *Balaena mysticetus* (Struthers, 1881) of reduced innominate bones, femur, tibia and fibula as well as the associated flexor and ex-
tensor muscles. No especial phylogenetic importance can be attributed to the absence of sebaceous and sweat glands and also of smooth muscles. Weber points out that the smooth muscles of the head as well as the sebaceous glands are lacking in the adult hippopotamus. In the young hippopotamus, however, sebaceous glands occur with the scattered long hairs. Some mammals lack sebaceous glands and others sweat glands.

In contradiction to the assertion of Albrecht and to the conclusion reached by Weber after a rather hasty dissection of the region of the external acoustic meatus of an adult porpoise, Huber (1934, p. 134, fig. 11) has demonstrated the persistence of ear muscles in a full-term fetus of *Monodon monoceros*. These vestigial ear muscles had previously been found in *Lagenorhynchus albirostris* (Murie, 1873b, p. 152) and *Globicephala melaena* by Murie (1873a, pp. 249–251), and subsequently were discovered in *Delphinus delphis* by Beauregard (1893, pp. 213–214), in *Phoecaena phocoena* by Boerninghaus (1904, pp. 192–214), in *Mesoplodon bidens* by Hanke (Kükenthal, 1914, p. 112), and in *Tursiops truncatus* as well as in fetuses of *Sibbaldus musculus* and *Balaenoptera acuto-rostrata* by Hanke (1914, pp. 497–503).

Weber (1887, p. 47) concludes that no one will assert that the most complicated type of hair construction makes its appearance before the generalized type. More recently, Japha's investigations (1911) have shown conclusively that as many as 80 sinus hairs are present around the mouth of some cetaceans and that they are actually modified mystacial and mental vibrissae. Although the bristles of these sinus hairs are vestigial, the sheaths of these hairs persist, and the blood sinuses therein have been elaborated. Each of these peculiarly modified sinus hairs is supplied with several hundred myelinated nerve fibers from infraorbital and mental nerves, and these nerve fibers connect with numerous tactile Pacinian corpuscles lodged within the hair sheath and immediate vicinity.

In the light of our present knowledge of the geological history of the Cetacea, the disappearance of teeth in the mysticete stock and the regressive remodeling and reduplication of the teeth in odontocetes as well as the concomitant loss of differentiated grasping and shearing teeth are to be interpreted as an adaptive alteration which brought into existence a feeding apparatus better adapted to the seizure and retention of the more numerous smaller prey.

Weber does not agree with Howes that the cartilaginous nodule on the inner edge of each thyrohyal is a remnant of the second branchial arch, since Dubois was unable to find any indication of a boundary between the ossified portion of the thyrohyal and the nodule of cartilage.

As regards the independent ossification of the transverse processes, Abel (1931, pp. 220–227, 267–275, figs. 1–4) has brought forth evidence to show that in case of the Eurhinodelphidae, Physeteridae, and Ziphiidae, the *Collum costae* has fused with the vestigial parapophysis of the dorsal vertebra, forming the mepophysis [= transverse process]. In the case of *Delphinus, Phocaena, Globicephala*, and *Delphinapterus*, however, the rudimentary *Collum costae* retains its connection with the shaft of the rib.
Mechanical changes in the relations of the bones of the odontocete skull, particularly in the region where the olfactory nerves originally found passage, have resulted in the closure of the opening in the cribriform plate and the concomitant lateral expansion of its component parts, the mesethmoid and ectethmoids, to completely cover the fontanelle on the anterior wall of the braincase between the medial margins of the frontal bones (Kellogg, 1928, p. 101, fig. 22).

An imperforate alisphenoid is not a universal characteristic of all odontocetes, for *Aulophyseter* and *Idiophyseter* are certainly exceptions to this statement.

The telescoping and remodeling of the cetacean skull have resulted in the displacement of the squamosal which has been pushed upward on the lateral surface of the parietal, eliminating entirely or reducing its exposure on the internal surface of the cranium. Notwithstanding the general impression that in the Cetacea the squamosal bone does not participate in the formation of the inner cranial wall, a fair amount of this bone is exposed between the periotic and the parietal on the skull of a 3 foot 6 inch fetus of *Balaenoptera borealis* (Ridewood, 1922, p. 259).

From a study of the chondrocranium in four fetal stages of *Megaptera*, Honigmann (1917, p. 78) is convinced that the Cetacea are descended from carnivorous Monodelphia.

Symphysial ankylosis of the opposite mandibles occurs to a varying extent among the odontocetes, the maximum length of symphysis being found in *Zarhachis flagellator* (Kellogg, 1924) and the minimum in *Globicephala* and *Phocaena*. The mandibles of mysticetes are united by a ligamentary symphysis.

The reported occurrence of a supra-angulare on a mandible of *Sibbaldus musculus* can be explained best as an anomaly, since no such reptilian homologues were found by Ridewood (1922) in mandibles of fetuses belonging to this and other species of mysticetes.

The incredible resemblance seen by Albrecht in the “similar and normal arrangement of the vascular and nerve foramina in the upper and lower jaws of many reptiles (especially *Mosasaurus*) and the Cetacea,” as well as the reduction in the number of these foramina in an ascending series from lower to higher mammals is hardly a true statement of the facts according to Weber, since as many as five foramina mentale occur in *Babirussa babyrussa* and they are numerous in *Orycteropus*.

The cochlea makes one and a half turns in most Recent cetaceans, though it makes two and a half turns in the Eocene archaeocetes. The cochlea is discussed in more detail on pages 118, 313–314.

It is true that the malleus is connected with the tympanic membrane solely by a ligament. The malleus naturally has remained within the epitympanic cavity, since its anterior process is ankylosed to the outer lip of the tympanic bulla. Inasmuch as life in the water necessitated a remodeling of the organ of hearing so that it would function for the reception of water-borne sounds, the osseous portions of the inner ear have undergone certain changes which brought about a diminishing utility for the tympanic membrane. “Whales have acquired an organ of hear-
ing in which resonance must play an important part, for the malleus is rigid; the tensor tympani muscle, whose function in land mammals is to make taut the ear drum, is vestigial; and in some species the stapes is immovable in the vestibule. The tympanic bulla is the relatively dense and heavy sounding box fastened to the periote by two thin pedicles, which can be set in vibration. Vibrations set up in these pedicles produce a corresponding amount of motion in the malleus, whose anterior process is likewise fused with the bulla between these pedicles, and it in turn transmits these vibrations to the incus and stapes. Another mechanical arrangement is thus acquired to take over the function ordinarily performed by the ear drum. Water-borne sound vibrations transmitted to the air contained in the tympanic bulla cause it to function as a sounding box, and its vibrations reach the cochlea by way of the ossicular chain and the vestibule” (Kellogg, 1928, p. 204). Boenninghaus (1904, pp. 345–350) has described the anatomical details which insure the insulation of the labyrinth against extraneous bone-conducted sound waves.

Weber argues that the Cetacea are true mammals and that they are not set apart from the Monodelphia [= Eutheria], notwithstanding the persistence of a number of primitive and generalized characteristics. The presence of highly modified sinus hairs, the vestiges in the fetus of the outer ear muscles, and mammary glands of the eutherian type are proof to Weber (1887, p. 47) that the Cetacea are derived from land mammals. Weber is also impressed by the construction of the cetacean uro-genital apparatus. The cetacean placenta is adeciduate and diffuse, reminding one of that of ungulates. If one holds that the diffuse placenta is the most primitive type, then according to Weber (1887, p. 43) the Cetacea may have some affinity with primitive placental mammals. The diffuse placenta of Phocaena phocoena was found by Wislocki (1933) to be the epithelial-chorial type, as described in certain artiodactyls (sow, hippopotamus, and camel), perissodactyls (horse and tapir), the pangolin (Manis), and lemurs (with the possible exception of Galago).

Weber (1887, p. 44) refers briefly to the structure of the bronchial branches in the Cetacea. Recent histological study reveals that the bronchial tree of a bottle-nosed porpoise (Tursiops truncatus) possesses an unusually developed cartilaginous armature. The cartilages of the dichotomous trachea and the bronchii are circular and closed. These cartilages extend downward to the sphincter openings into the air sacs. At the point where the bronchioles are reduced to a diameter of 0.5 mm. valves formed by sphincter muscles appear in their lumina. These valves are repeated in rapid succession to the terminations of these bronchioles, producing a series of small chambers or compartments. The architecture of the bronchial tree and of the air sacs in the lungs of Tursiops are considered by Wislocki (1929) to represent an extreme stage of specialization correlated with adaptation to aquatic conditions.

To Weber the aforesaid evidence indicates that the Cetacea originated during the Mesozoic from some generalized mammal standing midway between the ungulates and the carnivores. Subsequent research has shown that, notwithstanding
the wide-spread modifications in the nasopharynx, the respiratory apparatus, the gastro-intestinal and uro-genital tracts, the brain and the arteries that nourish it, the eye, the internal ear, and the skeleton, the derivation of the Cetacea from some eutherian mammal (Monodelphia) is supported by adequate anatomical evidence, for it is extremely unlikely that these organs would have evolved independently direct from some problematical promammal, duplicating in their basic morphological details those of eutherian mammals.

RESEMBLANCES OF THE ARCHAEOCETI TO THE TRICONODONTA

Stromer (1903c, p. 99) at one time stated that the Zeuglodon type of tooth can be derived from that of the Triconodontia, and that the articular position of the mandible is quite similar to that of the Jurassic Triconodonta. Later Stromer (1908b, p. 168) abandoned his belief in any direct connection between the Triconodontia and the Archaeoceti. One would infer from the comments of Stromer that he had been influenced originally by a statement by Osborn (1888, p. 242) that the tritubercular type of tooth can be traced back to a type with three cones in a line, that is the triconodont type, and the latter in turn to the haplodont reptilian cone. The evidence presented by Wortman (1902a, pp. 44–46) to show that the tritubercular crown of every complicated premolar and molar thus far known among placental mammals has arisen by the development of a posterior cusp on the heel and the addition of another cusp internal to the principal cusp or cone seems to have convinced Stromer that the teeth of the Triconodontia have no direct phylogenetic connection with those of archaeocetes.

Simpson (1928, p. 68, fig. 19) has figured the mandibles of European Jurassic Triconodontia, including Amphilestes, Phascolotherium, Triconodon, and Trioracodon. All these mandibles possess the diagnostic mammalian squamoso-dentary articulation, but lack a distinct angular process. In the case of Triconodon and Trioracodon, the condyle of the mandible is below the level of the cheek teeth. The molars always have three cusps arranged in a longitudinal series. Gregory (1934, p. 238) states that the “upper tooth row hung outside of the lower tooth row, so that the upper molars wore down on the inner side, the lower on the outer side, while one lower molar articulated with two upper molars. There was a heavy external cingulum on the upper molars and an internal cingulum on the lower molars; the molar teeth had two well-separated roots arranged in an antero-posterior plane—all these features reinforcing the strong cuspidation of the molars in establishing the fully mammalian status of the triconodonts.”

The combination of characters listed by Simpson (1928, pp. 171–175) for the Triconodontia, including (1) no jugo-lachrymal contact, (2) jugal reduced, (3) lachrymal reduced or wanting, (4) fenestrated palate, (5) basisphenoid (in Triconodon) with two small median foramina, presumably for entocarotid, situated in close proximity to large lateral foramina ovalia, (6) the mode of occlusion and mechanics of shearing use of the triconodont molar, and (7) the non-placental character of the mandible seem to eliminate all possibility of any phylogenetic
connection between them and placental mammals, and therefore also with the Archæoceti. The teeth of triconodonts do not alternate with each other. The shearing of the molars is effected by an oblique motion of a crest along a wearing surface. The teeth of triconodonts, according to Simpson (1933, pp. 129, 131), are essentially inadaptible, since they are so highly adjusted to one type of occlusion and to one direction of jaw motion. It is Simpson’s expressed belief (1929, p. 143) that the Triconodontia “represent another early side line, probably of equally remote derivation and equally independent of other mammals,” and so far as known became extinct at the end of the Jurassic.

RESEMBLANCES OF THE ARCHÆOCETI TO THE MARSUPIALIA

Ameghino (1905, pp. 237–238) contends that the archæocetes are not cetaceans, but belong instead to an independent order to which he in 1889 (pp. 44, 353, 895, 896) gave the name Hydrothereuta, and that this order is derived from the Sarcobelos. He admits that he had erred in placing the Squalodontidæ in that order. Ameghino believed that the transformation of the archæocetes for an aquatic life required a long period of time and that therefore one should look for the progenitor among the older Sarcobelos, as for instance the sparassodonts [= Boryhaenidae] or perhaps the Pedimanes [microbiotheres = Didelphïidae]. This relationship between the archæocetes and the marsupials is stated to be confirmed by the position of the jugal which extends backward on the zygomatic arch as far as the glenoid cavity, a condition not found among the creodonts. Therefore this structural peculiarity was said to disprove the contention of Fraas (1904a, p. 210) that the archæocetes descended from Proviswerra or some other similar Eocene creodont.

It is incontestable that the skulls of Recent genera of marsupials have the jugal extending backward on the zygomatic arch to the glenoid fossa. The construction of the zygomatic arch, however, does not appear to afford a very reliable basis for any demonstration of phyletic relationships. One of the characteristics of the skull in two families of Recent Insectivora, the Macroscelidæ and the Tupaiidæ, is the backward extension of the jugal on the zygomatic arch to the glenoid fossa. The division of the anterior element in the zygomatic arch, a condition that occurs not infrequently as an anomaly in a number of insectivores, is regarded by Wortman (1920), however, as strong presumptive proof that the upper element represents the jugal and the lower the quadrato-jugal. On the skull of a young adult female Rhynchocyon petersi (No. 182561, U. S. N. M.), Wortman (1920, p. 5, fig. 2) recognizes a quadrato-jugal on the under surface of the jugal which extends backward to the glenoid articular fossa. A somewhat similar construction of the zygomatic arch was described by Wortman for Tupaia (1920, fig. 4) and Gymnura (No. 14551, U. S. N. M.).

There are some points of unusual interest and importance in skulls of Recent marsupials that Ameghino failed to take into consideration. At least fourteen genera of Recent marsupials have an extravagantly inflated “alischénoid bulla.” This condition reaches its maximum development in Thalacomys, Perameles,
Bettongia, Myrmecobius, Phascolarctus, and Sarcophilus, and is present in varying stages of development in the remaining genera. A similarly developed "alisphenoid bulla" characterizes the skull of the Recent insectivore Macroscelides. Insurmountable difficulties at once arise when an attempt is made to derive the true pterygoid fossa of the Archaeoceti, Mysticeti, and Odontoceti from the structure represented by the "alisphenoid bulla" or air sinus. No true pterygoid fossa is present on the skulls of Recent marsupials. A distinct ectopterygoid or scaphoid fossa formed by the insinking of the ectopterygoid muscles and bounded internally by the pterygoid and externally by the freely projecting thin wing of the alisphenoid is present, however, in at least fifteen genera of Recent marsupials. This fossa is unusually large in some of the Macropodidae, especially Macropus, Petrogale, Dendrolagus, Onychogalea, Bettongia, and Aepyprymnus.

The relations of the squamosal on skulls of the Archaeoceti, Mysticeti and Odontoceti are exceptional among mammals. On all of these types the squamosal extends forward to reach the pterygoid. The foramen ovale is located in the cleft between the bifid anterior end of the squamosal and the postero-external limb of the pterygoid. In the case of the right whales, Balaena and Eubalaena, the anterior end of the squamosal is actually in contact with the palatine.

RESEMBLANCES OF THE ARCHAEOCETI TO THE INSECTIVORA

Matthew at one time suggested that the archaeocetes might have been derived from the Eocene insectivore type represented by Pantoleses as readily as from the Creodonta. Gregory thereupon (1910, pp. 418-419) made a critical analysis of the resemblances of the archaeocetes to the insectivores in general. Among the structural peculiarities listed by Gregory which tend to indicate an insectivore ancestry are (1) the antero-posterior arrangement of the incisors on the elongated premaxillaries, (2) the elongation of the rostrum, (3) the low anterior position of the orbits, (4) the triangular outline of the skull in palatal view together with the relatively weak jugal bones, (5) the large attachments for the temporal muscles and weak attachments for masseteric muscles, (6) the tubular postorbital region of the braincase resembling that of zalambdodont insectivores, (7) the shape of the mandible, and (8) the reduction of inner part and elongation of outer part of crown of cheek teeth superficially analogous to the Madagascar Hemicentetes. Gregory also concluded that the expansion of the tympanic bulla is an aquatic adaptation and like the closing in of the postnarial gutter by approximation of the pterygoid plates, thus carrying the posterior narial opening backward to the basicranial region, may have little phylogenetic significance.

The arrangement of the incisors in an antero-posterior series, according to Gregory (1910, p. 289), is probably derived from the intermediate condition preserved in Didelphis and Pantolettes in which the opposite incisor series are neither transverse nor antero-posterior in position. The spacing at intervals of the incisors, canine, and anterior cheek teeth one behind the other on the long narrow rostrum of the Potamogale skull is cited likewise by Döderlein as another resemblance to the
archaeocete skull. The hinder cheek teeth of *Protoctetus* according to Döderlein (1921, p. 54) are simply backward built trigonal teeth with three roots, which prior to this backward building could have been matched by the corresponding teeth of *Potamogale*.

It was Leche's (1907, p. 127) contention that, inasmuch as *Potamogale* is an aberrantly specialized aquatic offshoot of a *Microgale*-like insectivore and therefore a centetid, the molar cusp pattern is a derived type modified for a piscivorous diet. According to Leche (1907, pp. 46–47) the basal internal cusp is homologous with an upgrowth (hypocone) of the basal internal cingulum, the principal V-shaped cusp is homologous with the protocone, and the para- and metacones are represented by the reduced external cusps.

The contrary view is that the *Potamogale* molar consists of a reduced series of outer styril cusps and an enlarged series of inner cusps. As a result of a critical study of the problem of origin and cusp-homologies of the molar teeth, Gidley (1906, pp. 93–94) concluded that the internal basal ledge represents the protocone, the principal cusp at apex of the V is homologous with the paracone or para + metacone, and the outer styril cusps are developments of the cingulum. According to Gidley's view, the protocone (or the fused protocone and hypocone) is quite prominent on the *Potamogale* molar and still typical in form, while in *Hemicentetes* "the inner cusp (protocone and hypocone) has entirely disappeared." According to this interpretation of the cusp homologies, the conspicuous reduction of the inner side of the molar crown in *Hemicentetes* has resulted in the disappearance of the protocone (or protocone + hypocone) and a pronounced outward shifting of the paracone (or paracone + metacone), tending to approximate a fore-and-aft alignment with the para- and metastyles in the case of M1.

More recent discoveries indicate that the basic cusp pattern of the *Potamogale* molar is very old geologically. The molar construction of the New Mexican middle Paleocene *Palaeorctes puercensis* "is nearest to that of *Potamogale*" according to Matthew (1913, p. 312), "and even more than in *Potamogale* it approaches clearly and in all details to that of the normal tritubercular type, especially that of such early Eocene Insectivora as *Didelphodus* or *Palaeictops*." Matthew expressed the conviction that the molar construction of *Palaeorctes* "is in every respect a central and generalized type from which the diverse modern types are derivable," and also that strong support is given the conclusion that the principal cusp of the "zalambdodont upper molar is the connate paracone and metacone of the normal tritubercular molar," and that the basal internal crescent or cusp is the protocone. The basiocranial structure of *Palaeorctes* is more primitive than in Recent zalambdodonts, approximating that of early creodonts, and the construction of the otic bulla is comparable with that of the Recent *Oryzorctes* and *Microgale*. Although Gregory (1910, p. 240) at one time was inclined to accept Leche's conclusions in regard to the cusp homologies of the centetid molar, it would seem that in 1920 (1920a, pp. 218–225) he unhesitatingly accepted the interpretation of the zalambdodont molar cusp pattern advocated by Gidley and Matthew.
In so far as the cheek teeth are concerned, if one postulates a zalambdodont insectivore ancestry for the archaeocetes and holds that a reduction of the inner portion of the molar crown somewhat similar to that of *Hemicentetes* has been effected in *Protocetus*, then it follows that the more pronounced lateral compression of the molar of the latter is the result of a marked displacement of the paracone toward the outer side of the crown where it becomes the principal shearing cusp. This outward displacement of the paracone was then accompanied by a marked reduction of the external cingulum, the parastyle migrated inward to form the basal anterior cusp, the metacone became the larger hinder basal cusp, the meta-style was lost, and the protocone was reduced to a mere vestige. In view of our present knowledge of the cheek teeth of antecedent archaeocetes, it is rather hazardous to stress the importance of cusp homologies in so far as it may relate to the derivation of *Protocetus*.

Indisputable evidence is now available that the deciduous teeth of the upper Eocene archaeocetes are not only well developed, but are also not replaced until the animal attains adult size. The delayed replacement of the milk dentition of insectivores until the animal has attained adult dimensions is regarded by Leche (1907, pp. 38, 39, 60, 120, 140) as a very primitive mammalian character. Gregory (1910, p. 237) has recorded that the milk dentition persists into the fully adult stage of certain Oligocene Lepticidae.

With regard to the tympanic bulla of archaeocetes, which is involuted and shaped like in mysticetes and odontocetes, there exists certainly not even the remotest superficial resemblance to that of pinnipeds, insectivores, carnivores, or other terrestrial groups of mammals. The development of an involucrum, the conch-like conformation of the tympanic bulla as a whole and its attachment to the periotic by anterior and posterior pedicles, the peculiar sigmoid process, the ankylosis of the slender anterior process of the malleus to the outer lip of the bulla, and the acoustical isolation of the labyrinth taken together constitute a functional remodeling (Matthes, 1912, pp. 594–599; Kellogg, 1928, p. 204; van der Klaauw, 1931, pp. 37–39) that has not as yet been duplicated in any other mammal. Ridewood (1922, p. 242, fig. 4) has shown by his study of fetal mysticetes that the conch-like bulla arises solely by an increase in size of the original (ecto) tympanic or annulus tympanicus (the first formed part of this structure) and that no entotympanic is present. The peculiar remodeling of the tympanic ring in the Recent sireniens *Trichechus manatus* and *Hydrodamalis gigas* to resemble an involucrum is highly suggestive and indicates that for one reason or another a development somewhat similar to that of cetaceans has been retarded and furthermore the attachment of this ring to the periotic parallels that of the cetacean tympanic bulla. The condition of the tympanic in sireniens (van der Klaauw, 1931, pp. 11–12, 32–33) tends to confirm the belief that the cetacean tympanic bulla is an aquatic specialization. Accordingly the archaeocete tympanic bulla seems to represent a specialization of the simple tympanic ring and might be derived as readily from an insectivore type as from a creodont type.
The Recent zalambdodont insectivore *Potamogale* is pictured by Döderlein (1921, pp. 53–54) as having the nearest likeness in the external body form to the land dwelling ancestor of the Archaeoceti. As regards the general bodily appearance of *Potamogale*, Döderlein assigns especial importance to the length and relative thickness of the laterally compressed tail which at the base is not perceptibly differentiated from the body and tapers toward the rudder-like extremity. Döderlein sees in this cylindrical body continuing uninterruptedly into a thick powerful tail a remarkable resemblance to the cetacean body form. One may well question, however, the "primitiveness" of this fish-eating insectivore.

The insectivore otter *Potamogale* is highly specialized in an aquatic direction and there is no evidence that the hindlimbs can be used effectively for aquatic propulsion, for the legs are short and the toes unwebbed. According to Howell (1930, p. 29) *Potamogale* is something of a paradox, for the flattened tail is used as the sole means of aquatic propulsion, while in other types of aquatic mammals "a flattening of the tail follows acquisition of webbing by, and at times an increase in the size of, the hind feet." Dobson’s dissections (1883, pp. 100–106, pl. 9, figs. 11–13, pl. 10) show that the pectoral muscles of *Potamogale* are unlike the characteristic insectivore pattern. Howell (1930, p. 155) interprets this resemblance to conditions in the pinnipeds as fortuitous and "merely an intermediate stage in eventual convergence toward a similarity in appearance to pectoral conditions in the seals (Phocidae)."

Although a number of the structural details of the archaeocete skull are undoubtedly heritages from some primitive ancestral stock, characteristics of this kind do not point to a derivation from any particular known order of mammals. The brain, for instance, is characterized by having an elongated and slender olfactory peduncle that ends in an enlarged olfactory bulb. The maxillary branch of the trigeminal nerve (V₂) is transmitted by the sphenobital fissure. This seemingly represents the original mammalian condition, since it occurs also in monotremes. The optic nerve (II), which in some insectivores, marsupials and monotremes, passes through the sphenobital fissure, in archaeocetes pierces the orbitosphenoid as in most placentals mammals. The ophthalmic division of the trigeminal nerve (V₁), which in most mammals passes through the sphenobital fissure, follows the optic nerve through the orbitosphenoid and the optic foramen (see, figs. 31b, c, p. 109). The mandibular branch of the trigeminal nerve (V₃) issues from the cranium through the open tympano-periotic recess behind the alisphenoid and reaches the temporal fossa through the foramen ovale, which is located at the contact between the bifid anterior end of the squamosal and the postero-external limb of the pterygoid. A single post-parietal foramen is present on the lateral surface of each parietal. In marsupials and some insectivores, this foramen transmits a vessel that is connected with the venous system of the transverse sinus. The presence of a post-parietal foramen, however, does not imply that the ancestry of the archaeocetes can be traced directly to some insectivore.
RESEMBLANCES OF THE ARCHAEOCETI TO THE CREODONTA

The secodont character of the dentition, the presence of the typical eutherian dental formula 3. 1. 4. 3, the uniform tritubercular conformation of the upper molars as well as of Pm4, and the indicated presence of a small inner tubercle or cusp on Pm3 were held by Fraas to point toward a creodont ancestry for the lower middle Eocene Protocetus. Fraas (1904a, p. 210; 1905, p. 386) looks for the progenitor of the Archaeoceti to be found among the Proviverrinae, a subfamily of the Hyaenodontidae. To some extent at least Fraas was influenced in his views by characters exhibited by an imperfectly preserved skull of the lower Eocene Tritemnodon whitiae (Cope, 1884, pl. 25d, fig. 1). The dentition of this hyaenodont and also of related genera, including Sinopa, were subsequently figured by Matthew (1906, figs. 1–3). Further study of the teeth of these creodonts has led to some divergence of opinion among the several investigators who have interested themselves in this question. The remarkable disproportion between length of skull and length of entire skeleton, which according to Fraas (1904a, p. 216) characterizes the old creodonts and Protocetus alike, is not borne out by examination of the skeletons. In the case of Oxyaena lupina the skull constitutes about 13 per cent of the total length of the entire skeleton, in Patriofelis ferox about 12.6 per cent, and in Sinopa grangeri less than 10 per cent, but in Protocetus atavus there is reason to believe that the skull comprises about one-fourth of the entire skeletal length.

A creodont ancestry for the archaeocetes was likewise advocated by Andrews (1906, p. xxii), who goes on to state that inasmuch as the dentition of Protocetus, so far as the premolars and molars are concerned, “is practically that of a creodont,” its origin is clearly indicated “from members of that group, which may therefore have inhabited this region [i.e. Fayum] at a still earlier period.” Andrews furthermore concludes that the Fayum archaeocetes taken together with Protocetus atavus “form a series showing a complete transition, so far at least as the dentition is concerned, from the creodonts” to the more recent archaeocetes. Andrews (1906, p. xxii) directs attention to the fact that the cheek teeth of the four Fayum hyaenodonts, Sinopa, Apterodon, Pterodon, and Hyaenodon, illustrate four stages in the development of the cutting blade and in the reduction of the talon and the postero-internal cusp. Winge (1921, pp. 1–2, 12) also believed that Protocetus stands so near the Hyaenodontidae that “there would scarcely have been any reason to separate it from them” were it not for the fact that Protocetus represents one of the first of the archaeocete series.

To the arguments previously advanced to show that these hyaenodonts are related to the Archaeoceti, Matthew (1909, p. 315) adds the backward extension of the molar series upon the zygomatic arch, the shearing molars and trenchant premolars singularly like those of Hyaenodon, and the closing in of the postnarial gutter by approximation of the pterygoid plates, thus carrying the posterior narial opening backward to the basicranial region. Matthew, however, was convinced that the supposed resemblances were more apparent than real, and that the “chief
objection to regarding the three characters cited as evidence of real relationship is that they are specialized characters of *Hyaeenodon*, an Oligocene genus of cursorial adaptation and not present in its more generalized ancestors of the early Eocene, nor in any primitive Credonta.” It is of interest that Fraas (1904a, p. 210) had previously concluded that the absence of M₃ as well as the different conformation of Pm₃, Pm₄ and the upper molars remove the genera allocated to the Hyaenodontinae from further consideration and that similar objections eliminate *Palaeoictis* (Oxyaenidae). Granting that these points of resemblance between *Protocetus* and the creodonts do not indicate any relationship other than such as we should expect a primitive archaeocete would retain in common with members of other primitive orders, the possibility is not excluded that at an earlier period a somewhat similar sequence of stages in the remodeling of creodont cheek teeth may connect some predecessor of *Sinopa* with *Protocetus*.

Stromer (1908b, p. 169) has drawn attention to several structural peculiarities of the early hyaenodonts which in his estimation offset the resemblances cited by Fraas and Andrews. Among the points of difference that can be observed on the ventral side of the skull of *Sinopa* (Wortman, 1902b, pl. 10; Matthew, 1906, fig. 5) according to Stromer are the complete unlikeness of the auditory region, the position of M₃ with reference to the jugal portion of the zygomatic arch, the forward prolongation of the palatines to or beyond the level of anterior end of Pm₄, and the absence of any backward prolongation of the bony palate. To these objections may be added the entire absence on the skull of *Sinopa* of any indication of pterygoid fossae for the accessory air sinus of the middle ear, the absence of vaginal plates of the pterygoids, the arrangement of the incisors in a transverse series, and the more pronounced backward prolongation of the basicranium behind level of base of zygomatic arch. In *Sinopa* more than half of that portion of basicranium between M₃ and occipital condyles lies behind level of glenoid articular surface, while in *Protocetus* only about one-fifth is so situated. The position of the glenoid articular surface on the archaeocete skull is paralleled to a certain extent in *Hyaeenodon*, the several species of which according to Matthew (1906, p. 217) “differ very considerably in certain adaptive features of the base of the skull dependent upon the pushing backward of the glenoid articulation to a position opposite the occipital condyles.” This alteration of the hyaenodont skull, however, makes its appearance in the Oligocene *Hyaeenodon* and has not been observed in any of its precursors in the early Eocene.

Gregory (1910, p. 419) in commenting upon the creodont resemblances observes that the true molars of *Protocetus* exhibit only “a superficial resemblance to those of any hyaenodont” and that “the reduction of the inner side of the molar crown has been effected independently also in the Pinnipedia” and in *Hemicentetes*. Furthermore, he calls attention to the fact that no trace of the transverse arrangement of the incisors exists in any known archaeocete. This shifting in the position of the incisors may have been brought about in part by the forward extension of the premaxillaries. As regards the presence of the postorbital constriction, Gregory
states that in case of the creodonts it “is due not to any actual narrowing but to the very rapid broadening of the muzzle and zygomata in adaptation to carnivorous habits,” while in Protocetus it is largely secondary and apparently associated with “the reduction of the olfactory parts of the brain.”

Viewing the evidence presented as a whole, it is clear enough that no known creodont fulfills all the requirements of an archaeocete ancestor. Perhaps the most conspicuous deficiency in the documentary record is the lack of creodont endocranial casts that can be compared with those of archaeocetes. The comments of Spitzka in regard to the natural endocranial cast from the Bridger formation, which was subsequently named Megencephalon primaevus, were interpreted to indicate (Osborn, Scott, and Speir, 1878, pp. 21–22) that “the general outline, the course of the convolutions, and the line of the sutures offer strong presumptive evidence that the cast belongs to one of the aquatic carnivores.” This endocranial cast is figured by Bruce (1883, pp. 39–41, pl. 7, fig. 6) and his opinion, if correctly understood, is that it resembles the brain of a seal much closer than that of a dolphin. This is not surprising inasmuch as the conformation of the dolphin brain has undoubtedly been modified by the telescoping of the cranial bones, while the seal skull has not been similarly modified. Stromer (1909b, p. 169) observes that the development of the cerebrum as well as its furrows and ridges show that the brain of the middle Eocene Megencephalon primaevus represents a much higher stage than that of Dorudon.

RESEMBLANCES OF THE ARCHAEOCETI TO THE PINNIPEDIA

Giebel (1847, pp. 212, 221) and Jourdan (1861, p. 962) were among the first to place Zeuglodon [= Basilosaurus and Zygorhiza] in the order Pinnipedia, but neither one enumerated the structural peculiarities that indicate such a relationship. Brandt (1868, p. 359) expressed the belief that cetaceans and carnivores are connected by such intermediate forms as the archaeocetes, seals, and sea-otters.

Gill in at least one contribution (1870, p. 503) to this subject asserted that although the archaeocetes are “related on the one hand to the seals and on the other to the toothed cetaceans,” the relation to the latter is the more intimate, and that the archaeocetes may be combined with the odontocetes and the mysticetes into the order Cete, of which each represents a suborder. A year later, Gill (1871, p. 121) stated that the Pinnipedia and the Zeuglodontia “may indeed be considered as derivatives from the same original stock, and from the zeuglodont stem have probably descended, in different directions, the toothed and the whalebone whales.” In replying to criticism of this view by Professor Brandt (1872), Gill (1873a, p. 20) denied that he had intended to convey the idea “that the specialized denticetes and mysticetes of the Tertiary epoch could have originated in the epoch and from Tertiary zeuglodonts.”

A more exact statement of Gill’s views of this controversial subject are concisely given in the following quotation (1873b, p. 264):
"The tendencies of the specialization in the Pinnipedia, as the great reduction in size of the milk teeth, the decreasing differentiation of the other teeth, and the modifications of the form, are towards the Cete; the extinct Zeuglodons, and especially the Basilosauridae, even indicate the possibility, if not probability, of the derivation of the Cete from a Pinniped avus. At the most, however, it can only be claimed that no quadrupedal type now exists, or has left its remains, so far as is yet known, which so nearly fulfills the conditions of intervention between ordinary quadrupeds and mutilates [= Sirenia and Cete] as the Pinnipedia. It is possible, however, that the resemblances in question may be adaptive, and it must not be forgotten that similar tendencies, but in a very minor degree, are exhibited by a specialized lutrine type (Enhydris, or sea-otter)."

The fact that Huxley placed Zeuglodon and Squalodon in his Phocodontia, a suborder of the Cetacea, would seem to indicate that he conceded some degree of relationship between the archaeocetes and the seals. The sole remark that can be construed as supporting this view is Huxley’s statement that “the molar teeth have laterally compressed crowns with serrated edges and two fangs [= roots], resembling those of many seals, and Zeuglodon differs from all other Cetacea in the circumstance that some of its teeth have vertical successors.” Huxley asserted that the above-mentioned “fossil forms constitute connecting links between the Cetacea and the aquatic Carnivora.” Among the resemblances of the Phocodontia to the Cetacea listed by Huxley (1872, pp. 349–350) are the distinct and unankylosed cervical vertebrae, caudal vertebrae with transverse processes perforated vertically, large thick zygomatic processes of the squamosals, and expanded supraorbital processes of the frontals. The Phocodontia according to Huxley have a symmetrical skull and the nasals although short “are longer than those of any other cetacean.”

Marsh’s views are well stated in the following quotation (1877, p. 373):

“The Cetacea are connected with the marine carnivores through the genus Zeuglodon, as Huxley has shown, and the points of resemblance are so marked that the affinity can not be doubted. That the connection was a direct one, however, is hardly probable, since the diminutive brain, large number of simple teeth, and reduced limbs in the whales, all indicate them to be an old type, which doubtless branched off from the more primitive stock leading to the carnivores.”

By the characters of their embryonic teeth “anlagen,” according to Julin (1880, pp. 87–88), the mysticetes are shown to have been derived from some toothed whale, probably related to the squalodons, and the latter is connected with the Pinnipedia through the zeuglodons.

Thompson staunchly advocated the thesis that the archaeocetes have no direct affinities with the Cetacea, but have instead the closest possible relation with the pinnipeds. Aside from the supposed resemblances of the teeth of Basilosaurus and Zygorhiza to those of pinnipeds, especially Stenorhynchus [= Lobodon] and Otaria, Thompson (1890, pp. 2–3) cites certain peculiarities of the archaeocete skull, such as the entire absence of telescoping, the broad nasal bones, the conformation of the fronto-nasal sutures, the pinched-in parietal region, the sagittal and lambdoidal crests, the vertical triangular occiput and the width of the interval
ventrally between the small occipital condyles, all of which are said to agree "line for line" with the skulls of *Arctocephalus* and *Otaria*. The lateral extension of the frontals to form the broadened supraorbital processes is held to have arisen from an exaggeration of the postorbital processes of the *Otaria* skull. It is likewise stated by Thompson that the pterygoid is a blunt hooked process like that of carnivores, and that the cochlea makes two and a half turns, or one more than in the Cetacea.

Dames (1894, pp. 204–205) seems not to have been greatly impressed by Thompson's evidence for the pinniped nature of the archaeocete skull, especially with respect to *Arctocephalus* and *Otaria*. Dames points out that as regards the Otariidae no accessory denticles are developed on the cutting edges of the crown of the haplodont cheek teeth, although a few small tubercles are present on the well-developed cingulum, the canines are unlike the incisors, and also the conformation of the occiput is quite unlike that of archaeocetes. Dames correctly concludes that the archaeocete skull with its elongated rostrum, backward shifted narial aperture, and anteriorly extended narrow premaxillaries is utterly unlike the pinniped skull. Even in the case of the highly specialized skull of the male sea-elephant (*Mirounga angustirostris*), the premaxillaries are not extended forward conspicuously beyond the ends of the maxillaries, the incisors are arranged in a transverse series, the rostrum is noticeably shorter than the cranium, the mastoid is inflated, and the conformation and attachment of the tympanic bulla is entirely different from that of archaeocetes. The *Mirounga* type of specialization according to Gregory (1910, p. 416) "is clearly only a development of the normal phocid type and is separated from the cetacean type by a host of significant differences."

Furthermore, Dames (1894, p. 206) observes that the notches for the jugular leash on the hinder end of the basicranium constitute an important structural distinction from the pinniped skull. Müller (1849, p. 38) before Dames likewise had observed that these jugular incisures were remarkably like those on the dolphin skull. Thompson erred in his interpretation of the damaged pterygoid on the basicranium of the *Zygorhiza kochii* skull figured by Müller (1849, pl. 4). The true characteristics of the pterygoids are shown in the illustrations reproduced elsewhere in this review (figs. 30, 79).

Another important point emphasized by Dames is that there is hardly another cranial structure so characteristic of the Cetacea as the tympanic bulla. The possession of a typical tympanic bulla with a well-developed involucrum by the archaeocetes is fairly conclusive evidence of a cetacean relationship and excludes *a priori* the Pinnipedia from consideration. As regards Thompson's quotation from Müller (1849, p. 12) that the cochlea of *Zygorhiza kochii* makes two and a half turns, or one more than in the Cetacea, Dames held that this is to be interpreted as a heritage from its land-dwelling progenitor. Müller's figures (1849, pl. 1, figs. 2–3) and especially the figure of the same specimen published by Carus (1849, pl. 39A, fig. iv) show a compactly coiled cochlea. To supplement this evidence, a right periosteal of *Zygorhiza kochii* was sectioned, exposing the cochlea. It was found that the turns of the cochlea are almost vertical in relation to the
antero-posterior axis of the periotic, while in all Recent odontocetes the turns of the cochlea are approximately horizontal to the same axis. The change in the direction of the central conical pillar around which the cochlear tube winds seems to have accompanied the shifting of the *tractus spiralis foraminosus* from the antero-inferior wall approximately at the bottom of the internal acoustic meatus to the fundus of the meatus. X-ray photographs were made of the periotics of all the genera of Recent odontocetes. In case of a few genera the cochlea was filled with molten lead and the bone comprising the ventral face of the *pars cochlearis* was removed to expose the true position of this structure. It was found that the cochlea of Recent odontocetes makes from one and a half to possibly two turns. The cochlea of Recent odontocetes is distinctly elongated and there is an obvious "unwinding" of the turns at the base. The alterations in the cochlea which have been brought about in the course of time are no more remarkable than the remodeling of the skeleton as a whole. In its gross structure, the archaeocete periotic agrees point for point with those of Recent cetaceans, not only in the type of attachment to the braincase, but also in the presence of identical structures, as for instance the anterior and posterior processes, the *pars cochlearis*, the fossa for the head of the malleus, the *fossa incudis*, the Fallopian aqueduct and facial canal, the fossa for the stapedial muscle, and the excavated *hiatus epitympanicus*. It will be observed also that the positions of the *fenestra ovalis*, the *fenestra rotunda*, the cerebral orifices of the *aquaeductus cochleae* and the *aquaeductus vestibuli*, the internal acoustic meatus, the *foramen singulare*, and the entrance to the *aquaeductus Fallopii* are identical in the periotics of both groups and that the general conformation of all these structures is so close that it can hardly be questioned that a near relationship is indicated.

Thompson's comments on the archaeocete mandible are traceable to the incorrect restoration of the mandible of *Basilosaurus cetoides* published by Koch (1851, pl. 7, fig. 3). Although Thompson asserts that the archaeocete mandible differs in several important details from that of *Delphinus*, it does not necessarily follow that this applies to all odontocetes. Dames observes that there are other odontocetes, as for instance *Physeter*, which have mandibles of somewhat similar shape, the similarity being most obvious in (1) the proportion of length to height, (2) the gradual increase in height of ramus from front to rear, (3) the length of the symphysis, and (4) the angle formed by the divergence of the opposite rami behind the symphysis. Mandibles of *Inia* and *Stenodelphis*, both of which have a well-developed coronoid process, exhibit a somewhat closer resemblance to the archaeocete mandible. The most conspicuous development of the coronoid process is found in *Platanista*. The ankylosis of the mandibles of archaeocetes is listed by Thompson (1890, p. 4) as another difference from the Cetacea. This is refuted by the undoubted ankylosis of the mandibles of *Physeter, Inia, Lepotes, Platanista, Zarhachis, Schizodelphis, Acrodelphis*, and *Eurhinodelphis*.

Curiously enough Thompson also asserted that the entrance to the alveolar canal in the archaeocete mandible is by no means as large as the gigantic cavity in
the dolphin mandible, notwithstanding the fact that Müller (1849, p. 13) had described the extraordinary large size of this opening. Even though this assertion were partially correct, no relationship to the Pinnipedia would be indicated in view of the rather tiny size of the alveolar foramen in mandibles of the latter. Even more startling is the statement by Thompson that the archaeocete mandible lacks the *processus angularis* and that one finds a parallel of this condition in the seal. So far as known no *processus angularis* is recognizable on any odontocete or archaeocete mandible. Conversely, as pointed out by Dames (1894, p. 207), all Recent pinnipeds without exception possess this process, but in different degrees of perfection. Furthermore, the condyle of the archaeocete mandible is quite like that of odontocetes and does not even remotely resemble that of pinnipeds.

In all the above-mentioned points there is no direct resemblance to the short compact mandible of pinnipeds which on the contrary corresponds more closely to the type of mandible possessed by land carnivores. It is thus obvious that Thompson not only was unfortunate in the choice of comparative material, but also that he failed to interpret correctly the evidence before him.

As regards the vertebrae, Dames concluded that Thompson selected such characters as would best fit with his preconceived notions and passed over all others in silence. The pinniped features of the archaeocete atlas are, according to Thompson, (1) the presence of broad transverse processes pierced by a foramen, (2) the semilunar form of the fossa for the reception of the odontoid process of axis, and (3) the shape of the articular surfaces. On the atlas of most pinnipeds, the transverse processes are expanded horizontally and compressed dorso-ventrally, but in case of *Zygophora*, *Dorudon*, and *Basilosaurus* these processes are expanded in a vertical direction and compressed antero-posteriorly. Furthermore, the archaeocete atlas possesses a well developed backward projecting hypapophysis which either is lacking or is vestigial on those of pinnipeds, including the Miocene *Alloodesmus* (Kellogg, 1931, figs. 9–12), but is very well developed in some odontocetes, especially *Inia geoffrensis*, *Eurhinodelphis cocheteuxi* (Abel, 1931, pl. 19, fig. 3e), and *Zarhachis flagellator* (Kellogg, 1924, pl. 12).

On the archaeocete axis the broad longitudinal ridge on the dorsal face of the short plug-like odontoid process, which is set off on each side by a wide groove, is continuous posteriorly with a ridge of almost the same width on the dorsal face of the centrum. This type of odontoid process according to Thompson is minutely reproduced in the pinnipeds. The odontoid process on the axis of *Phoca* and *Erignathus* is certainly not similarly modified. A somewhat closer resemblance is exhibited by the odontoid process on the axis of the otarids *Eumetopias*, *Arctocephalus*, and *Callorhinus*. A somewhat similarly modified odontoid process is found in several terrestrial carnivores, for instance *Felis onca*, *Hyaena crocuta*, *Gulo luceus*, and also the aquatic *Enhydra lutris*. Dames correctly decided that the possession of a strongly developed odontoid process does not demonstrate any

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1 The atlases of *Monachus monachus* (No. 219069, U. S. N. M.) and its Miocene precursor, *Monotherium maeoticum* (Nordmann), seem to be the sole exceptions to this statement.
closer affinity with the pinnipeds than with the insectivores or even with the macropods. It is likewise true that a similar odontid process is developed on the axis of *Inia geoffrensis* and a number of fossil odontocetes, including *Priscodelphinus grandaevus* Leidy (Cope, 1890, fig. 2).

Thompson (1890, p. 5) would have one believe that the greatly elongated and downward directed ventral transverse processes, the lateral arterial foramina, as well as the contour of the neural canal of the sixth cervical of *Zygorhiza kochii* are duplicated on the corresponding cervical of *Phoca vitulina*. Even a cursory examination of the cervical vertebrae of phocids and otarids will convince one that the ventral transverse processes are relatively short, conspicuously expanded antero-posteriorly, and directed more downward than outward. The sixth as well as the other post-axial cervicals of archaeocetes do not resemble those of pinnipeds any closer than they do those of some terrestrial carnivores. The rather close agreement which Dames (1894, p. 208) supposed existed between the cervicals of archaeocetes and *Stenodelphis blainvillei* is not confirmed by actual comparison of the two cervical series. The sixth cervicals of *Stenodelphis* and *Lepotes* have short ventrally directed transverse processes, their antero-posterior diameter being about equivalent to their length. It is rather curious that the ventral transverse processes on the fifth cervicals of *Inia geoffrensis* and *Kentriodon pernix* should exhibit the closest approach to those on the sixth cervical of archaeocetes, while the serially homologous cervicals are quite unlike each other. Dames does not assign any particular importance to the non-ankylosis of the cervical vertebrae in *Inia, Platanista*, and the archaeocetes.

Thompson contends that the dorsal vertebrae of archaeocetes, with their short transverse processes and distinct horizontally placed posterior zygapophyses are like those of seals, and that vertebrae of this type are not found among the Cetacea. The presence of distinct horizontally placed postzygapophyseal facets on the anterior dorsals and short transverse processes on the hinder dorsals of some archaeocetes are heritages from less-modified precursors and need not be sought for among the recent Odontoceti, which have undergone a longer period of adaptation to an aquatic habitat. At least one of the middle Eocene archaeocetes, *Protocetus atanus*, has nearly vertical articular facets on the postzygapophyses of the hinder dorsal vertebrae and of the lumbar vertebrae. Dames, however, erroneously stated that the centra of archaeocetes lack lateral facets for articulation with rib capitula.

Thompson attempts to draw a parallel between the *Basilosaurus* lumbers with remarkably elongated centra, low position of the transverse processes, and forward projecting metapophyses which arise high up on the neural arch, and the corresponding vertebrae of seals. Some of the characters given for the lumbar vertebrae, as for instance the conformation and position of the transverse processes, length of neural spine, and size of neural canal are not peculiar to the archaeocetes, for they can be matched in the Odontoceti. The statements of both of these investigators in regard to the dorsal and lumbar vertebrae of archaeocetes have no especial significance, since the vertebrae under discussion at that time were so im-
perfectly preserved. That the trunk vertebrae of some of the smaller archaeocetes are wholly cetacean in character will be seen by a comparison of those of *Zygorhiza kochii* with those of *Eurhinodelphis* (Abel, 1931).

One observes in the Archaeoceti according to Fraas (1905, pp. 384–386), a peculiar combination of pinniped and cetacean characters, since the anterior part of the body, including the forelimbs, finds its closest counterpart in the pinnipeds, while the hinder part of the body resembles a cetacean. Fraas, however, was inclined to believe that the supposed resemblances observed in the teeth of the Archaeoceti and the Pinnipedia have no especial significance, but are another illustration of the phenomenon of convergence, and that the manifold resemblances in skull construction are to be explained by a common creodont ancestry (Fraas, 1904a, p. 220).

On comparison it will be observed that *Zygorhiza kochii* has a forelimb, which in so far as functional adaptation is concerned exhibits a remarkable resemblance to that of a fur seal. Judging from the peculiarities of the component parts of the *Zygorhiza* forelimb, one might infer that structurally it had passed beyond the adaptive stage present in the fur seal.

The figure of the *Basilosaurus* scapula published by Müller (1849, pl. 27 fig. 2) is in part inaccurate and in part restored. According to Dames (1894, p. 210), an examination of the original of this figure shows that (1) the spine is figured much stronger than it actually is, (2) the acromion is shown with a high ridge which is not present on the original, and (3) the coracoid process is obviously broken off. Yet these structures are cited by Thompson (1890, pp. 6–7) as demonstrating affinity with the pinnipeds. An essentially complete scapula of *Basilosaurus* is figured on page 63 (fig. 20). The archaeocete scapula, it is true, has held more closely to that characteristic of land carnivores. This is correlated with the stage in the transformation of the forelimb, which happens in this instance to correspond somewhat closely to that of pinnipeds.

According to Gregory (1910, p. 417) the “humerus shows, it is said, a curious mingling of pinniped with cetacean characters (Lucas, 1895), but this neither proves that the zeuglodonts are related to the pinnipeds, nor casts any just suspicion upon their relationship with the Cetacea, since the latter is probable on other grounds.” Lydekker (1893, p. 559) on the other hand was convinced that beyond the fact that the humeri of archaeocetes and pinnipeds “have a strongly developed deltoid crest, there is not the most remote resemblance between the two.” The archaeocete humerus has a large deltoid crest, distinct tuberosities, transversely placed head, and a well-developed trochlea. The slender ulna retains a distinct olecranon process and the bent radius is slightly widened distally. Thus the forelimb has a hinged and non-rotary elbow joint, slightly movable wrist, and metacarpal bones with ball-like distal extremities.

Dames (1894, p. 210) dismisses Thompson’s statements in regard to the phalanges by saying that those designated as such (Burmeister, 1847, p. 984) are in part portions of the sternum and in part fragments of chevron bones. This
conclusion does not appear wholly justified in so far as it may apply to Müller’s description (1851, p. 246) of the finger bones obtained by Koch on his second visit to Alabama. The distal club-like enlargement of the ribs seems to be peculiar to the archaeocetes.

With regard to the pelvic girdle, our knowledge is limited at present to that of Basilosaurus cetoides. The innominate bones of pinnipeds, of which Zalophus and Phoca may be taken as representative types, have a robust ilium which is turned outward and an exceedingly large elongated obturator foramen. In Basilosaurus, however, the atrophied condition of the ilium, the small size of the obturator foramen, and the relative dimensions of the post-acetabular portion of the innominate bone indicate a far more advanced specialization than is shown by any known pinniped.

The presence of a large third trochanter on the femur, according to Lucas (1900a, p. 330) “need not be considered surprising, since, however distant the relationship may be between Zeuglodon and the seals, it is a relationship that seems to exist, and Scott and Wortman both consider the seals to be descended from the primitive carnivores, through the creodonts, and these are characterized by the presence of a third trochanter on the femur.” The presence of a third trochanter on the atrophied Basilosaurus femur is undoubtedly a heritage from some earlier progenitor and does not necessarily denote any near relationship to the Pinnipedia.

After having discussed in considerable detail the rather dubious evidence adduced by Thompson, Dames arrives at the conclusion that the archaeocetes are not pinnipeds, and that they on the contrary are cetaceans and most certainly odontocetes. Furthermore, Dames asserts that all the peculiarities of Recent Cetacea, especially the Odontoceti, either in one or another stage of development or else in the process of completion, are present in the archaeocetes. The retention of the normal carnivore contact-relationship of the parietals, frontals, and nasals are said to connect the archaeocetes with their land-dwelling progenitors, since aquatic life has not as yet brought about any obvious reduction or overlapping of the elements in the archaeocete skull. The elongation of the rostrum and the accompanying forward extension of the premaxillaries on the archaeocete skull are interpreted by Dames (1894, p. 211) as the initial step in the remodeling process that later followed the path culminating in the odontocete type of skull, since any fast swimming animal dwelling exclusively in water necessarily requires a pointed snout for cutting through the water, and in case of lung-breathers the outer narial aperture for intake of air must be placed higher on the head. The construction of the skull in the region of the orbit is cited as evidence that this portion of the archaeocete skull has not as yet felt the full effect of the remodeling influences associated with an aquatic habitat but has retained the essential characteristics of that of land carnivores. On the other hand a typical cetacean tympanic bulla has been acquired and the transformation of the mandible along the lines of that characteristic of odontocetes has been completed.
Gidley (1913, p. 654) expressed his views as to the origin of the archaeocetes in the following words:

"The high degree of specialization which they had attained in the development of the body and limbs, combined with the retention of so many primitive characters, would indicate a very ancient origin for these animals, and if derived from the same stock as the seals or sea-lions or direct from the early creodonts, their branching-off point must have dated back to a time most remote, certainly before the various natural groups of creodonts appearing in the early Eocene were sufficiently differentiated to be recognized."

The present investigation has not revealed any facts that conflict with the ideas expressed in Gidley's statement.

RESEMBLANCES OF THE ARCHAEOCETI TO THE EDENTATA

So far as known, no one has actually suggested that the archaeocetes have been derived from the edentates, though there have been those that advocated such a relationship between the Recent Cetacea and the Edentata. Blainville (1816, p. 109) seems to have been the first to suggest that the Cetacea may represent an anomalous aquatic modification of the edentate stock.

Many years later, Beddard (1902, p. 120) revived the idea of an edentate ancestry for the Cetacea and listed certain structural peculiarities which in his opinion merited serious consideration, including: (1) The existence of remnants of a hard exoskeleton, of which vestiges are said to persist in the porpoise, (2) the double articulation of the rib to the sternum in balaenopterids, comparable to conditions in the great anteater, (3) the fusion of some of the cervical vertebrae, (4) the share the pterygoids take in the formation of the hard palate, and (5) the vena cava in the porpoise in common with many edentates diminishes in size, instead of increasing, as it approaches the liver.

The supposed existence of remnants of an osseous exoskeleton in the Cetacea rests upon the rather dubious assumption that the low rugosities on the anterior margin of the dorsal fin of Phocaena spinipinnis Burmeister and along the dorsal ridge of Neomeris phocaenoides (Cuvier) constitute a vestige of this dermal armature (Kükenthal, 1893, pp. 251–258, pl. 16), and that fossilized remains of an osseous dermal armor had been found associated with the skeletons of Basilosaurus cetoides (Dames, 1894, p. 219; Lucas, 1904) and Delphinopsis freyeri (Abel, 1901). As regards Neomeris, a histological examination of the skin on the dorsal ridge convinced Howell (1927, p. 6) that, although a local thickening of the epidermis exists, neither any indication of cartilage nor of a center of ossification can be discerned. The so-called "Panzerplatten" of Basilosaurus (Müller, 1849, p. 34) have since been shown definitely to belong to an Eocene leathery turtle (Psephophorus sp.), but no satisfactory explanation has as yet been given for the nodular-like impressions on the matrix inclosing the Delphinopsis skeleton (Abel, 1901, pp. 301–303, pl. 20; Winge, 1921, pp. 56–58).

The detailed relations of the ribs with the sternum in balaenopterids are not strictly homologous with the conditions found in the giant anteater. The two
places of articulation of the distal end of the first rib to the sternum in *Balaenoptera physalus* are described and figured by Struthers (1871, p. 117, pl. 7, fig. 4) as follows: (1) The end of the lateral wing of the trilobate sternum, covered by cartilage, is connected on its posterior edge by ligaments to a roughened area located on the anterior border of this rib, and (2) a short cartilage belonging to the anterior part of the distal end of this rib is joined by a ligament to the backward projecting xiphoid process of the sternum. No remnants of the mesosternum have been found in any mysticete. As an individual variation in the finback, the proximal end of the first rib is occasionally split by a short cleft, making it bicipital. The explanation generally accepted for this condition is that a cervical rib is fused with the rostral surface of the first rib.

Before taking up in detail the relations of the ribs to the sternum in *Myrmecophaga tridactyla*, it is necessary to state that seven free vertebrae constitute the cervical series, the first rib (articulating with the first dorsal vertebra) is not bicipital, and its distal end is connected by ligaments solely with the end of the lateral wing of the pre sternum. The second rib, however, has a double connection with the sternum, the anterior angle of its distal end being connected by ligaments with the posterior border of the lateral wing of the pre sternum and the remainder of its distal end being connected by ligaments with a sternal rib which articulates in part with the postero-external angle of the short broad posterior process of the pre sternum and in part with the antero-external angle of the first section of the mesosternum.

Likeness does not invariably denote relationship. Ankylosis of the centra of several cervical vertebrae does occur in the armadillos, but not in the anteteaters. Mechanically induced convergences, such as the shortening and strengthening of the neck by ankylosis of the vertebrae, can hardly have any genetic significance.

The anomalous construction of the palatal surface on skulls of *Myrmecophaga tridactyla* and *Tamandua tetradactyla* is more nearly comparable to conditions in the archaeocete than in the mysticete skull. In both of these anteaters the palatal surface is extended backward to the level of the external auditory meatus by the meeting on the mid-line of the greatly widened pterygoids. Furthermore, skulls of *Myrmecophaga* and *Tamandua* have a pterygoid fossa for an accessory air sinus, communicating with the tympanic cavity, which is completely inclosed by the pterygoid and the alisphenoid. This fossa produces a noticeable oval prominence on the side of the palatal surface. In the mysticetes, however, the closing in of the postnarial gutter is effected by the backward prolongation of the palatines, a modification that reaches its maximum development in *Balaena mysticetus*, and the fossa for the accessory air sinus of the middle ear is inclosed solely by the pterygoid. These structural conditions in the anteater skulls do resemble superficially those in the mysticetes, and certainly they are in no way associated with aquatic adaptation. Inasmuch as the palate in skulls of other edentates is not similarly modified, the condition found in the anteater skulls is quite likely a secondary modification, standing in some relation to the strengthening of the basicranium to compensate
for the extraordinary lengthening of the rostrum or to their highly specialized feeding habits.

Bearing in mind the numerous adjustments that have been effected in the Recent Cetacea, and the direct relation of increase or decrease in the size of the blood-vessel supplying some particular organ to the functional demands or physiological activities of the latter, which are conditioned by the particular circumstances of the environment, it is obvious that undue importance should not be assigned to resemblances such as the dimensions of the vena cava.

The frequent occurrence of retia mirabilia as well as the multiplication and cylindrical shape of the teeth (Weber, 1887, p. 52) in members of both orders are interesting resemblances that have no phylogenetic significance.

It is remarkable also according to Beddard (1901, p. 96) "that in the Cetacea we find precisely what is found in the manatee and the sloth—the decrease of the cervical region by the presence of an additional rib belonging to the last cervical, and the increase of the cervical region by the apparent dropping of a rib." No exception can be taken to the first part of Beddard’s statement. In the case of *Balaenoptera borealis* (Schulte, 1916, p. 488) the first rib is bicipital, the anterior head articulating with the seventh cervical vertebra. *Trichecus* (Flower, 1885, p. 42) and *Choloepus hoffmanni* (Flower, 1885, p. 48) have only six cervical vertebrae. As regards the increase of the cervical region by the apparent dropping of a rib, this condition occurs in only one Recent cetacean. No ribs are attached to the first dorsal vertebra of *Neobalaena marginata* (Beddard, 1901, pp. 93, 96). The first and second dorsal vertebrae lack ribs in all species of *Bradypus* (Flower, 1885, p. 48). A search of the literature and an examination of the skeletons of sirenians failed to reveal the basis for the inclusion of the manatee in the second part of Beddard’s statement. All of the genera referred to the family Dugongidae have seven cervical vertebrae. No extinct sirenian has as yet been described that has a larger number of vertebrae in the neck.

Ameghino (1905, p. 244) postulates a hypothetical ancestral stock (Archaeopelta) of mammals as the original source from which were derived the Cetacea, Monotremata, and Edentata. The present-day monotremes were considered to represent an excessively specialized branch of the Cretaceous Peltateloidea (the progenitors of the armadillos), while the Cetacea were derived from an ancestral stock common to both at an earlier epoch. Confirmation of this view, according to Ameghino (1905, p. 240), is shown by the presence of such characters as haplodonty, homodonty, and polyodonty in both the Cetacea and the Edentata. Schlosser (1907, p. 466) rather appropriately remarked that such views need not be taken seriously.

RESEMBLANCES OF THE ARCHAEOCETI TO THE ARTIODACTYLA

Flower (1883a, p. 394) laid especial emphasis on the resemblance of Recent Cetacea to suilline artiodactyls in the elongated larynx, complex stomach, simple liver, reproductive organs, and fetal membranes. The archaeocete type of skull
according to Flower presents as many likenesses to one of the primitive pig-like ungulates as to that of a seal, "except in the purely adaptive character of the form of the teeth." It is also the contention of Flower that "the structure of the Cetacea is, in so many essential characters, so unlike that of the Carnivora that the probabilities are against these orders being nearly related," although he does concede that the teeth of archaeocetes "approximate more to a carnivorous than to an ungulate type."

These resemblances cited by Flower may possibly according to Gregory (1910, p. 420) "be connected with the derivation of the artiodactyls from creodonts." The prolongation of the larynx (Hein, 1914) into the posterior nares in both the Recent Cetacea and the hippopotamus as noted by Flower is quite likely another instance of convergent modification and in the case of the Cetacea may according to Gregory "be regarded as an aquatic development of the retrovelar larynx of insectivores."

In the majority of odontocetes the first chamber of the stomach is actually a dilation of the oesophagus, but in the ziphiods, "notwithstanding the many chambers, all are true gastric chambers, lined by glandular epithelium" (Benham, 1901, p. 120). In ruminants, the first chamber of the stomach constitutes a reservoir, since no digestive fluids reach the food stored there, while in the case of odontocetes the first division is a "macerating chamber" into which digestive fluids from the gastric region of the stomach are discharged. Beddard (1902, pp. 347–348) takes exception to the supposed resemblances observed in the cetacean stomach (Jungklaus, 1898), since there may be as few as four chambers in the rorqual and as many as fourteen in ziphiods. As a further objection, Beddard states that the "essential difference between the whale's and the ruminant's stomach is this: in the latter the stomach is primarily divided into two portions, of which the first is non-digestive and is clothed with oesophageal epithelium. The second, the abomasus, is the digestive region. The first part is again divided into three compartments [rumen, reticulum, and omasus]. In the whales, on the other hand, it is the digestive part which is again subdivided, while if the first part is divided it is not markedly so as in the ruminants."

The cetacean liver is a compact organ, relatively simple in conformation and less lobulated than in many mammals. Schulte (1916, p. 451) found in a fetus of *Balaenoptera borealis* that the left lobe was smaller than the right lobe in all dimensions, but the Spigelian lobe was large and peculiar in the great development of its processus papillaris. Although Flower was impressed by the resemblance of the cetacean liver to that of artiodactyls, it has been observed that the unlobulated condition of this organ is not a distinguishing feature of all artiodactyls, for in the Camelidae according to Owen (1868, vol. 3, p. 478) the under surface of the liver is subdivided into many small polygonal lobules. In the opinion of Owen (1868, vol. 3, p. 463), however, the cetacean liver exhibits more resemblance to the human liver.

As regards the reproductive tract, Flower does not specify any particular structural resemblance to the Artiodactyla. Ommanney (1932, p. 440), however,
states that in the camel “the ovary lies in a pavilion provided by the oviducal funnel,” and that a similar condition “has been noted in some Cetacea.” Murie (1875a, p. 285) found in *Globicephala melaena* that the broad ligament and the fimbrize of the oviducal funnel form “a delicate arched covering or pavilion which overarches the ovary.” In ruminants, the ovary is lodged in a pouch-like recess formed by a folding of the broad ligament like that described by Turner (1871, pp. 470–471) for *Orcinus*.

Inasmuch as the adeciduate and diffuse placenta of *Phocaena* (Wislocki, 1933) is definitely an epithelio-chorial type, like that described for artiodactyls (sow, hippopotamus, and camel), perissodactyls (horse and tapir), the pangolin (*Manis*), and lemurs (with possible exception of *Galago*), no close relationship to artiodactyls alone can be demonstrated. After reviewing the structure of the male and female reproductive tracts, Ommenney (1932, p. 409) remarks that “it will be seen that among these groups [i.e. Insectivora, Fissipedia, Pinnipedia, Artiodactyla, and Perissodactyla] there is little comparison with the Cetacea, since points of resemblance in any group are negated by equally important differences.”

As regards the highly convoluted brain of Recent Cetacea, Weber (1904, pp. 126, 562) directs attention to the fact that the concentric gyri which surround the Sylvian fissure are likewise present in the brains of Carnivora and Ungulata. Although he considered the origin of the Archaeoceti to be rather uncertain, Weber (1904, p. 581) thought that the construction of Recent Cetacea pointed toward derivation from the primitive Condylarthra and therefore the progenitor of the archaeocetes should likewise be sought among the representatives of that order.

**RESEMBLANCES OF THE ARCHAEOCETI TO THE PERISSODACTYLA**

Anthony (1926, pp. 99–101) contends that the structures (skeleton and dentition) on which palæontologists base their conclusions as to the affinities of the archaeocetes are precisely those that might be expected to be the most malleable under the influence of morphogenic factors. Furthermore, if it were possible to examine the least malleable organs, such as the viscera and the central nervous system, one might reach somewhat different conclusions. The characters of the cheek teeth and of the skeleton that have been cited to show a direct relationship between archaeocetes and creodonts may on the contrary be interpreted according to Anthony (1926, pp. 109–111) as adaptive convergences and not as heritages from a common ancestor. Anthony failed to reach any decision in regard to the precise relationships of the Archaeoceti. At the end of his memoir, he reiterates his uncertainty by remarking that if the archaeocetes are creodonts adapted to an aquatic life, then they are not related to the Recent Cetacea, or if on the contrary they are descendants of the primitive Condylarthra, then they belong in the same phylum as the Recent Cetacea.

Strong evidence for the derivation of Recent Cetacea from primitive quadrupedal mammals is found by Anthony (1926, pp. 97–98, 133) in the persistence of
certain vestigial structures, as for instance the remnants of the pelvis and the hind-limb, the muscles of the manus, the turbinate bones in mysticetes, the olfactory bulb in mysticetes, the conjunctival glands, the muscles of the external ear, and the sinus hairs. Although the evidence as Anthony sees it revealed in the soft parts of Recent Cetacea suggests a close relationship between them and the Perissodactyla, on his phylogenetic chart (p. 133) the Recent Cetacea are derived directly from the early Condylarthra, while the Perissodactyla are shown as descendants of the Phenacodontidae and near related forms and they in turn from the early Condylarthra.

Anthony takes the view that there is no adequate morphological evidence to connect the Recent cetaceans with the carnivores, either in the visceral organs or in the nervous system, or in other structural conditions. On the contrary, beginning with Hunter (1787), experienced anatomists, including Flower (1838a), Pouchet, Beauregard, Bouvier (1889), and Neuville, have noted morphological details which approximate conditions in the ungulates. Among the structural peculiarities common to Recent Cetacea and the Ungulates, which are considered by Anthony as infinitely more important than some that have been cited in the past, are the following: (1) Alone with the perissodactyls, cetaceans possess a lateral diverticulum at the entrance to the narial fossae [pp. 118–121]; (2) cetaceans like the perissodactyls and Hyrax possess a diverticulum of the eustachian tube [pp. 117, 121–123]; (3) the communication of the two pleura through the anterior mediastinum is found in cetaceans and the Equidae (Neuville, 1923, pp. 38–39); (4) the tapetum chorioideum of the eye of cetaceans like that of ungulates is constituted by the superposition of thin lamellae of conjunctival tissue, piled up like the leaves of a book, while in the Carnivora, Fissipedia as well as Pinnipedia, it is constructed of superimposed cellular layers that can be dissociated into nucleated cellular elements [A. Rochon-Duvigneaud in Anthony, 1926, pp. 123–127]; (5) the os penis is absent in both cetaceans and ungulates but is generally present in the Carnivora, Fissipedia as well as Pinnipedia [p. 127]; (6) the multilobed or convoluted ovary of cetaceans with its numerous protuberant Graafian follicles exhibits very great affinities with that of Hyrax, and according to Champy [in Anthony, 1926, p. 127] is distinguished from the carnivore ovary by a series of important details; (7) like in perissodactyls, one observes in male cetaceans, particularly in ziphoids, the frequent persistence of Müller’s ducts [pp. 127–128]; (8) as is the case in numerous ungulates (Perissodactyla, Suidae, Hippopotamidae, Tylopoda, and Tragulidae), cetaceans have a non-deciduate and diffuse placenta, while the Carnivora on the contrary possess a deciduate and zonary placenta [p. 128]; (9) the presence of the hippomanes body in the fetal membranes of cetaceans is another resemblance to the Perissodactyla [p. 129]; (10) like most ungulates, cetaceans bear but a single young, while the Carnivora generally have large or small litters [p. 129]; (11) by the long period of gestation, cetaceans approach ungulates and are thus distinguished from the Carnivora in which gestation is always relatively short [pp. 129–130]; and (12) in the case of cetaceans, the young at birth
is bulky and very much advanced, the neopallium of its brain presenting the same folds as that of an adult. It is exactly the same in the case of ungulates, while on the contrary new-born Carnivora are of small bulk in comparison to the adult, little advanced in their development, and their neopallium presents as yet only fundamental folds.

The Ungulata are not considered to constitute a natural group by most paleontologists. Anthony likewise holds that the Artiodactyla are widely removed from the Perissodactyla. Therefore, inasmuch as some of the morphological details which have been utilized to demonstrate a genetic relationship with the Cetacea are common to both the Artiodactyla and the Perissodactyla, it is obviously difficult to differentiate between seemingly deep-seated characters and certain resemblances which after all may be either simply primitive placental heritages or additional instances of convergent or parallel development. Of the anatomical characters listed by Anthony, two alone (Nos. 3 and 4) are so far as known peculiar to the Perissodactyla and the Cetacea.

As regards the construction of the main blow-hole cavity, and the anterior and posterior narial diverticula in the odontocetes, recently made dissections by Raven and Gregory (1933) and Huber (1934) tend to show that the complicated spiracular sacs which open into the narial passages are aquatic specializations associated with the water-adapted breathing mechanism. Huber’s researches (1934, pp. 122–125, 132–134) on Tursiops and Monodon show that with the contraction of special muscles the external orifice of the blow-holes is closed, compressing the spiracular cavity and the premaxillary diverticula, and as a result the air contained therein exerts sufficient pressure to force the plugs firmly into the dorsal entrances to the bony narial passages. These diverticula have not been found in the mysticetes by any of the anatomists who have studied the nasal apparatus.

In the Recent Equidae, as well as in the tapir and rhinoceros, the true nasal passage is complicated by the addition of lateral diverticula, giving rise to the so-called false nostril. Gregory concluded that the upper or "lachrymal" fossa of the extinct Equidae probably lodged a greatly enlarged nasal diverticulum. Furthermore, Gregory (1920b, p. 268) states that "it can be shown conclusively that the fossæ in question in the Equidae arose within the family and are not truly homologous with those of Artiodactyla, that there were no such fossæ in the primitive placental mammals of the Paleocene and Eocene, and that the Artiodactyla and Perissodactyla were not derived from a common stem family but are widely distinct orders." There is no paleontological evidence to show that such diverticula were possessed by the early condylarths, as is implied by Anthony’s hypothesis.

Furthermore, Murie (1873a, pp. 246–247, fig. 2) has described nasal structures in an artiodactyl (Saiga tartarica) which he considers to be "veritable homologues of the cetacean spiracular sinuses and their rudimentary nasal cartilages." Nasal diverticula are thus known to occur in odontocetes, perissodactyly, and artiodactyly.
The significance of peculiar specializations, like the diverticulum from the eustachian tube, which has developed along somewhat different paths in the Mysticeeti, Odontoceti, Hyracoidea, and Perissodactyla, is not clear. In the Mysticeti (and also Archaeoceti) this diverticulum is lodged within the osseous walls of the pterygoid fossa, but among the Odontoceti it probably attains its maximum development in Delphinus where it is extended forward as a rostral air sac on the under surface of the maxillary. In the Recent Equidae and the tapir, these diverticula form large guttural sacs, but only vestiges of these structures are preserved in the rhinoceroses.

One may well question the genetic importance of a single structure like the anterior mediastinum, inasmuch as the entire respiratory mechanism (Müller, 1898; Howell, 1930, pp. 315–322) has been so extensively modified for aquatic habits.

As regards the comparative anatomy of the eyes of the Mysticeti and Odontoceti, Püttter (1902, pp. 386–389) has listed in tabular form the resemblances and differences that exist when they are compared with those of pinnipeds. Of all the complex structures that constitute the eye, the histology of the tapetum choroideum seems to be the sole important structural detail that is peculiar to the Equidae and the Cetacea. We have indubitable evidence that optical, physiological, and structural adjustments for under-water vision have been effected in the eyes of cetaceans (Kellogg, 1928, pp. 195–198). The porpoise eye has no cones in the retina. Nocturnal animals as well as those accustomed to faint or subdued light generally have eyes that lack cones in the retina. On the contrary diurnal mammals have eyes with rods and cones in the retina. Rochon-Duvigneaud does not discuss the significance of the histological structure of the tapetum choroideum in relation to the retina.

Contrary to Anthony’s assertion, the os penis is known to be present in at least one mysticete, the Atlantic right whale (Turner, 1913, p. 919, fig. 24).

The ovaries of whales differ from those “of most other mammals in their highly convoluted condition and the prominence of the frequently numerous corpora lutea and [Graafian] follicles, which give the surface a very irregular appearance” (Mackintosh and Wheeler, 1929, p. 382). The persistence of a similar type of ovary in both the Hyracoidea and the Cetacea strengthens evidence from other sources that both have retained a number of heritages from primitive placentals. Weber (1904, p. 710) and Gregory (1910, pp. 360–364) have discussed the peculiarities of the Hyracoidea which distinguish them from all other ungulates. Although their precise affinities may be obscured by recently acquired specializations, the evidence as summarized by Gregory suggests that the Hyracoidea represent “an offshoot of the stock which gave rise to the insectivores, creodonts, condylarth, periphytids, etc.” Champy does not list the important structural details that distinguish the cetacean ovary from that of carnivores, nor does he point out any resemblances to the perissodactyl ovary. Certain primitive features are, however, discussed by Ommanney (1932, p. 440) including the absence of any peritoneal covering or “tentorium” to enclose the ovary, which either lies free upon or is lodged
in a pouch-like recess formed by the folding of the broad ligament (as described by Turner, 1871, pp. 470–471, for Orcinus), and suspension of the ovary in the abdomen by a plica diaphragmatica, recalling conditions in monotremes and insectivores.

The persistence of the Müllerian ducts in male cetaceans is undeniable, but here we are dealing with the retention of structures which exist at some embryonic stage in all placental mammals, and usually disappear with the formation of the permanent kidneys. A great variety of conditions are found in male cetaceans ranging from the complete absence of any trace of the Müllerian system like in Balaenoptera physalus (Ommannay, 1932, p. 382), through stages of extreme reduction, as for instance the sac-like depression in Kogia breviceps (Benham, 1901, p. 125), to the extreme development, a two-horned structure resembling an uterus bicornis, found in Mesoplodon (Anthony, 1922, pp. 85–89). The lower part of these Müllerian ducts sometimes persists as a small unpaired cavity (Sinus pectoralis) which sinks into or is surrounded by the prostate gland, as for instance in primates, many carnivores, insectivores, and Balaenoptera as described by Daudt (1898, p. 295). In certain perissodactyls (horse, donkey and zebra) as well as in Monodon monoceros and Delphinapterus leucas the Müllerian ducts are represented by a cæcum (Vagina masculina), bifid at its tip. These ducts attain their maximum development in rodents (beaver), artiodactyls (goat and reindeer), and some carnivores, where the Müllerian system (Uterus masculinus) is constituted for a short distance by a central canal which bifurcates, forming two long lateral horns between the vasa deferentia, like in Mesoplodon. Embryonic survivals, such as the Müllerian system in males, are possessed by mammals simply because these development stages have never been lost during growth.

The adediate and diffuse placenta of cetaceans, at least in the case of Phocaena phocoena (Wislocki, 1933), is of the epithelioc-chorial type, resembling the described conditions in certain artiodactyls (sow, hippopotamus, and camel), perissodactyls (horse and tapir), the pangolin (Manis), and lemurs (with possible exception of Galago). The occurrence of this type of placenta in such widely separated types as lemurs, pangolins, and artiodactyls removes much of the genetic importance attributed to its coexistence in perissodactyls and cetaceans.

After listing the primitive and distinctive features in the urino-genital system of the Cetacea, Ommannay (1932, p. 442) remarks that “besides many extremely primitive characters indicating not necessarily origin from, but affinity to some very primitive Insectivore-like mammal, the greatest number of points show resemblance to the Ungulata, especially the Perissodactyls.”

It is incontestible that an “allantoic” body, corresponding to the “hippomanes” body met with in the fetal membranes of a mare, has been found floating freely in the allantoic fluid of Platanista (Anderson, 1879, pp. 492–493) and Delphinus (Chabry and Boulart, 1883, p. 575). Dastre (1879, vol. 2, pp. 545–554; see also, Jenkinson, 1906, pp. 90–93) noted the presence of these bodies in the amniotic liquid of certain artiodactyls (sheep, cow, and pig). These chorial plaques or masses appeared first at a fetal length of 10 to 30 mm., but disappeared at full
term. Since they were most plentiful during the period of maximum intensity of ossification (qualitative), Dastre regarded these chorial plaques as constituting some sort of a reserve where phosphatic substances accumulated, awaiting the moment of their utilization in the fetal organism. We thus observe that the "hippomanes" are calcareous concretions (Needham, 1931, vol. 3, pp. 1286–1287) containing calcium phosphate and glycogen, that they float free in the amniotic liquid of at least some odontocetes, artiodactyls, and perissodactyls, and that they may be associated in some manner with the calcium metabolism of the embryo. Inasmuch as Anthony holds that the Artiodactyla as well as the Carnivora are derived from the Creodonta, the presence of these bodies in artiodactyls greatly weakens this portion of his argument. It is also of some interest in this connection that Hamlett (1935) has found hippomanes in the yolk-sac cavities of *Lemur fulvus* and *Phaner furcifer*, but no allantoic hippomanes were found in the limited series examined.

Blue and fin whales are normally polyoestrus, the ovaries shedding a single ovum at each ovulation. In a very small percentage of cases, the ovaries liberate several ova at one ovulation (Wheeler, 1930, p. 413). The frequency of twin fetuses recorded by Risting (1928) for finback and blue whales taken in the Antarctic seas is less than 1 per cent. There are also a number of records of multiple fetuses for whalebone whales. Seven fetuses were taken from a female blue whale at South Georgia in 1924–25 (Risting, 1925; 1928, p. 101). A female finback caught at Hellis Fjord, Iceland, on July 10, 1909, had six fetuses (Haldane, 1910, p. 117), and the same number were found in a female finback at the Getares whaling station in southern Spain. There are also several records for three fetuses. One can with equal propriety argue that the occasional occurrence of multiple fetuses is an indication of relationship with the Carnivora. Favoring this view also is the occurrence of eight teat "anlagen" in the earliest fetal stages of *Phocaena* (Kükenthal, 1893, p. 356).

Tabulated statistical data on fetuses gives "a period of gestation of slightly over ten months in the case of blue whales, and of eleven and a half months in the case of fin whales" (Mackintosh and Wheeler, 1929, p. 428). Anthony accepts a gestation period of ten months for some odontocetes (*Delphinus* and *Phocaena*). At the time Anthony was studying this question, the duration of the gestation period in certain mustelids had not been accurately determined. The gestation period for the fisher (*Martes pennanti*) as determined by breeding them in captivity is according to Frank G. Ashbrook (personal communication) from 350 to 360 days. For the marten (*Martes americana*) the gestation period lasts from 259 to 275 days (Ashbrook and Hanson, 1930). The duration of the gestation period of cetaceans thus does not differ markedly from that of some Mustelidae. Returning again to the perissodactyls we find that the gestation period for the horse is given by Anthony as 347 days and for the rhinoceros 16 months. All of the above-mentioned types thus have an exceptionally long gestation period, but such an accord is not necessarily an indication of genetic relationship.
The body of the new-born cetacean most certainly is disproportionately large as compared with the mother and also very much advanced in development. At birth the young cetacean becomes a free-swimming individual, dependent upon its own exertions not only to escape from being drowned, but also to suckle its mother, and to avail itself of such protection as the mother may be able to render against predatory enemies. The mental and physical capacities of the new-born cetacean must be developed sufficiently to cope with the aquatic environment, since it cannot be hidden like the young of land-dwelling mammals until such time as it is physically able to make concerted use of its faculties.

Certain topographic features of a brain belonging to a *Megaptera* fetus, particularly the concentric arrangement of a series of curved fissures around the Sylvian fissure (= gyrus lunaris of Anthony) of the cerebral hemisphere, according to Anthony (1925; 1926, p. 118) tend to show that the neopallium of cetaceans approaches closer to that of ungulates than to that of carnivores. He states (1925, p. 681) that the period during embryonic development when these fundamental folds of the cerebrum are observable is relatively short. Turner, however, has described the brains of *Monodon monoceros* (1890, p. 136, fig. 32) and also of *Balaenoptera acutorostrata* (1890, p. 136) in which the convolutions on the cranial surface of the neopallium surmounting the Sylvian fissure are likewise divided by curved fissures into four great arcuate tiers. It is to be noted, however, that Anthony does not deny that a similar concentric arrangement of fissures characterizes the carnivore brain. He remarks that it was not possible for him to compare the morphology of the neopallium in cetaceans with that of ungulates. Since then the microscopic structure of the cerebral cortex of *Tursiops truncatus* has been studied by Langworthy (1932).

Langworthy is convinced that aquatic adaptation has produced marked changes in the central nervous system of the porpoise (*Tursiops truncatus*) and that the chief factor contributing to the differentiation and growth of the cerebral cortex is the great influx of sensory impulses, particularly auditory stimuli from the cochlear nerve. The fore-brain has rotated to such an extent that the Sylvian fissure extends in a vertical direction. The cerebral hemispheres are large, the convolutional pattern of sulci and gyri is extremely complex, and the whole brain is fore-shortened antero-posteriorly. A primitive architecture exists in the cerebral cortex, the cells being few and the cell layers poorly differentiated. Furthermore, according to Langworthy (1932, p. 478) “many of the sections of the cerebral cortex of the porpoise described here have a primitive structure very similar to the undifferentiated cortex described by Watson in Insectivora,” and also the “general structure of the area frontalis is similar in the porpoise and the cat” (p. 479).

Some of the resemblances cited by Anthony can be explained as primitive placental heritages, a few seem to have been built up by the processes of convergent and parallel development, and the inconclusive nature of others is readily apparent.
RESEMBLANCES OF THE ARCHAEOCETI TO THE SIRENIA

Proof of the relatively near kinship of the Cetacea (and Archaeoceti) to the Sirenians is found according to Gill (1873b) in the common character of atrophy of the hindlimbs and pelvis, the pisciform shape of the body, and adaptation for habitual life in the water. He explicitly states (1873b, p. 264) that “the extinct zeuglodonts, and especially the Basilosauridae, even indicate the possibility, if not probability, of the derivation of the Cetea from a pinniped avus, ... nor is there any cogent evidence, apparently, against the descent of the sireniants from a mutilate descendant of a proto-pinniped ancestor.” It is far more credible, in the opinion of Gill (1873b, pp. 262–263), “that the ordinary cetaceans and the sireniants are derivatives from a common original stock—a generalized gyrencephalic type—whose form had already been modified for continued aquatic life by the reduction or atrophy of the hinder members, and that the existing orders represent the extreme specialization in diverse directions from such a common type, than that the two forms have independently diverged from two ambulatorial types.”

The morphology of Recent Cetacea (Weber, 1904, pp. 552–584) and Sirenia (pp. 727–740) on the contrary offers convincing evidence that the resemblances cited by Gill are purely convergent adaptations. The cumulative paleontological evidence, also, supports the view that the Sirenia approach the Proboscidea (Gregory, 1910, pp. 407–409) and that they are not genetically related to the Cetacea.

It has been claimed by Beddard (1902, p. 120) that Haeckel advocated some sort of a genetic alliance between the Sirenia and the Cetacea. This observation is not entirely accurate, as may be readily seen by reading Haeckel’s comments on this question. We find that Haeckel (1895, p. 564) asserts that the deep-seated and extraordinary modifications of the body, particularly the fish-like shape, which characterize his “Legion Cetomorpha” are particularly important and instructive, for they demonstrate that complete adaptation to life in the water brought about entirely similar results in the descendants of three orders of terrestrial placental mammals. This triphyletic convergence in the outward appearance of the three orders (Sirenia, Mysticeti, and Odontoceti) comprising the Cetomorpha is explained by Haeckel (1895, p. 564) as the mechanical consequence of functional adaptation and progressive hereditary transmission. Convergence has affected not only the external body form and the hide, but also the inner soft parts and the skeleton. Nevertheless deep-seated differences in the construction of certain organs, as for instance the nasal passages, clearly demonstrate the polyphyletic character of the Cetomorpha. According to Haeckel (1895, pp. 562–563) the Sirenia are descendants of herbivorous placentals, the toothed whales (including Zeuglodon) are derived from carnivorous placentals, while the whalebone whales came from a third order. He accepts Kükenthal’s view (1893, pp. 348–349) that the toothed and the whalebone whales stand in no direct phylogenetic relationship, but that on the contrary they are derived from two distinct groups of terrestrial mammals.
RESEMBLANCES OF THE ARCHAEOCETI TO THE MYSTICETI AND ODONTOCETI

The problem of the origin of the Archæoceti as well as their relationships to the Odontoceti and Mysticeti have long engaged the attention of anatomists, cetologists and palæontologists. Owen (1839), after having studied the remains of Basilosaurus cetoides submitted for examination by Harlan, concluded that the microscopic structure of the crowns of the teeth and the implantation of the roots in distinct alveoli, as well as the persistence of anterior and posterior epiphyses ankylosed to the vertebral centrum and the conformation of the neural arch was adequate proof that this animal belonged to some cetaceous mammal, "intermediate between the cachalot [Odontoceti] and the herbivorous species [Sirenia]." Müller (1849, pp. 5, 31) studied critically the imperfectly preserved cranial and skeletal remains belonging to Basilosaurus and Zygoryzsa which has been assembled by Koch in Alabama and arrived at the conclusion that, although these archæocetes possess structural peculiarities suggesting a position intermediate between the pinnipeds and the cetaceans, they actually belong in the Cetacea.

Gill (1870, p. 502; 1872, p. 93) groups the archæocetes in a suborder equivalent in importance to the Odontoceti and the Mysticeti. Brandt (1873a, p. viii) places the archæocetes and the squalodonts as families in a tribe subordinate to the Odontoceti. Dames (1894, p. 219) likewise concludes that the archæocetes should be allocated among the Cetacea, but holds that there are no valid grounds for separating them as a suborder distinct from the Odontoceti. On the other hand Fraas (1904a, p. 220) is convinced that the Archæoceti comprise an extinct subgroup of the Credodonta, and that the observed resemblances to the Cetacea have been effected by convergent development during adaptation to life in the water. Fraas emphatically asserts that the Archæoceti are completely separated from the Cetacea. Weber's later view (1904, p. 584), that the line of cetacean ancestry goes back to prototypal archæocetes, differs considerably from that expressed by Fraas, for he believes that the Mysticeti were "detached very early from animals, which likely stand near to Zeuglodon, and from them also developed the Odontoceti."

The concept that the Archæoceti are not only primitive eutherians adapted to habitual life in the water but also Cetacea is definitely established according to Stromer (1908b, pp. 158–167) by the comparative analysis he has given for some 88 structural characteristics. Stromer (1908b, p. 174), however, considers that the Archæoceti constitute a series entirely distinct from the Odontoceti, the former during the upper Eocene developing gigantism and the latter, differentiating more slowly, breaking up into several families which continued their parallel evolutionary development. Stromer is willing to agree with Weber (1886, p. 243) that Basilosaurus constitutes one of the unsuccessful attempts of the archaic cetacean stock to create another side-branch, and holds (1908b, p. 171) that it is now firmly established that the Mysticeti and the Odontoceti in their evolutionary
history have been separated for a very long time, although both had a common ancestor.

Abel (1913, p. 220) employs the term Archaeoceti in a much broader sense than any other investigator and allocates the Microzeuglodontidae, Patrocetidae, Agrophididae, and Zeuglodontidae (including Protocetus, Eocetus, Dorudon, Basilosaurus, etc.) to this order. The Zeuglodontidae are considered by Abel to be an aberrant offshoot from some stem-ancestor among the creodonts, while the Microzeuglodontidae are given a central position ancestral to the Mysticeti and to all of the Odontoceti with the exception of the Delphinidae (sensu latu).

According to Winge (1921, p. 15) "the genera of zeuglodonts taken together form the section Archaeoceti, the source from which all the higher cetaceans have originated." It has been the contention of other investigators that, if the Archaeoceti are true cetaceans, structural resemblances will be more marked in the early archaic toothed whales than in Recent odontocetes and mysticetes. Hence transitional structural conditions or at least some of the initial steps in the remodeling process that eventually led to the development of typical odontocetes and mysticetes should be found when these archaic toothed whales are compared with archaeocetes. The arguments thus far advanced by those interested in this problem have centered around the structural peculiarities of the upper Eocene Agrophius pygmaeus, the late Oligocene or Miocene Microzeuglodon caucasicus, and Patrocetus ehrlichii.

Stromer (1908b, p. 173) has discussed the possibility that the Odontoceti may be connected with a Protocetus-like prototypal cetacean through an Agrophius-like intermediate stage. He lays especial emphasis on the remarkable similarity to the archaeocetes in the width of the temporal fossae, the not greatly retracted nasal opening and the part the parietals take in the construction of the cranial roof of the Agrophius skull. Nevertheless the overlapping of the cranial bones shows that Agrophius pygmaeus (True, 1907) is more highly differentiated than any known member of the Archaeoceti and the single preserved serrated cheek-tooth is far in advance of the orbit. The association of Agrophius (Kellogg, 1928, p. 49) with the odontocetes rather than with the mysticetes rests on a much sounder basis, for this archaic toothed whale undoubtedly represents a somewhat distantly related precursor of the squalodonts, which include a number of diverse types. There is reason to believe that Agrophius at least represents a morphological stage through which the toothed whales may have passed in their development and that the subsequent remodeling of the odontocete cranium was accomplished by a forward movement of the occipital region until the supraoccipital shield came in contact with the frontals.

The manifold resemblances of the Archaeoceti to the Squalodontidae, according to Stromer (1908b, p. 172), in such details as the auditory apparatus, the projecting anterior ends of the premaxillaries, and the dentition, as well as the circumstance that in Dorudon the first (milk) dentition is not replaced until full size is attained, while in the Recent Odontoceti (Kükenthal, 1893, p. 420) it is the first
dentition that persists as the functional one, can not be attributed to convergence, but on the contrary indicate a direct near relationship. Within the family Squalodontidae (Squalodon, Prosqualeodon, and Neosqualodon), Stromer sees a transitional series that connects them with the as yet unknown older and smaller Protocetus-like archaeocetes.

The pterygoid fossæ of the Dorudon skull seemingly indicate relationship with the Mysticeti. Although as regards the whalebone, the mandible, and the thorax the Mysticeti are more advanced, they are otherwise less specialized than the Odontoceti. Therefore Stromer (1908b, p. 172) considers it quite probable that the Mysticeti were detached from the common stem before the appearance of Protocetus and that they were less altered than the more closely connected later Archaeoceti and Odontoceti.

Convincing proof is found by Dart (1923, pp. 637, 643) in endocranial casts for the concept that the archaeocetes were deflected from the main path of cetacean evolution and that they, or at least the genera represented among the endocranial casts studied by him, were not the ancestors of the Cetacea. These archaeocetes could not have given rise to Prosqualeodon davidii according to Dart (1923, pp. 639–640), for the actual bulk (750 c.c.) of the latter's endocranial cast is slightly less than that (785 c.c.) of the middle Eocene Dorudon intermedius. In accordance with Marsh's law of increasing brain weight, the progenitor of Prosqualeodon must have possessed a considerably smaller brain than that of this middle Eocene archaeocete. Furthermore, in the archaeocetes the olfactory peduncle is attached to the ventral surface of the fore brain in the characteristically mammalian fashion, while in Prosqualeodon the nipple-like olfactory apparatus is inserted somewhat higher on the anterior end of the forebrain. The relative atrophy of the optic chiasmic region is demonstrated even in the middle Eocene archaeocetes by the contraction of the area between the olfactory peduncles and the tuber cinereum. Conditions are entirely different on the endocranial cast of Prosqualeodon, where there is evidence of an initial expansion of the basal area between the insertion of the olfactory peduncles and the tuber cinereum. Crossing this basal interspace is a well-marked optic chiasma, indicating elaborate visual capacities—"an utter impossibility in the offspring of the zeuglodonts here described at any epoch" (Dart, 1923, p. 641). The idea that the ancestors of the Recent Cetacea went through a stage of expansion of the basal regions of the brain, not displayed by any of the archaeocetes studied by Dart (1923, p. 642), receives additional support from the conformation of the antero-ventral portion of the fore brain of Prosqualeodon.

In marked contrast to the archaeocetes according to Dart (1923, p. 641), "the evolution of the cetacean stock, while it depended to some degree upon an initial trigeminal specialization, was not effected by any sudden reliance upon this sense to the neglect of other important senses, but depended upon an orderly and balanced correlation of this hypertrophy with a concurrent aggrandissement of the visual and auditory senses."
Miller (1923, pp. 3–4, 11–12) like Stromer (1908b, p. 172) takes the view that the transition from the archaeocete type of skull to that of the toothed whale (Odontoceti) involves simpler principles than is the case for the whalebone whales (Mysticeti). He argues, however, that the archaeocete skull is highly specialized in a direction toward elongation and narrowing of the post-rostral region, and that the cranial architecture “appears to be removed from rather than antecedent to the line of development which led to the telescoped, broadened condition of the post-rostral region seen in the skulls of all modern Cetacea.” Furthermore, the dentition of the archaeocetes “appears to have been, even in such an aberrant type as Basilosaurus, uniformly undergoing a simple and not very unusual process of reduction in the normal mammalian manner, a tendency which would not lead by any known process to the remarkable and unique condition of polyodonty through which the modern cetacea have either once passed or are now in.” While it appears doubtful to Miller, that the known archaeocetes “were ancestral to any of the Recent whales it seems probable that they came from a terrestrial stock which was nearly related to the latter’s forerunners; and there can be little question that in certain details of structure they possess features which are morphologically intermediate between those of early land mammals and those of some living cetaceans.”

The humerus of Microzeuglodon caucasicus (Lydekker, 1893, p. 559, pl. 36, fig. 2) is an important link in the history of the transformation of the odontocete forelimb, for it has retained a distinct deltoid crest, a head similar to that of archaeocetes, both proximal tuberosities, and a reduced distal trochlea for limited flexion with radius and ulna. This humerus, measuring 4.4 inches in length, is characterized by the compressed form of the shaft, the prominence of the deltoid crest, and by the “circumstance that the radius and ulna articulated to the distal end by means of two slightly convex facets set obliquely to each other, the one being anterior and the other posterior” (Lydekker, 1893, p. 560).

According to Abel (1905, p. 36), Microzeuglodon caucasicus can be considered as the point of origin for the more recent squalodonts, and the former doubtless has predecessors with a dentition analogous to that of Zeuglodon and therefore is derived like the archaeocetes from the creodonts. There can be no doubt today, states Abel (1905, p. 34), that the upper Eocene genus Zeuglodon is not the source for the derivation of the squalodonts, since it is “so specialized in a single direction that it is useless to search for an intermediate type connecting Zeuglodon and the Squalodontidae.” To Stromer (1908b, p. 173), however, the lack of adequate comparable skeletal material hinders further consideration of the possibility that Microzeuglodon may play an intermediate rôle between the Squalodontidae and the Protocetus-like smaller Archaeoceti. In the opinion of True, Microzeuglodon caucasicus does not bridge over the gap between the Archaeoceti and the Odontoceti. True (1908a, p. 386) contends that the position of the teeth on the rising anterior edge of the coronoid process of the mandible and “the form of the humerus—particularly the quite good articular facets—appear to me to indicate that this is a zeuglodont, with no very strong leaning toward Squalodon. If this be con-
ceded, there is no way at present in which to connect the Cetacea with any group of land mammals.” These objections led Abel (1913, p. 207) to a restudy of this problem. Abel does not accept True’s conclusions in regard to the archaeocete nature of the mandible, but on the contrary expresses the belief that the intervals between the hinder cheek teeth on the steeply rising anterior edge of the coronoid process constitute a deep-seated distinction between Microzeuglodon and the archaeocetes.

Abel (1913, p. 215) believes that a Protocetus-like type with teeth conditions as in Microzeuglodon caucasicus was the starting point for the Patriocetidae stock. Thus according to Abel (1913, p. 219) from prototypal archaeocetes have evolved the Microzeuglodontidae and they in turn gave rise to the Patriocetidae, the precursors of the older mysticetes. In the Microzeuglodontidae, the most primitive family of archaic cetaceans according to Abel, the hinder mandibular cheek teeth are not dwarfed, the crowns of these teeth are serrated on both cutting edges, and the teeth are not closely crowded but are separated by distinct intervals. The essential alterations that have been effected in skull construction during the evolvement of the Patriocetus stage from a pre-Protocetus stage are explained by Abel as consequences of the shifting of the dorsal nasal opening toward the rear, the atrophy of the temporal muscles thus permitting a widening of the roof of the cranium, and the remodeling of the teeth for a grasping function.

The most obvious peculiarity of the braincase of Patriocetus (Abel, 1913, pl. 6) is the thin ledge-like projection from the parietal that extends backward from the supraorbital process of the frontal to the apex of the supraoccipital and overhangs the temporal fossa. Abel states that the postero-internal extremity of the maxillary stops at the antorbital line and is not extended backward above the frontal along with the ascending process of the premaxillary (which extends backward to the parietal), but instead the hinder end of the maxillary slides under the supraorbital process of the frontal. The last-mentioned detail appears to be substantiated by the published photograph of the skull (Abel, 1913, pl. 2), indicating that an infraorbital plate or process of the maxillary is present. If the contact between the frontal and maxillary has been correctly interpreted, the normal mammalian relationship of these bones has been retained and is not materially different from the relations of these bones in Eubalaena and in the archaeocete type of skull.

As additional proof for the rôle which Patriocetus ehrlichii [=Patriocetus grateloupii (Meyer)] is supposed to play as a connecting link between the archaic whales and the mysticetes, Abel (1913, p. 186) makes use of Kükenthal’s theory (1893) that in the course of ontogenetic development the many-cusped teeth divided into as many single teeth as there were cusps on these teeth. Among some thirty finwhale embryos, Kükenthal (1893, pp. 430–437) found several that had 53 conical crowned teeth “anlagen” in each upper jaw, of which a part (in varying numbers and in different positions) were united in larger aggregations, some comprising as many as four single teeth. These teeth are resorbed later during embryonic growth.
On applying this hypothesis to Patriocetus Abel finds that if one reckons each cusp as a potential single tooth, by adding up not only the crown points of the four anterior grasping teeth, but also the seven cusps on each of the seven two-rooted cheek teeth, a total of 53 single teeth can be obtained by division. This is the same number of teeth that Kükenthal found in each upper jaw of finwhale embryos. Accordingly Abel believes that there can be no doubt that Patriocetus represents the starting point for the mysticete embryonic dentition. With this conclusion, Kükenthal (1922, p. 73) is not willing to agree unconditionally, for he holds that the mysticete embryonic dentition is derived from a heterodont set in which the cusps are arranged one behind the other on the tooth crown like those of fish-eating mammals, and that one is not justified in saying that the ancestors of the mysticetes are to be sought among the archaic whales, especially not Patriocetus.

More recent palæontological evidence indicates that Microzeuglodon and Patriocetus were almost if not quite contemporaneous. Furthermore, at least one member of the mysticete stock (Cetotheriopsis lintianus (Meyer)) is associated with Patriocetus in the white sands of the Linz basin in Austria. Since the architecture of the skull of Microzeuglodon is wholly unknown and our knowledge of the mandible limited to a hinder fragment containing the four posterior cheek teeth, the possibility that it may represent a morphological stage which eventually was remodeled along the lines of Patriocetus can only be advocated on purely hypothetical grounds.

One may visualize (Kellogg, 1928, p. 47) the steps in the transformation of an archaeocete type of skull to that of some of the Eocene archaic toothed whales, but skulls demonstrating the actual stages have not as yet been found. Assuming that the skulls of these archaic toothed whales have been derived from the archaeocete type of skull, one must necessarily concede that the outer edge of the maxillary immediately in front of the supraorbital process of the frontal and the tooth-bearing portion of the maxillary, which projects backward beside the jugal below the orbit, must degenerate or be eaten away in order that the maxillary may be pushed back over the supraorbital process of the frontal. The jugal must lose its connection with the maxillary and fuse to the ventral surface of the lachrymal bone. The lachrymal bone must continue to retain its position at the anterior margin of the supraorbital process of the frontal, but must be shifted so that it comes to lie on the ventral instead of the lateral face of the maxillary. Granting that these alterations were effected in the course of time, what became of the hinder cheek teeth that were located on the maxillary below the anterior end of the orbit on all known archaeocete skulls? On all squalodont skulls the maxillary cheek teeth are increased to at least eleven and the hindermost molar is located considerably in advance of the orbit, while the maxillary has been shoved backward to the supraoccipital, concealing the frontal.

In the view of the limitations imposed by the actual mechanical construction of the archaeocete type of skull, it is difficult to see how this type of cranial archi-
tecture could be remodeled more readily in the direction leading to the odontocete type of skull than to that of a mysticete. On the contrary, the mysticete skull and particularly the older types that have been referred to the mysticete line of descent, as for instance Archaeodelphis (Kellogg, 1928, pp. 180–181) and Protocetus, possess a type of cranial architecture that does not involve as many deep-seated mechanical difficulties in the hypothetical alteration of the archaeocete type of skull as are necessitated to perfect a generalized odontocete skull from the same source.

In the foregoing review of conflicting opinions, one sees that the more recent students of this problem are convinced that the separation between the Odontoceti and the Mysticeti has been one of long duration, and that no known archaic toothed whale possesses the structural details necessary for the demonstration of the actual mechanical method by which the archaeocete skull was transformed into that characteristic of either of these suborders. It will be observed also that the paleontological record of the Cetacea prior to the Miocene is wholly inadequate for a satisfactory demonstration of descent in any particular direction, and that the lack of adequate skeletal remains of archaic cetaceans from the Oligocene and the later Eocene constitutes a serious obstacle to the accurate elucidation of the steps by which such a transformation might have been effected. Furthermore, in all the attempts that have been made to reconstruct the line of descent of Recent Odontoceti and Mysticeti some wholly unknown prototypical cetacean that antedated the appearance of Protocetus atavus is postulated as the original source for the derivation of all the Recent Cetacea as well as the Archaeoceti.

There have been several, however, among those that have studied the Recent Cetacea, notably Kükenthal and his students, who have consistently argued that the Archaeoceti, Odontoceti, and Mysticeti are each derived from entirely different land-dwelling progenitors.

As an advocate of the diphyletic origin of the Recent Cetacea, Kükenthal (1893, pp. 348–349) contends that the Mysticeti and the Odontoceti are not directly related to one another and that the existing similarities in various organs are merely instances of convergence. Among the structural peculiarities which led Kükenthal to this conclusion are: (1) the deep-seated differences in the construction of the nose, particularly the dissimilar mechanisms for closing the external nostrils in the Odontoceti [pp. 322–326, 348] and the Mysticeti [pp. 343–348], (2) the obliteration in adults and the marked degeneration in fetal stages of the Regio olfactoria, the transformation of the hinder upper accessory diverticula, and the reduction of the ethmoid bone muscles to membranous structures, all of which distinguish the Odontoceti from the Mysticeti, the latter having a distinctly formed though reduced Regio olfactoria and three ethmoid muscles [p. 347], (3) the union in adult Odontoceti of the upper portions of the nasal passages to form a very large roomy spiracular sac (in very small fetuses the two nasal openings are almost completely separated from one another [p. 327]), a structure which is entirely lacking in the Mysticeti [p. 348], (4) one external nostril in the Odontoceti and two external nostrils in the Mysticeti [p. 348], (5) the existence of remnants of a former osseous
exoskeleton, perhaps similar to that of an armadillo, in the Odontoceti [p. 257] and the non-existence of such remnants in the Mysticeti, and (6) the occurrence in the Odontoceti of sinus hairs on both sides of the upper jaw exclusively in fetal stages (with the exception of *Inia* and *Lagenorhynchus*—see Kükenthal, 1914, p. 44) and then only as vestigial structures, while in the Mysticeti, in the fetus like in the adult, more numerous specialized sinus hairs are present on the lips [p. 358].

In opposing this contention Weber (1904, p. 584) argues that the Mysticeti and the Odontoceti have a monophyletic origin and emphasizes that only on the basis of a blood relationship may the existence of the following similarities be explained: (1) the three divisions of the stomach, (2) the position of the testis in consequence of withdrawal of the *descensus*, (3) the construction of the brain, (4) the construction of the mammary glands, (5) the alteration of the forelimb, (6) the presence of conjunctival glands, and (7) the conditions in the middle ear. It does not appear reasonable to Weber that such a specialization would have resulted twice in non-blood related groups.

To this argument, Kükenthal (1922) replies that (1) the partition of the stomach into three divisions in both groups is in reality a phenomenon of adaptation, since the occurrence of teeth in the fetus demonstrates that the mysticetes were fish eaters before they turned to plankton, and in a number of specific details the stomach (Jungklaus, 1898) is less differentiated in the Mysticeti than in the Odontoceti [p. 83]; (2) the position of the testicle is not the same in both groups, testicody (i.e. the abdominal position of the testicle) is secondary, and according to Freund (1912, p. 1151) the torsion of the testicles is a new acquisition, while the incompleteness of the *descensus* (see also Ommanney, 1932, pp. 387–388) may readily be explained as the result of the sinking below the surface level of an organ that might offer resistance to the water [p. 84]; (3) the similarities in the construction of the brain indicate that the progenitors of the Odontoceti and the Mysticeti belonged to a group of mammals whose cerebrum was characterized by the sagittal course of its principal sulci, and also the extraordinary increase of convolutions is probably secondary [p. 83]; (4) the conditions in the skin [including the mammary glands] are to be interpreted as convergences; (5) while the construction of the pectoral flipper in both groups, including the complete envelopment of the fingers, the transformation of the entire limb into an elastic plate movable only at the shoulder joint, and the loss of the nails may argue against diphyletic origin, these similarities are the result of adaptive convergence, since there are fundamental dissimilarities, including the presence of only four fingers in the mysticete manus (the so-called thumb of *Balaena* being identified as the prepollex) and of five fingers, as well as hyperdactylyism also, in the odontocete manus; (6) the occurrence of conjunctival glands in both groups is traced by Püttter (1902) to a secondary chemical adaptation for protection of the cornea against the action of sea-water, causing a functional change in the tear gland, an enlargement of Harder’s gland, and the accompanying formation of a subconjunctival stratum connecting both glands to augment the greasy secretion; and (7) the many similarities in the middle ear are all adaptive,
representing a specialization for reception of water-borne sounds, and furthermore
the elimination of the external auditory passage from sound conduction has taken
place in a totally different and entirely independent manner in the two groups
[pp. 81–82].

These contradictions of statement in regard to identical anatomical structures
subserving the same function show how difficult it is even for such eminent experts
as Kükenthal and Weber to come to some sort of an agreement in regard to the
relative importance to be assigned to similarities and dissimilarities, for by one the
resemblances are classed as convergences (adaptive) and by the other as a demon-
stration of blood relationship (non-adaptive).

Kükenthal devoted more than thirty years to an intensive study of the mor-
phological peculiarities of the Recent Cetacea, and throughout this period he and
his students stoutly defended the hypothesis of the diphyletic origin of the Odonto-
ceti and the Mysticeti. In his last discussion of this problem, Kükenthal (1922)
summarized the evidence obtained in these studies and selected certain structural
peculiarities of each group that in his opinion merited serious consideration. Kük-
enthal tells us that the Recent Mysticeti have (1) the Regio incisiva in small
embryos separated from the rest of the fore part of the palate, but blending in the
course of embryonic development with the upper lip folds which end near Stenson’s
opening (Freund, 1912, pp. 1116–1117) [p. 80], (2) the Pars cochlearis of the otic
capsule from the beginning completely isolated from the basal cartilage mass of
the chondrocranium, except for a precartilaginous connection in front, correspond-
ing to the Lamina supracochlearis (Honigmann, 1917, pp. 65, 78) [p. 76], (3) the
tympanic bulla and periotic enveloped by layers of fatty, elastic and spongiosae
tissues, the elongated posterior process of the periotic being firmly wedged in be-
tween exoccipital and squamosal (Hanke, 1914, pp. 504, 513–514, 517) [p. 81], (4)
no vestige of the auricular cartilage [p. 81], (5) no complicated arrangement of di-
verticula, valves, and nasal muscles [p. 80], (6) nostrils which are closed by water
pressure, the upper portions of the membranous walls of nasal passages being
pressed together since they touch each other when relaxed (Gruhl, 1911, pp. 406–
408) [p. 80], (7) two external nasal openings (nostrils) [p. 80], (8) retained an ol-
factory apparatus, although reduced [p. 82], (9) one nasoturbinal [p. 82], (10)
olfactory epithelium on the ethmoturbinal [p. 82], (11) the epithelial boundary
located at equator of lens of eye (Pütter, 1902, pp. 384, 388), and upper eyelid
broadened, thus moving the eye slit downward [p. 82], (12) lost the organs of taste
(Wolf, 1911, p. 52) [p. 82], (13) a narrow ösophagus, with uniform lumen [p. 83],
(14) the junction of ösophagus with first division of stomach located on the right
side and near proximal end of the latter (Jungklaus, 1898, p. 81) [p. 83], (15) an
enlargement of the second division of the stomach (abomasus or rennet bag) (Jung-
klaus, 1898, p. 81) [p. 83], (16) the stomach as a whole less differentiated than in
the Odontoceti, the divisions being not sharply separated from one another and
having broad communicating openings (Jungklaus, 1898, p. 81) [p. 83], (17) the
spleen (single organ) located on distal end of first division of stomach (Jungklaus,
1898, p. 82) [p. 83], (18) the testicles of male located in a more lateral position [p. 84], (19) the vulva and anus of female separated by a distinct perineum [p. 85], (20) no remnants of hard exoskeleton [p. 79], and (21) the tail dorso-ventrally flattened in smaller embryos of balaeopterids, but relatively shorter than in larger embryos and adult animals [p. 80].

The Recent Odontoceti, however, have (1) the Regio incisiva in small embryos in broad communication with rest of palate, like in most land mammals (Freund, 1912, p. 1118) [p. 80], (2) the Pars cochlearis of the otic capsule (Phocaena, de Burlet, 1913, p. 541) in direct continuous connection with basal cartilaginous mass of chondrocranium (Honigmann, 1917, p. 78) [p. 76], (3) the tympanic bulla and periotic acoustically isolated by surrounding air-filled sinuses and attached to cranium by ligamentary connections (Boenninghaus, 1904, pp. 281–286; 225–231) [p. 81], (4) a vestige of the auricular cartilage buried beneath the skin [p. 81], (5) a complicated arrangement of diverticula, valves, and nasal muscles (see Huber, 1934) [p. 80], (6) nostrils which are closed by muscular compression of air in the diverticula, thus forcing the plugs that function as valves into the bony nasal passages (Gruhl, 1911; see also Huber, 1934) [p. 80], (7) one external nasal opening (nostril) [p. 80], (8) lost all traces of an olfactory apparatus (see Kellogg, 1928, p. 201) [p. 82], (9) no nasoturbinal [p. 82], (10) no ethmoturbinal and no olfactory epithelium [p. 82], (11) the epithelial boundary located on the hinder surface of lens of eye (Pütter, 1902, pp. 384, 388) and a peculiar tilting of the retina (Pütter, 1902, p. 297) [p. 82], (12) the organs of taste persisting in a reduced condition (Wolf, 1911, p. 50; see also Sonntag, 1922, pp. 640–646) [p. 82], (13) a wide and flexible cesophagus [p. 83], (14) the junction of the cesophagus with first division of stomach (masticatory division) located at apex of the latter (Jungklaus, 1898, p. 81) [p. 83], (15) the first division of the stomach the longest (Jungklaus, 1898, p. 81) [p. 83], (16) the third division of the stomach (with mucous glands) often divided into a number of successive sections, the divisions being sharply separated by septa, in whose center are the communicating openings (Jungklaus, 1898, p. 81) [p. 83], (17) the spleen (usually a number of secondary divisions) located on the dorsal side of the first division of the stomach (Jungklaus, 1898, p. 81) [p. 83], (18) the testicles of the male located on the ventral belly wall [p. 84], (19) the vulva and anus of the female lying in a common groove in the skin and encased by a common sphincter [p. 85], (20) remnants of a hard exoskeleton, horny scales with calcareous sediments beneath them (Kükenthal, 1893, pp. 251–258, pl. 16; see also Howell, 1927, p. 6) [p. 79], and (21) a round twisted tail in smaller embryos, later compressed from side to side, but relatively longer than in larger embryos and adult animals.

In estimating genetic relationships, investigators, whether consciously or not, are disposed to stress the importance of details with which they are most familiar and to minimize those that are in conflict with the view they are advocating. Since genetic affinity is assessed by noting degrees of resemblance in morphological details and by interpreting the significance of differences, it is not surprising that an examination of the Recent Odontoceti and Mysticeti should lead such competent anatomists as Kükenthal and Weber to diametrically opposed conclusions.
To evaluate intelligently the opinions of these experts, it is necessary to have a clear understanding of adaptive and non-adaptive anatomical categories. It is the contention of Kükenthal (1922, p. 75) that exclusive reliance on the reasoning employed by comparative anatomists, that is the degree of similarity corresponds to the degree of relationship, must lead to errors. To overcome this difficulty he has therefore endeavored to distinguish between characteristics directly related to aquatic adaptation and those that are heritages from their terrestrial ancestors. Furthermore, he believes that it is desirable to consider not only the form but also the function of the organ, and whether or not similar conditions exist in other unrelated aquatic mammals, as for instance the Sirenia and the Pinnipedia. The measure of success that Kükenthal has attained in his objective analysis of anatomical details will be appraised by each individual reader in accordance with his own viewpoint and experience.

No satisfactory evidence has been presented to show that all structures will be modified during adaptation to life in the water, or that modification will proceed at equivalent speed or even in the same direction in all the various types of cetaceans subjected to this influence. This is particularly true of the auditory apparatus, for fundamentally the construction of the tympanic bulla, the petrotic and the middle ear is identical in the Odontoceti and the Mysticeti. Granting that the degeneration of the external auditory meatus and the pinna has not followed the same path in both suborders, these details do not outweigh in importance the fact that no other aquatic mammal has the osseous auditory apparatus constructed like that of the Mysticeti, Odontoceti, and the Archaeoceti. Since numerous examples of embryonic additions to or falsifications of the original ancestral type have been cited by embryologists, some may question the genetic significance of the fetal structures listed by Kükenthal. The palæontological record of the Odontoceti clearly shows that the remodeling of the facial portion of the skull has resulted in a profound transformation of the nasal region (Kellogg, 1928, p. 201) and that adaptive alterations in the olfactory apparatus and in the nostrils were therefore necessary. Adaptive alterations have undoubtedly been effected in the stomach, as Kükenthal admits, which tend to conceal some of the original details of construction in this organ. Inasmuch as partial descent of the testes characterizes both groups, the precise position of it in the body cavity is of doubtful genetic significance, as is also the occurrence of a perineum separating the vulva and the anus in the female mysticete, for in both the Balaenidae and the Odontoceti the anus lies within the hinder commissure of the vulva and is surrounded by the same sphincter muscle (Ommannay, 1932, p. 392). In consequence of the substitution or addition of certain parts, the remodeling of others, and the complete elimination of some structures, the two orders of Recent Cetacea are quite unlike each other in a number of details.

The conclusion (Kellogg, 1928, pp. 41–42) that cetaceans living and extinct represent a multiserial group consisting of several lines of descent appears to be borne out not only by osteological and paleontological, but also by anatomical evidence. That at least three distinct lines of descent are represented among the
known Cetacea is evidenced by the general acceptance among mammalogists of the three suborders, of which the Archaeoceti or zeuglodonts at present are known to have been in existence at a more remote time than the Odontoceti or toothed whales; while the known geological history of the Mysticeti or whalebone whales, with the possible exception of Archaeodelphis patrius, is much shorter and does not date at present farther back than the Oligocene. The exigencies of an aquatic mode of living are such that the members of the several families of these three suborders assumed a similar outward appearance in conformity with streamline requirements, a mechanically induced convergence which is likewise manifested in many other unrelated groups of aquatic vertebrates, but there is no palaeontological evidence to support any assumption of a remodeling of originally unlike parts to a similar adaptive use. The directions in which the members of these three suborders, collectively and individually, subsequently developed were predetermined by peculiarities in existence in the skulls of their progenitors before the tendency toward the foreshortening of the braincase and the telescoping of the bones had been made manifest. The resemblances between these three suborders are such as to suggest a rather close blood relationship of the original ancestral forms and common descent from some broad-headed stock in which the critical cranial elements were united by squamous instead of dentate sutures. No extinct cetacean skull known exhibits proof of descent of an archaic toothed whale from any known archaeocete, or presents structural conditions necessary to form the basis for the elaboration of the mysticete and odontocete types of skull from a common progenitor.

**SUMMARY**

Anatomists quite generally seem convinced that the brain, viscera, and other soft parts are "notoriously" conservative. They are often inclined to over-emphasize the influence of the animal's environment on such parts as the skeleton, limbs, or teeth, and to minimize the same influences when anatomical details are under discussion. Skeletal characters, cranial foramina, and the construction of the teeth can not be ignored entirely when an explanation is sought for resemblances in anatomical details.

It can not be denied by those capable of appreciating the evidence, which has been made available by numerous investigators, that profound morphological and physiological alterations have been effected in the various organs and tracts of the cetacean body. The functioning of the entire cetacean body is conditioned by adjustments necessitated by an exclusively aquatic existence. Even the reproductive tract is specialized for aquatic parturition, the brain while superficially similar to certain mammals exhibits nevertheless many specialized features, including the complexly folded cerebral hemispheres which owe their differentiation not to the usual olfactory and optic impulses but to those originating in the cochlear nerve, and furthermore the digestive, urinary, vascular and respiratory tracts are similarly adjusted for the requirements of habitual life in the water.
In summation, it would appear that the evidence seems to point toward the concept that the archaeocetes are related to if not descended from some primitive insectivore-creodont stock, but that they branched off from that stock before the several orders of mammals that reached the flood tide of their evolutionary advance during the Cenozoic era were sufficiently differentiated to be recognized as such. Morphologically the archaeocetes seem to stand relatively near to the typical Mysticeti and Odontoceti, although all three suborders were separated from each other during a long interval of geologic time. It is not necessary to assume that any known archaeocete is ancestral to some particular kind of whale, for the archaeocete skull in its general structure appears to be divergent from rather than antecedent to the line of development that led to the telescoped condition of the braincase seen in skulls of typical cetaceans. On the contrary it is more probable that the archaeocetes are collateral derivatives of the same blood-related stock from which the Mysticeti and the Odontoceti sprang.

In the absence of actual annectent fossil types, the more important items of evidence may be summarized as follows:

1. The Archaeoceti were adapted to aquatic conditions of life prior to the middle Eocene.

2. The most primitive known archaeocetes occur in the middle Eocene of Egypt and of Nigeria.

3. The upper Eocene archaeocetes of the Fayum, of England, and of the southern United States obviously represent a more advanced stage in specialization than the middle Eocene forms.

4. Archaeocetes are unknown in formations of Eocene age on the Pacific and Indian Ocean coasts. This gap in the documentary record, however, can not be regarded as conclusive proof of the actual absence of archaeocetes in these oceanic areas during Eocene time.

5. The true place of origin and the ancestry of the Archaeoceti can not be demonstrated conclusively from the available evidence. The arguments advanced, however, for some insectivore-creodont like precursor seem to have a more adequate basis than those adduced for an ungulate ancestry or for any other theory of descent.

6. The Archaeoceti are related to the Mysticeti and the Odontoceti.

7. It is unsafe to attempt to determine the phylogenetic relationships of the Recent Cetacea to any assumed ancestral stock solely by the examination of resemblances and differences in their highly adapted organ systems, for these structures are perhaps of all bodily parts the most rigorously adapted to cetacean functional needs. Furthermore, phylogenetic conclusions should never rest on the evidence of any single anatomical character, however important, but always on the cumulative testimony of as many non-adaptive hereditary features as can be marshalled for examination.

By projecting backward the known facts of embryology, comparative anatomy, and osteology of the Recent Cetacea on what information is available
concerning the extinct forms, one gains a limited conception of the general trend of evolutionary development from the more generalized to the highly specialized living types, from which it is possible to interpret the source of some of the diverse modifications that have been effected. Our conception of the nature of the generalized prototype must necessarily be hypothecated on the general assemblage of morphological details that characterize the Archaeoceti, the Odontoceti, and the Mysticeti.

The hypothetical ancestor of the Archaeoceti must have had an elongated body, with rather long trunk, a laterally compressed tail similar perhaps to that of the fish-eating river otter among Recent carnivores and Potomogale among the insectivores, and small hind limbs. The ancestral stock may be sought among types which possess skulls with the following structural peculiarities:

1. An elongated rostrum, with incisors arranged in an antero-posterior series and not in a transverse series as in known creodonts and carnivores;
2. Hinder cheek teeth extended backward on maxillary considerably behind level of anterior end of jugal;
3. Inner portion of crown of cheek teeth reduced and outer portion elongated;
4. A tubular intertemporal region for olfactory apparatus;
5. A prominent supraorbital process of the frontal and a low orbit;
6. Retracted nasal bones and well-developed turbinal bones;
7. Strong lambdoidal crests and at least a visible sagittal crest; and
8. Mandible characterized by fairly large entrance to alveolar canal, a nonhooked coronoid process, and condyle placed below level of the molars.

On the basis of the existing knowledge of the skeletons of archaeocetes, one may expect to find the following structural peculiarities in the skeletal elements of their immediate precursors:

1. Scapula with high blade, curved vertebral margin, large acromion arising from near anterior border, slender coracoid process, a narrow supraspinous (pre-spinous) fossa and a large infraspinous fossa;
2. Humerus with large articular head, well-developed greater tuberosity and smaller lesser tuberosity, prominent deltoid crest, a large radio-ulnar trochlea, and no entepicondylar foramen;
3. Radius and ulna articulated with one another and with humerus, forming a hinged elbow joint; ulna with fairly large olecranon process;
4. Movable wrist (mobility of wrist reduced in archaeocetes), with scaphoid and lunar elements separate and not ankylosed; metacarpals with ball-like distal ends; and phalanges not reduced in number;
5. Flexibility of neck reduced by presence of well-developed lateral processes on cervical vertebrae; atlas with hypapophysis; axis with protuberant odontoid process and high neural spine; and sixth cervical with elongated downward-projecting lower transverse processes;
6. A firm articular connection between successive dorsal and lumbar vertebrae, the articular facets on the postzygapophyses being nearly vertical;
7. A least two differentiated sacral vertebrae;
8. Caudal vertebrae differentiated by the presence of hypapophysae for articulation with chevron bones;
9. A differentiated sternum; manubrium enlarged; mesosternum divided into several segments; and xiphisternum elongated;
10. Innominate bone with a reduced ilium, an elongated postacetabular region, a large acetabulum with cotyloid notch, and an obturator foramen; and
11. Femur with third trochanter.
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PLATES
Plate 1

_Basilosaurus cetoides_ (Owen)


_Zygorkiza kochii_ (Reichenbach)

PLATE 2

Basilosaurus cetoides (Owen)

Skull, No. 4674. Fig. 1, lateral view, left side, about \( \frac{1}{6} \) nat. size; Fig. 2, lateral view, right side, about \( \frac{1}{6} \) nat. size; Fig. 3, posterior view, about \( \frac{1}{10} \) nat. size. United States National Museum, Washington, D. C. Upper Eocene, upper Jackson formation, Choctaw County, Alabama.
BASILOSAURUS CETOIDES
Plate 3

Basilosaurus cetoides (Owen)

Thoracic region of mounted skeleton, No. 4675. The first to fourteenth dorsal vertebrae, inclusive, as well as the neural spines of the fifth, sixth, and seventh cervical vertebrae are shown. About 1/3 nat. size. United States National Museum, Washington, D. C. Upper Eocene, upper Jackson formation, Choctaw County, Alabama.
PLATE 4

Basilosaurus cetoides (Owen)

Plate 5

_Basilosaurus cetoides_ (Owen)

Ninth to thirteenth lumbar vertebrae, inclusive; first and second sacral vertebrae; and first and second caudal vertebrae, No. 12261. About \( \frac{1}{2} \) nat. size. United States National Museum, Washington, D. C. Upper Eocene, upper Jackson formation, Choctaw County, Alabama.
PLATE 6

Basilosaurus cetoides (Owen)

BASILOSAURUS CETOIDES
Plate 7

*Basilosaurus cetoides* (Owen)

Figs. 1 to 4, halves of two mesosternal segments, No. 4675. About \(\frac{1}{4}\) nat. size.

Figs. 5 to 8, lateral views of manubrium and three mesosternal segments, No. 4675. About \(\frac{1}{4}\) nat. size.

Figs. 9 to 12, dorsal views of manubrium and three mesosternal segments, No. 4675. About \(\frac{1}{4}\) nat. size.

PLATE 8

_Basilosaurus cetoides_ (Owen)

Fig. 1, external view of anterior end of left mandible, No. 13690. About 1/4 nat. size.
Fig. 2, external view of anterior end of right mandible, No. 13690. About 1/4 nat. size.
Fig. 3, internal view of anterior end of right mandible, No. 13690. About 1/4 nat. size.
Fig. 4, anterior end of right premaxillary with I₁ in situ, No. 13690. About 1/4 nat. size.
Fig. 5, external view of right Pm₃, No. 13690. About 1/4 nat. size.

United States National Museum, Washington, D. C. Upper Eocene, Ocala limestone (upper Jackson formation), Houston County, Georgia.
Plate 9

Prozeuglodon isis (Andrews)

Fig. 1, posterior view of skull, No. 11787. About 3/8 nat. size. Württembergische Naturkundliche Sammlung, Stuttgart, Germany. Lower upper Eocene, Birket-el-Qurun stage, Fayum, Egypt.

Fig. 2, posterior view of skull, No. 14381. About 3/8 nat. size. American Museum of Natural History, New York, N. Y. Lower upper Eocene, Birket-el-Qurun stage, Fayum, Egypt.
Plate 10

Zygorhiza kochii (Reichenbach)

Skull, No. 11962. Fig. 1, dorsal view; Fig. 2, ventral view. About \( \frac{1}{4} \) nat. size. United States National Museum, Washington, D. C. Upper Eocene, upper Jackson formation, Choctaw County, Alabama.
Plate 11

Zygophyza kochii (Reichenbach)

Skull, No. 11962. Fig. 1, lateral view, about ½ nat. size; Fig. 2, posterior view, about ½ nat. size. United States National Museum, Washington, D. C. Upper Eocene, upper Jackson formation, Choctaw County, Alabama.
PLATE 12

_zygorhiza kochii_ (Reichenbach)

**Fig. 1.** Internal views of cheek teeth in left maxillary of skull, No. 11962; a, Pm2; b, Pm3; c, Pm4; d, M1; and e, M2; about nat. size.

**Fig. 2.** External views of cheek teeth in left maxillary of skull, No. 11962; a, Pm2; b, Pm3; c, Pm4; d, M1; and e, M2; about nat. size.

PLATE 13

_Zygorhiza kochii_ (Reichenbach)

Fig. 1, external views of anterior teeth in left premaxillary and left maxillary of skull, No. 11962; a, I2; b, I3; c, C; d, Pm1; about $\frac{1}{4}$ nat. size.

Fig. 2, internal views of anterior teeth in left premaxillary and left maxillary of skull, No. 11962; a, I2; b, I3, c, C; d, Pm1; about $\frac{1}{4}$ nat. size.

Fig. 3, detached teeth from mandibles, No. 11962; a, left Pm4; b, right Pm4; c, left Pm3; d, right Pm2; e, left Pm2; f, right M3; and g, right M1; about $\frac{1}{2}$ nat. size.

ZYGORMA KOCHII
Plate 14

*Zygorkiza kochii* (Reichenbach)

Figs. 1 and 2, right mandible, No. 11962. Fig. 1, external view; Fig. 2, internal view. About $\frac{1}{4}$ nat. size.

Fig. 3, ventral view of manubrium of sternum, No. 12093. About $\frac{1}{5}$ nat. size.

Fig. 4, ventral view of mesosternal segment, No. 4748. About $\frac{1}{5}$ nat. size.

PLATE 15

*Zygorhiza kochii* (Reichenbach)

**Fig. 1**, right periotic *in situ*, No. 11962. Showing relations of periotic to the hinder end of pterygoid fossa, the lateral descending process of basioccipital, the notch for jugular leash, and the squamosal. The posterior process of the periotic is wedged in between the paroccipital process and the squamosal; the anterior process and the outer face of the periotic are pressed against the squamosal. About nat. size.

**Figs. 2 and 3**, left periotic, No. 10855. **Fig. 2**, cerebral view; **Fig. 3**, ventral view. About nat. size.


*Protocetus sp.*

**Figs. 4, 5 and 6**, anterior dorsal vertebra. **Fig. 4**, anterior view; **Fig. 5**, lateral view; **Fig. 6**, posterior view. About nat. size.

Bureau of Economic Geology, University of Texas, Austin, Texas. Upper middle Eocene, Crockett formation [= upper Cook Mountain], Texas.
Plate 16

*Zygorhiza kochii* (Reichenbach)

**Fig. 1**, dorsal view of basihyal, No. 12063. About \(\frac{1}{2}\) nat. size. Upper Eocene, upper Jackson formation, Choctaw County, Alabama.

**Figs. 2 to 3**, thyrohyals, No. 4678. **Fig. 2**, ventral view of right thyrohyal; **Fig. 3**, lateral view of left thyrohyal. About \(\frac{1}{4}\) nat. size. Upper Eocene, Ocala limestone (upper Jackson formation), Clark County, Alabama.

**Fig. 4**, left stylohyal, No. 4679. About \(\frac{1}{2}\) nat. size. Upper Eocene, upper Jackson formation, Choctaw County, Alabama.

**Figs. 5 to 6**, ribs, No. 4678. **Fig. 5**, first rib on left side; **Fig. 6**, fifteenth rib on right side. About \(\frac{1}{2}\) nat. size. Upper Eocene, Ocala limestone (upper Jackson formation), Clark County, Alabama.

United States National Museum, Washington, D.C.
Zygophyllum komati (Reichenbach)

PLATE 18

_Dorudon osiris_ (Dames)

Skull, No. M. 10228. Fig. 1, dorsal view; Fig. 2, ventral view. About 1/4 nat. size. British Museum (Natural History), London, England. Upper Eocene, Qasr-el-Sagha stage, Fayum, Egypt.
Plate 19

*Dorudon osiris* (Dames)

Skull, No. M. 10228. Fig. 1, lateral view, about \( \frac{1}{2} \) nat. size; Fig. 2, posterior view, about \( \frac{1}{7} \) nat. size. British Museum (Natural History), London, England. Upper Eocene, Qaar-el-Sagha stage, Fayum, Egypt.
Plate 20

Dorudon osiris (Dames)

Skull, No. 11626. Fig. 1, dorsal view; Fig. 2, ventral view. About 1/2 nat. size. Württembergische Naturaliensammlung, Stuttgart, Germany. Upper Eocene, Qasr-el-Sagha stage, Fayum, Egypt.
PLATE 21

Dorudon osiris (Danes)

Skull, No. 11626. Fig. 1, lateral view, about ½ nat. size; Fig. 2, posterior view, about ½ nat. size. Württembergische Naturhistorische Sammlung, Stuttgart, Germany. Upper Eocene, Qasr-el-Sagha stage, Fayum, Egypt.
Plate 22

*Dorudon osiris* (Dames)

Fig. 1, external views of cheek teeth in right maxillary of skull, No. 14382; a, Pm2; b, Pm3; c, Pm4; and d, M1; about nat. size.

Fig. 2, external views of cheek teeth in left maxillary of skull, No. 14382; a, Pm2; b, Pm3; c, Pm4; d, M1; and e, M2; about nat. size.

American Museum of Natural History, New York, N. Y. Upper Eocene, Qasr-el-Sagha stage, Fayum, Egypt.
Plate 23

Dorudon osiris (Dames)

Mandibles, No. 11417. Fig. 1, external view of right mandible; Fig. 2, external view of left mandible. About $\frac{1}{3}$ nat. size.

Left mandible, No. 11627. Fig. 3, external view; Fig. 4, internal view. About $\frac{1}{3}$ nat. size.

Württembergische Naturlänsammlung, Stuttgart, Germany. Upper Eocene, Qasr-el-Sagha stage, Fayum, Egypt.
DORUDON OSIRIS
Plate 24

*Dorudon stromeri* (Kellogg)

Skull (type specimen), No. 1004. XII. 134e. Fig. 1, dorsal view; Fig. 2, ventral view.

About \( \frac{1}{2} \) nat. size. Paläontologische Sammlung, Alte Akademie, Munich, Germany.

Upper Eocene, Qaar-el-Sagha stage, Fayum, Egypt.
DORUDON STROMERI
PLATE 25

*Dorudon stromeri* (Kellogg)

Skull (type specimen), No. 1904. XII. 134e. Fig. 1, lateral view, about $\frac{1}{2}$ nat. size; Fig. 2, posterior view, about $\frac{1}{2}$ nat. size. Paläontologische Sammlung, Alte Akademie, Munich, Germany. Upper Eocene, Qasr-el-Sagha stage, Fayum, Egypt.
PLATE 26

*Dorudon zitteli* (Stromer)

Fig. 1, lateral view of skull, No. 11235; about \( \frac{1}{3} \) nat. size.

Fig. 2, lateral views of cervical and dorsal vertebrae, No. 11235; about \( \frac{1}{3} \) nat. size.

Württembergische Naturkundesammlung, Stuttgart, Germany. Upper Eocene, Qasr-el-Sagha stage, Fayum, Egypt.

*Dorudon stromeri* (Kellogg)

Fig. 3, deciduous teeth (type specimen), No. 1904. XII. 134c; a and b, deciduous canines; c, d and e, deciduous incisors; f, right Dpm\( \frac{1}{2} \); g, left Dpm\( \frac{1}{2} \); and h, M\( \frac{1}{2} \); about \( \frac{1}{3} \) nat. size.

Paläontologische Sammlung, Alte Akademie, Munich, Germany. Upper Eocene, Qasr-el-Sagha stage, Fayum, Egypt.
DORUDON ZITTELI AND DORUDON STROMERI
PLATE 27

Dorudon stromeri (Kellogg)

Mandibles (type specimen), No. 1904. XII. 134e. Fig. 1, external view of right mandible; Fig. 2, external view of left mandible. About $\frac{1}{2}$ nat. size. Palæontologische Sammlung, Alte Akademie, Munich, Germany. Upper Eocene, Qasr-el-Sagha stage, Fayum, Egypt.

Dorudon zitteli (Stromer)

Right humerus, No. 11417b. Fig. 3, external view; Fig. 4, internal view. About $\frac{1}{2}$ nat. size Württembergische Naturaliensammlung, Stuttgart, Germany. Upper Eocene, Qasr-el-Sagha stage, Fayum, Egypt.
PLATE 28

Dorudon intermedius (Dart)

Skull, No. 1904. XII. 134a. Fig. 1, ventral view; Fig. 2, dorsal view. About ¼ nat. size

Paläontologische Sammlung, Alte Akademie, Munich, Germany. Lower upper Eocene.

Birket-el-Qurun stage, Fayum, Egypt.
PLATE 29

Dorudon intermedius (Dart)

Skull, No. 1904. XII. 134a. Fig. 1, lateral view, about 1/2 nat. size; Fig. 2, posterior view, about 1/3 nat. size. Paläontologische Sammlung, Alte Akademie, Munich, Germany

Lower upper Eocene, Birket-el-Qurun stage, Fayum, Egypt.
Plate 30

*Dorudon intermedius* (Dart)

Skull (type specimen), No. M.10173. Fig. 1, dorsal view; Fig. 2, ventral view. About 1/2 nat. size. British Museum (Natural History), London, England. Lower upper Eocene, Birket-el-Qurun stage, Fayum, Egypt.
PLATE 31

Dorudon intermedius (Dart)

Skull (type specimen), No. M.10173. Fig. 1, lateral view, about \( \frac{3}{8} \) nat. size; Fig. 2, posterior view, about \( \frac{1}{4} \) nat. size. British Museum (Natural History), London, England. Lower upper Eocene, Birket-el-Qurun stage, Fayum, Egypt.
Plate 32

Kekenodon onamata Hector

Teeth (type specimen), No. Ma.69. Fig. 1, canine from (?) right mandible; 1', cross section of crown; 1'', longitudinal section of root; 1'''', transverse section of root; Fig. 2, canine from (?) left maxillary; Fig. 3, internal view of left Pm4 and cross section of roots; Fig. 4, internal view of left Pm2; 4', posterior view of left Pm2; Fig. 5, internal view of right Pm3; Fig. 6, external view of right Pm4; 6', anterior view of right Pm1; 6'', transverse section of roots of right Pm3; Fig. 7, internal view of right Pm3; 7', posterior view of right Pm3; Fig. 9, dorsal view of left tympanic bulla; 9', ventral view of left tympanic bulla; Fig. 10, ventral view of left periotic; all about ³⁄₄ nat. size. Fig. 11, left Pm4 (same as Fig. 3); Fig. 12, right Pm4 (same as Fig. 6); Fig. 13, external view of right M2; Fig. 14, right Pm3 (same as Fig. 7); Fig. 15, left upper (?) canine (same as Fig. 2); Fig. 16, external view of right Pm3 (see Fig. 5); Fig. 17, lower right canine (same as Fig. 1); all about ³⁄₄ nat. size. [Figs. 1 to 10], after Hector, 1881, pl. 18 Dominion Museum at Wellington, New Zealand. Lower Miocene, Ototaran stage, Waitaki Valley, New Zealand.
PLATE 33

Eocetus schweinfurthi (Fraas)

Skull (type specimen), No. 10986. Fig. 1, lateral view. About ½ nat. size. Württembergische Naturaliensammlung, Stuttgart, Germany. Upper middle Eocene, lower Mokattam series, near Cairo, Egypt.
PLATE 35

Protocetus atavus Fraas

Left ear region of skull (type specimen), No. 11084. Fig. 1, basicranium tilted to show hypoglossal foramen at base of notch for jugular leash, foramen ovale at end of falciform process of squamosal, the fossa epitubaria on squamosal for processus tubarius of tympanic bulla, and the periotic bone; Fig. 2, view showing relations of periotic to squamosal, exoccipital, and alisphenoid. About nat. size. Württembergische Naturaliensammlung, Stuttgart, Germany. Lower middle Eocene, basal lower Mokattam series, near Cairo, Egypt.
Plate 36

Pontogeneus priscus Leidy

Figs. 1 to 3, fifth cervical vertebra (type specimen), No. 13668. Fig. 1, anterior view; Fig. 2, posterior view; Fig. 3, lateral view. About nat. size. Academy of Natural Sciences of Philadelphia. Upper Eocene, Jackson formation, Ouachita River, Louisiana.

Pontobasileus tuberculatus Leidy

Figs. 4 to 5, one root and adjacent portion of crown of a cheek tooth (type specimen), No. 11216. About ½ nat. size. Academy of Natural Sciences of Philadelphia. Locality not definitely known.
Plate 37

*Pontogeneus brachyspondylus* (Müller)

Figs. 1 and 2, third lumbar vertebra, No. 776. Fig. 1, lateral view; Fig. 2, anterior view. About $\frac{1}{8}$ nat. size.

Figs. 3 and 4, twelfth lumbar vertebra, No. 2211. Fig. 3, anterior view; Fig. 4, ventral view. About $\frac{7}{8}$ nat. size.
