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A NEW FOSSIL CETACEAN.

BY G. M. ALLEN.

WITH ONE PLATE.

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No. 1.— *A New Fossil Cetacean.*

By Glover M. Allen.

In the course of revising the collection of fossil mammals in the Museum, an unlabeled cranium was found, which was so largely embedded in a hard fine-grained marl, that its true nature was not at first appreciated. The specimen, after this matrix had been carefully chiseled away, proves to be of unusual interest. It lacks the vertex of the brain-case, the jugals, and most of the rostrum including the tooth-bearing parts of the maxillae and premaxillae. What remains, however, is fairly well preserved and clearly pertains to a toothed cetacean of a very primitive type, related apparently to the Eocene Agorophius, but differing in certain important details from the only known cranium hitherto referred to that genus. It is therefore doubly unfortunate that so important a specimen should be quite without record of locality, horizon, discoverer, or donor. It lay by itself in a tray without label or catalogue number, having probably been put aside just as received many years ago. The likelihood is that it was sent to Louis Agassiz in the early days of the Museum, possibly from some locality in the southeastern United States, at the time when he was planning a memoir on "Phocodon" (see Wyman, Amer. journ. sci., 1850, ser. 2, **10**, p. 230, footnote). One or two barnacle bases on the upper side indicate that it lay for a time, partly exposed, in the sea.

In the hope that there might be characteristic Foraminifera in the marly matrix, a sample from within the brain-cavity was submitted to Dr. Joseph A. Cushman, who very kindly examined it and reports that "there are a few Foraminifera contained in it, most of which are not well preserved. A few, however, seem to show that the material is probably Upper Eocene (Jackson) in age, and its general appearance would seem to indicate that it came from the Gulf Coastal Plain of the United States, probably from Alabama."

The cranium belonged to a dolphin-like animal, probably some five or six feet long. Obvious peculiarities are its relatively narrow and flattened brain-case, wide mastoid diameter, elongate flattened nasals, parietals forming part of the vertex, the relatively small and prominent occipital condyles, and the long and forward-sloping instead of vertical nasal passage with the remnant of a dorsal chamber above the main part of the nasal cavity. These characters, notwithstanding the lack of corroboration from the teeth, are sufficient to indicate its

relationship to the Mesoceti as defined by Dames (1894). While it possesses several primitive features in common with Prosqualodon, its relationship is perhaps nearer to Agorophius, with both of which it may be associated in Abel's family, Agorophiidae, whose three known members, while perhaps in no case directly ancestral to the more developed Squalodontidae, yet indicate previous stages in evolution.

Though quite as primitive in many respects as Agorophius, the new fossil shows so many points of difference that it seems worthy of rank as a separate genus.

Archaeodelphis, gen. nov.

Diagnosis.— A long-beaked dolphin-like cetacean; teeth unknown, but apparently long-rooted, probably resembling those of Agorophius and Prosqualodon; nasals long, narrow, and flattened dorsally; maxillae covering the anterior three fourths of the orbital portion of the frontals; orbit large, with thickened rim and prominent postorbital process; parietals meeting across the vertex of the skull behind the orbits; zygomatic process of squamosal relatively small, with small and nearly horizontal glenoid fossa; mastoid region thickened and produced obliquely downward and backward to or beyond the posterior edge of the condyles which are small and protuberant. Palatals large, expanded anteriorly, separated medially for more than half their length at the back end and by a deep notch at the front end of their combined margin; pterygoids widely sundered, their free margins partly overarching the narial passage. A well-marked nasal chamber is present above the anterior end of the passage, and the vomer forms a cylinder that completely encloses the basal end of the mesethmoid cartilage.

The genus is based on the specimen here described.

Archaeodelphis patrius, sp. nov.

Type-specimen.— A cranium, M. C. Z. 15,749 (Cat. Fossil Mamm.) lacking the bones of the vertex, the jugals, the teeth, and all but the basal portion of the rostrum.

Locality and horizon.— Probably from Jackson formation of the Upper Eocene of the southeastern United States, possibly Alabama, as suggested by the Foraminifera from the matrix.

Description.— A striking characteristic of the dorsal aspect is the narrow rectangular outline of the nasals whose inner anterior corners seem to have been slightly produced to form a blunt median point. They completely roof over the front end of the nasal passage so that the anterior nares open forward, a primitive character common also to the Archaeoceti. At either side of the nasals appears the base of an intermaxillary, its width about equal to that of a single nasal, its termination at about five eighths the length of the nasal, where it abuts against an anterior prolongation of the frontal. Laterally the proximal end of the maxilla extends back to the level of the base of the nasals, and overspreads about three fourths of the orbital process of the frontal dorsally, reaching the edge of the orbit about half way down

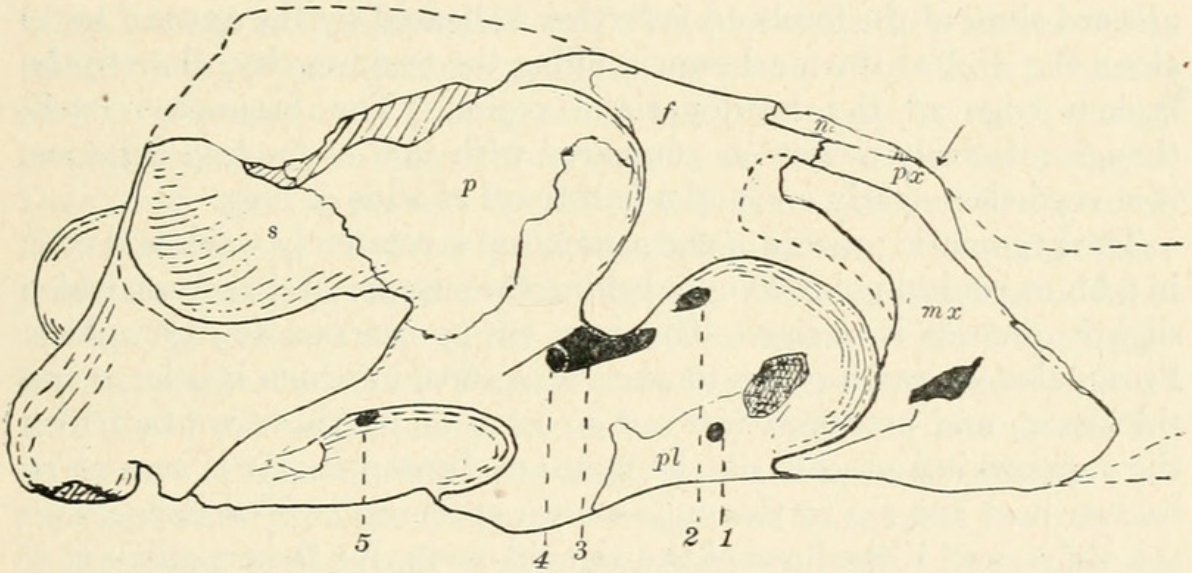

Fig. 1.— Side view of the cranium, from a photograph. *f*, frontal; *mx*, maxillary, part of base (the dotted line shows the limit of its backward extension); *n*, nasal; *p*, parietal; *pl*, palatal, ascending portion; *px*, premaxillary, basal end; *1*, sphenopalatine foramen; *2*, optic foramen; *3*, orbital fissure; *4*, foramen rotundum; *5*, foramen ovale.

on its anterior rim; below this point it forms the front portion of the orbit. Posterolaterally the frontal is produced to form a tapering supraorbital process, whose decurved point is separated from the zygomatic process of the squamosal by about one third the length of the temporal fossa. Its median portion at the point of least interorbital width shows a depression on each side of the cranial axis narrowing to a point forward, which probably received corresponding anterior processes of the parietals. In Agorophius there is also a median prolongation of the parietals fitting into a corresponding depression of the frontals but the projection is simple, not bifurcate.

Of the parietals themselves very little remains in the specimen save a portion of the lateral wing of each, (Fig. 1, *p*), whose lower boundary is faintly traceable on the inner wall of the temporal fossa, whence it extends forward as a narrowing border on the posterior rim of the supraorbital process.

In Agorophius the highest point of the dorsal profile is formed by the base of the maxillaries, back of which the summit of the skull extends on a nearly horizontal though very slightly depressed plane, to the vertex of the supraoccipital. In Archaeodelphis, on the contrary, there was obviously a gradual upward slope of the profile (Fig. 1) which, if the parietals were in place, must have been continued a slight distance to the junction with the supraoccipital, where, as in recent dolphins, the highest point of the profile must have been. This upward slope of the forehead is further indicated by the upward bevel along the edge of the marl matrix filling the brain-cavity, close to the broken edge of the frontoparietal region. The brain-case itself, though relatively narrow as compared with that of modern dolphins, is nevertheless nearly one and a half times as wide as long.

The zygomatic process of the squamosal is relatively weak and ends in a blunt conical point 30 mm. behind the supraorbital process, which slightly exceeds it in size. This is in strong contrast to Agorophius, Prosqualodon, and modern toothed cetaceans, in which it is large and thickened, and produced forward so as to be nearly in contact with the supraorbital process (in the figure of Agorophius, it is seen to be broken near the tip in the only known specimen). Correlated with this difference, is the form of the glenoid cavity for the articulation of the jaw. In Archaeodelphis the cavity is nearly flat, and faces almost ventrally, though the posterior border, evidently forming a distinct postglenoid process, appears to be slightly broken away. Medially the articulating surface extends for a distance nearly equal to its length. In Agorophius, Prosqualodon, and Patriocetus, as in the modern dolphins, the articulating surface is relatively larger and includes the concave ventral (or anterior) face of the zygomatic process. This difference evidently implies in Archaeodelphis a more precise limitation of the movements of the jaw, to insure a certain amount of shearing action between the opposing sets of teeth, in addition to their seizing function (the main use of teeth in modern cetaceans). Possibly such a cutting action enabled Archaeodelphis to feed upon small armored fishes, such as the young of ganoids. It may be regarded as a primitive feature, inherited from the supposed creodont or carnivorous ancestors.

Most remarkable is the development of the exoccipitals and their extension backward, outward, and downward, thereby greatly increasing the massive aspect of the mastoid region. A somewhat similar appearance is shown by Agorophius and Prosqualodon but in these genera the exoccipitals do not extend so far backward, hardly surpassing the base of the condyles, whereas in Archaeodelphis they equal or exceed the protuberant condyles and are produced strongly downward below them.

The occipital condyles are very different from those of modern cetaceans. In the Delphinidae their articulating surface is relatively large and almost continuous with the surrounding bones of the occiput so that the head rests firmly upon the atlas with its correspondingly enlarged and flattened anterior facets. In Archaeodelphis on the contrary, as well as in Agorophius and Prosqualodon, they are relatively smaller but very much more protuberant and are set off by a distinct neck or constriction. Their greatest axis is not quite vertical though much more nearly so than in most modern cetaceans, as for example, Delphinus. An approach to this condition, however, is found in Platanista among the more primitive living forms. This much more primitive condition was doubtless correlated with free instead of fused cervical vertebrae, a fact which, taken in connection with the enlarged mastoid region for muscle attachments, indicates a very much greater mobility of the head both up and down, and sidewise, than in modern cetaceans. Probably with the more forward-opening nostrils, the rostrum rather than the vertex of the head was first thrust above water in breathing, or the front of the head merely elevated from the horizontal position when near the surface, as a seal might do.

Very fortunately the base of the rostrum and most of the lower portion of the cranium were embedded in the matrix, so that it has been possible by clearing this carefully away, to disclose the structure of these important parts. Contrary to the condition shown by the type-specimen of Agorophius in which the nasals, intermaxillaries, and vomer seem to have been loosely attached, and have become lost, these bones in Archaeodelphis are strongly soldered together. A very remarkable and interesting development of the vomer and adjacent bones is seen in a front view of the rostrum (Fig. 2) which in the specimen is broken short off so as to give nearly a vertical section. The dorsal three fourths of the premaxillaries are considerably thickened with outward-flaring inner faces bounding the sides of the nasal opening. Their ventral fourth encloses the vomer whose lateral wings are here expanded to form a cylindrical tube, containing the mesethmoid

cartilage. This tube was obviously continued forward with its supporting rod of cartilage to give strength to the rostrum, as in the Denticeti. At its base, the tube separates the two intermaxillaries medially for a space of 9 to 14 mm. and is continued dorsally as a thin knife-like partition quite to the under side of the nasals, so as to divide the nasal chamber longitudinally. There appears to be also a vertical wing on each side lining a portion of the outer wall of the nasal opening. Ventrally, the vomer is continued as a median keel from the rostral cylinder and appears on the palatal aspect as a narrow line separating the maxillaries. Viewed from the posterior narial opening,

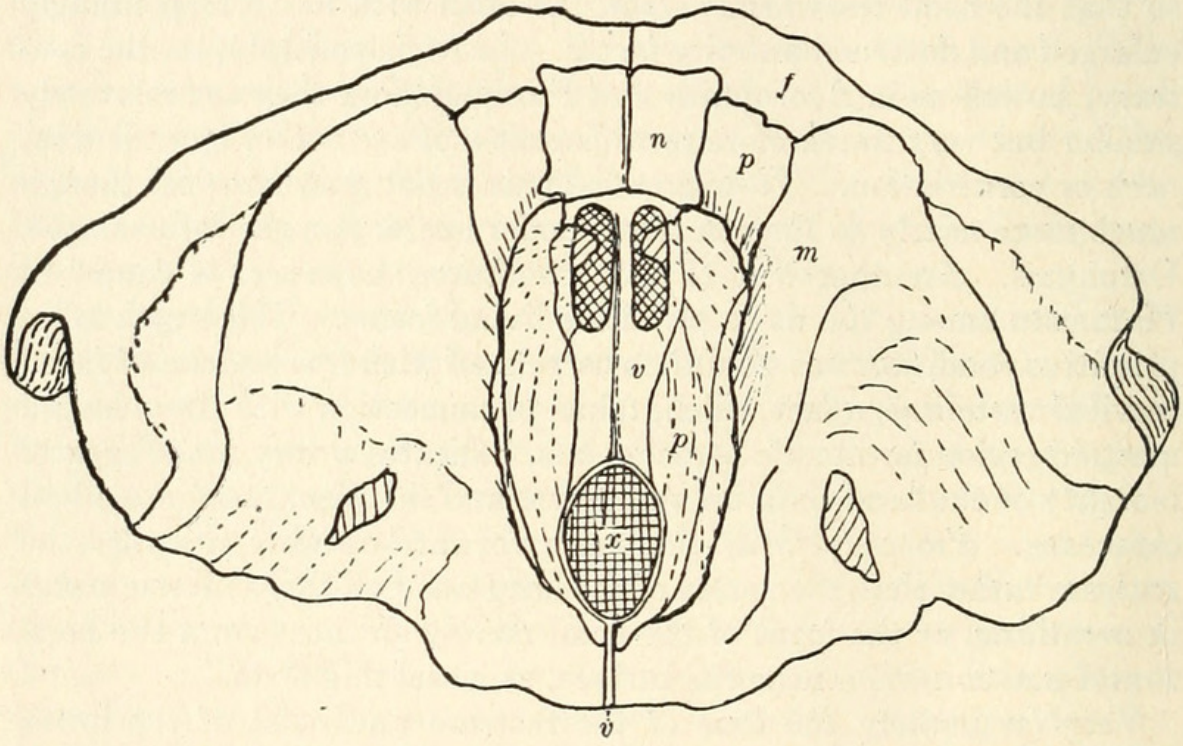

Fig. 2.— The cranium in front view, from a photograph. *f*, frontal; *m*, maxillary; *n*, nasal; *p*, premaxillary; *v*, vomer, forming a rostral tube to enclose, *x*, the mesethmoid cartilage.

the backward extension of this tube is seen to become laterally compressed, and continuing its course in the plane of the palate, abuts against the wall of the nasal cavity some 30 mm. from the opening of the posterior nares. With the apparent exception of Ceterhinops, no similar rostral tube is known in other cetaceans, for, as in Prosqualodon (Abel, 1912) it is usually open dorsally at the base and the mesethmoid cartilage, more or less ossified, appears at the base of the rostrum between the intermaxillaries.

The posterior part of the narial passage is flattened dorsoventrally,

with divergent sides, and is largely enclosed by the arching palatals and the incurved pterygoids, except medially where these bones are separate below. Behind the pterygoids the narial passage viewed from below, is continued as a broad shallow trough with raised and slightly divergent sides, nearly to the foramen magnum, much as in modern dolphins, except that this portion of the narial passage lies nearly in the plane of the palate instead of being bent at an angle with it. This angle is obvious in Agorophius (True, 1907, plate) as well.

The palatal region, so important for its diagnostic characters in the Cetacea, is beautifully preserved except for the tooth-bearing parts of the maxillaries. In most extinct cetaceans, however, this aspect of the skull is seldom preserved or figured so that full comparisons are not as yet possible. In the specimen, only the basal portions of the maxillaries between the tooth-rows remain. Here a slight longitudinal groove-like depression is indicated on each side of the median line, corresponding perhaps, with the shallow palatal grooves seen in Delphinapterus. The palatal bones are perfect and lie in a plane very slightly depressed from that of the maxillaries. As usual in Cetacea, as well as in seals, the tooth-rows lie anterior to the front margin of the palatals. Each palatal is expanded at its forward end, where its outline is strongly convex, so that there is a distinct emargination at the median portion of their combined front edges. Together they nearly fill the space between tooth-rows, and are in contact medially for a trifle less than one third their length before diverging evenly at their posterior ends. At the ventral edge of the orbit each sends up a dorsal branch at right angles to the palatal portion. Just above this edge and close to the anterior margin of the ascending wing is a small but distinct sphenopalatine foramen (Fig. 1, **1**).

The pterygoids are relatively small, their ventral portion incurved so as partly to embrace the opening of the posterior nares. They are widely separate and their posterior margins divergent.

Laterally, on either side of the trough that continues the narial passage, is a deep groove with sharply defined boundaries, extending forward as far as the pterygoid bone. About half way on the length of this groove opens the large foramen ovale, (Fig. 1, **5**) its course continued laterally as a shallow furrow. The orbit shows three large foramina for nerves. Slightly above and in advance of its center is the optic foramen of relatively small size (Fig. 1, **2**). Below and behind this is the very large orbital fissure (foramen lacerum anterius) deeply excavated in the wall of the orbit, while close against it posteroexternally, and separated only by a thin bony partition is the fora-

men rotundum (for the second division of the fifth nerve) lying in the same deep groove with the orbital fissure (Fig. 1, **3** and **4**).

What appears to be the opening of the lachrymal canal lies just below and ahead of the optic foramen, where the outline of a small lachrymal bone can be faintly traced, wedged in between the ascending process of the palatine and the base of the orbital portions of frontal and maxillary. The antorbital foramen perforates the latter just exterior to the lachrymal, and appears in the section of the broken rostrum as a large triangular orifice with its point directed downward.

The tympanic bullae are lost, and were evidently but loosely attached as is usual in Cetacea. The petrous and mastoid portions of the ear-bones, however, are still present, and as in some of the more primitive existing cetaceans, (Balaena, Platanista) are firmly wedged between exoccipital and squamosal. The petrosum is small (17 × 11.5 mm.), roughly egg-shaped, with its long axis directed anteroposteriorly, and lies close against a bony eminence bounding the inner side of the glenoid fossa. The mastoid portion (28 mm. long) extends obliquely outward and backward to the periphery, expanding to a width of 20 mm. where it reaches the outer surface of the cranium. A notch separates it from the postglenoid process.

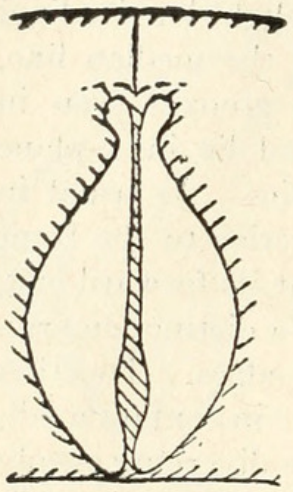

Fig. 3. — Diagrammatic cross-section of nasal passage at base of rostrum, to show the vestigial dorsal nasal chambers.

The nasal cavities are fortunately preserved intact and were, with some difficulty, quite cleared of matrix on one side of the median septum formed by the vomer. The greater part of their vertical diameter is taken by the narial passage itself which extends from the laterally compressed anterior opening, obliquely backward and downward, expanding laterally as it approaches the posterior nares. Directly back of the anterior narial opening and wholly above the air-passage itself, is a pocket extending backward and nearly cut off below by a blunt projection of the outer wall of the cavity, so that a distinct dorsal division of the nasal chamber (Fig. 3) is formed, a primitive feature of which no vestige remains in modern cetaceans. Stromer (1903, pl. 11, fig. 1–3) has shown sections of the nasal cavity of *Zeuglodon* (*Basilosaurus*) *zitteli* in which there is a much better developed olfactory chamber, similarly situated, and wholly cut off ventrally from the main air-passage by a *lamina terminalis* extending inward

from the outer wall of the cavity. He found also indications of naso- and maxillo-turbinals. It is therefore probable that the blunt projection from the outer wall of the nasal cavity, above referred to, is the remnant of a *lamina terminalis*, but there is no indication of turbinal bones, which probably had atrophied.

Measurements.— The following dimensions indicate the size of the cranium:

	mm.
Tip of nasals to end of occipital condyles	180
Front edge of palatal bone to same point	158
Anteroposterior length of temporal fossa	92
Length of right orbit	54
Length of nasals	41
Combined width of nasals	38
Width across front of orbits	145
Mastoid width	180
Least width between temporal fossae	64
Combined width of palatal bones	69
Width across occipital condyles	57
Approximate width across supraorbital processes (twice one half)	190
Height of muzzle at tip of nasals	70

Summary of Relationships.

Of primitive cetaceans whose skull characters are sufficiently known to admit of comparison with Archaeodelphis, three genera stand out as bearing a considerable degree of similarity to it, namely, Agorophius, Prosqualodon, and Patriocetus. The first of these, with the single species *A. pygmaeus*, is still known from the type-specimen only — now lost — the history and peculiarities of which have been fully set forth by True (1907). Although the intermaxillaries and nasals as well as most of the inferior side of the cranium of this specimen were not preserved, still it bears obviously a general superficial resemblance to Archaeodelphis in the somewhat flattened profile, the great anteroposterior extent and the breadth of the temporal fossae, and the resulting narrowness of the region separating the two fossae anteriorly. This narrow isthmus in both genera, is formed dorsally by the parietals which instead of being excluded from the peak of the cranium as in modern cetaceans, meet behind the frontals at the dorsal line. Further points of resemblance are found in the shape of the brain-case and in the great lateral extent of the orbital portion of the frontal with its well-developed and tapering postorbital process.

Both species, further, have small and prominent occipital condyles, indicating a considerable mobility of the head. On the other hand, Archaeodelphis differs from Agorophius in many important characters, both primitive and progressive. Thus its basicranial axis is not bent at an angle with the plane of the palate, whereas in Agorophius the fragments of basioccipital and basisphenoid remaining, clearly form a distinct angle with the palate, foreshadowing the considerable angle seen in many modern dolphins; again, the zygomatic process of the squamosal is but weakly developed in Archaeodelphis whereas in Agorophius it is large and well arched for the extensive jaw-articulation, in addition to being much more produced forward. On the other hand, Archaeodelphis is the more progressive in its higher vertex and shows a special development of the mastoid region downward and backward. A comparison of nasals, intermaxillaries, and vomer is not possible, but since these parts are lost in the type-specimen of Agorophius, it may be that they were less solidly fused than in Archaeodelphis. In the latter, the extraordinary formation of the vomer, completely enclosing the mesethmoid cartilage in a tube and dividing the nasal cavity by a thin bony septum is possibly a specialization; while the retention of elongate, narrow nasals well solidified with the surrounding bones and a distinct olfactory chamber dorsal to the main air-passage are primitive characters.

From his study of the three known specimens of Prosqualodon, from the Miocene of Patagonia, Abel (1912) has shown, that although possessing many primitive characters, such as the low vertex, narrow brain-case, broad zygomatic processes, parietals meeting at the vertex behind the frontals, and large temporal fossae, it shows nevertheless a great advance over Agorophius in many respects, and though hardly ancestral to Squalodon, yet foreshadows many of its delphinoid characters, such as the reduction of the nasals, the greater anteroposterior compression of the cranium, more nearly vertical nasal passages, and relatively smaller temporal fossae. Its teeth Abel interprets as being more specialized than in the squalodonts, and as a further progressive character, the intermaxillaries are toothless. It has a well-marked maxillary notch as in squalodonts and modern dolphins.

In comparison with Patriocetus, a new generic term proposed by Abel (1912, p. 69) for *Squalodon ehrlichii*, Archaeodelphis is at once distinguished by the absence of the pronounced overhanging ledge that partly roofs over the front end of the temporal fossa, somewhat as in the zeuglodonts (Basilosaurus). The zygomatic process of the squamosal is large as in Agorophius and Prosqualodon, and as in the

former the dorsal profile of the brain-case is nearly flat. The basicranial axis seems to be bent slightly to form an angle with the plane of the palate. As True (1907) had previously indicated, this cetacean seems very different from typical Squalodon, though its characters are still imperfectly known. The recent discovery of a well-preserved example in the upper Oligocene at Linz (König, 1911) should help to elucidate its relationships when the promised studies of Dr. Abel on this important specimen are published.

There seems to be no close relationship between Archaeodelphis and the zeuglodonts, which, as lately shown by the studies of Dames (1894), Stromer (1903), Fraas (1904), and Andrews (1906), appear to be only remotely connected with the more typical cetaceans (Mesoceti and Denticeti) if not a wholly independent offshoot from a primitive creodont stock. They reached their maximum development in both size and skeletal modification during Eocene times, and then became extinct. Their ancestry, however, seems to be clearly indicated through the discovery by Fraas (1904) of the skull of a small species (*Protocetus atavus*) from the lower Middle Eocene of Mokattam, near Cairo, Egypt. This was a primitive surviving type, contemporaneous with more evolved types that inhabited the same Eocene seas. Its dentition, however, instead of exhibiting the usual compressed premolars and molars with serrate edges, is like that of a typical creodont.

So far as can be judged from the specimen here described, Archaeodelphis stands as a very primitive cetacean, probably nearest related to Agorophius of known forms, and to be associated tentatively with it in a separate family, Agorophiidae. It represents a dolphin-like animal belonging in a general way to a type ancestral to the Squalodontidae and through them to the more modern delphinoids.

A word may be added as to Leidy's genus Ceterhinops. This was founded on a fragment of a cranium which included portions of maxillae, premaxillae, vomer, and frontal. The vomer formed at its base, a cylindrical tube, much as in Archaeodelphis, and this was continued dorsally as a thick bony septum quite separating the nasal passages. The figure given by Leidy (1877, pl. 34, fig. 7) indicates, however, a skull of different configuration, perhaps lacking such nasal bones as Archaeodelphis possessed, and having the basal ends of the premaxillae tapering to a point between the frontal and the maxillae. Its fragmentary nature renders a further comparison difficult, but indicates a possible relationship. Leidy's specimen came from the Ashley River phosphate beds of South Carolina.

REFERENCES.

Abel, Othenio.

1912. Cetaceenstudien. III. Mitteilung: Rekonstruktion des schädels von *Prosqualodon australe* Lyd. aus dem Miozän Patagoniens. Sitzb. K. akad. wiss. Wien, math.-nat. cl., **121**, pt. 1, p. 57–75, pl. 1–3.

Andrews, C. W.

1906. A descriptive catalogue of the Tertiary Vertebrata of the Fayûm, Egypt. London, 4to, 38, 324 pp., illustr.

Dames, W. B.

1894. Ueber zeuglodonten aus Aegypten und die beziehungen der Archaeoceten zu den übrigen cetaceen. Palaeont. abhandl., **5**, no. 5, 36 pp., 7 pls.

Fraas, Eberhard.

1904. Neue zeuglodonten aus dem unteren Mitteleocän vom Mokattam bei Cairo. Geol. palaeont. abhandl., **10**, 24 pp., 3 pls.

König, Anton.

1911. Ein neuer fund von *Squalodon ehrlichii* in den Linzer sanden. Jahresb. Mus. Franc.-Carol. Linz, **69**, p. 109–121, pl. 1.

Leidy, Joseph.

1877. Description of vertebrate remains, chiefly from the phosphate beds of South Carolina. Journ. Acad. nat. sci., Phila., ser. 2, **8**, p. 209–261, pl. 30–34.

Stromer, Ernst von.

1903. Zeuglodon-reste aus dem oberen Mitteleocän des Fajûm. Beitr. palaeont. u. geol. Oesterreich-Ungarns, **15**, pt. 2–3, p. 65–101, pl. 8–11.

True, F. W.

1907. Remarks on the type of the fossil cetacean *Agorophius pygmaeus* (Müller). Smithson. contr. knowl., 8 pp., 1 pl.

EXPLANATION OF THE PLATE.

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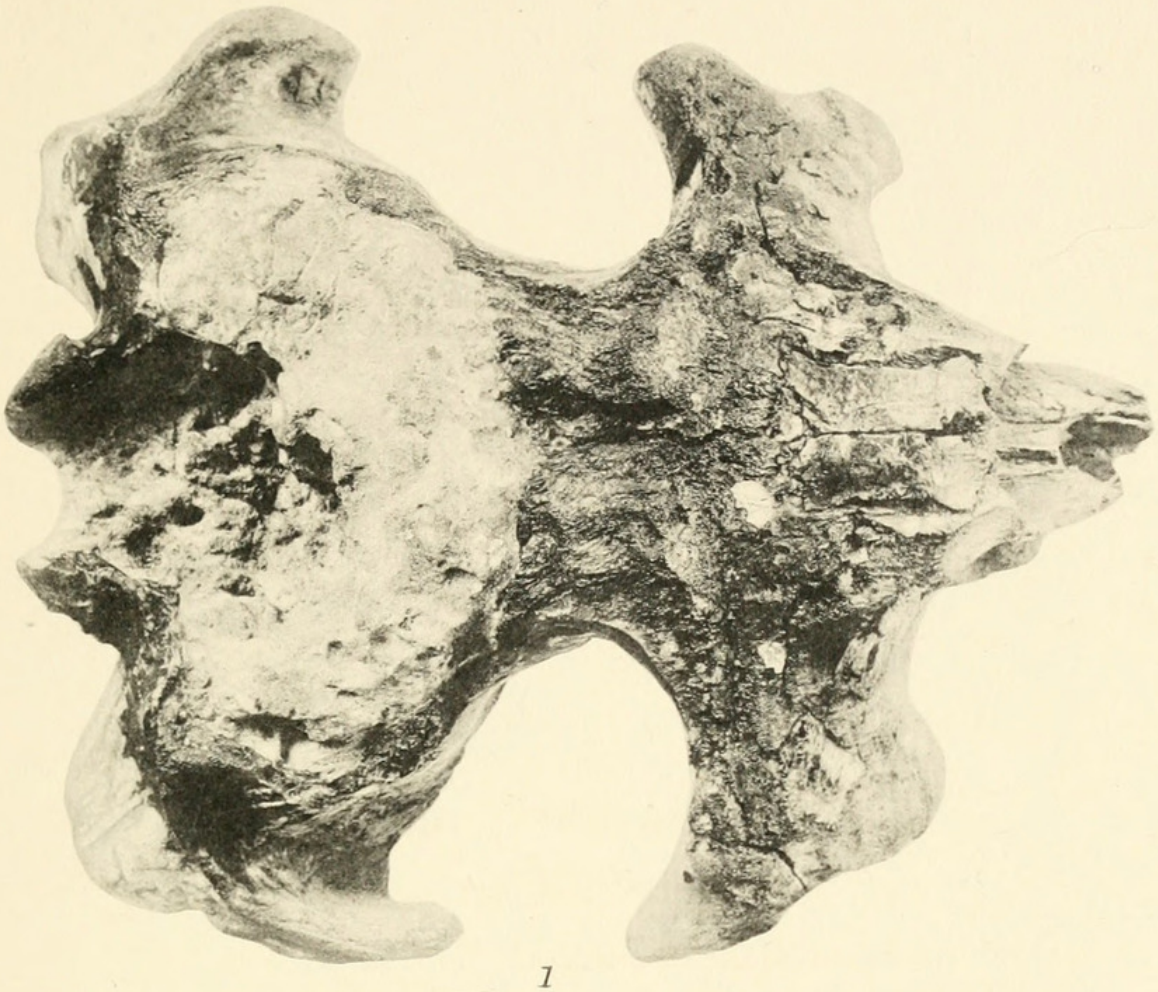
Archaeodelphis patrius Allen.

Fig. 1. The type-cranium from above.
Fig. 2. The same from below.



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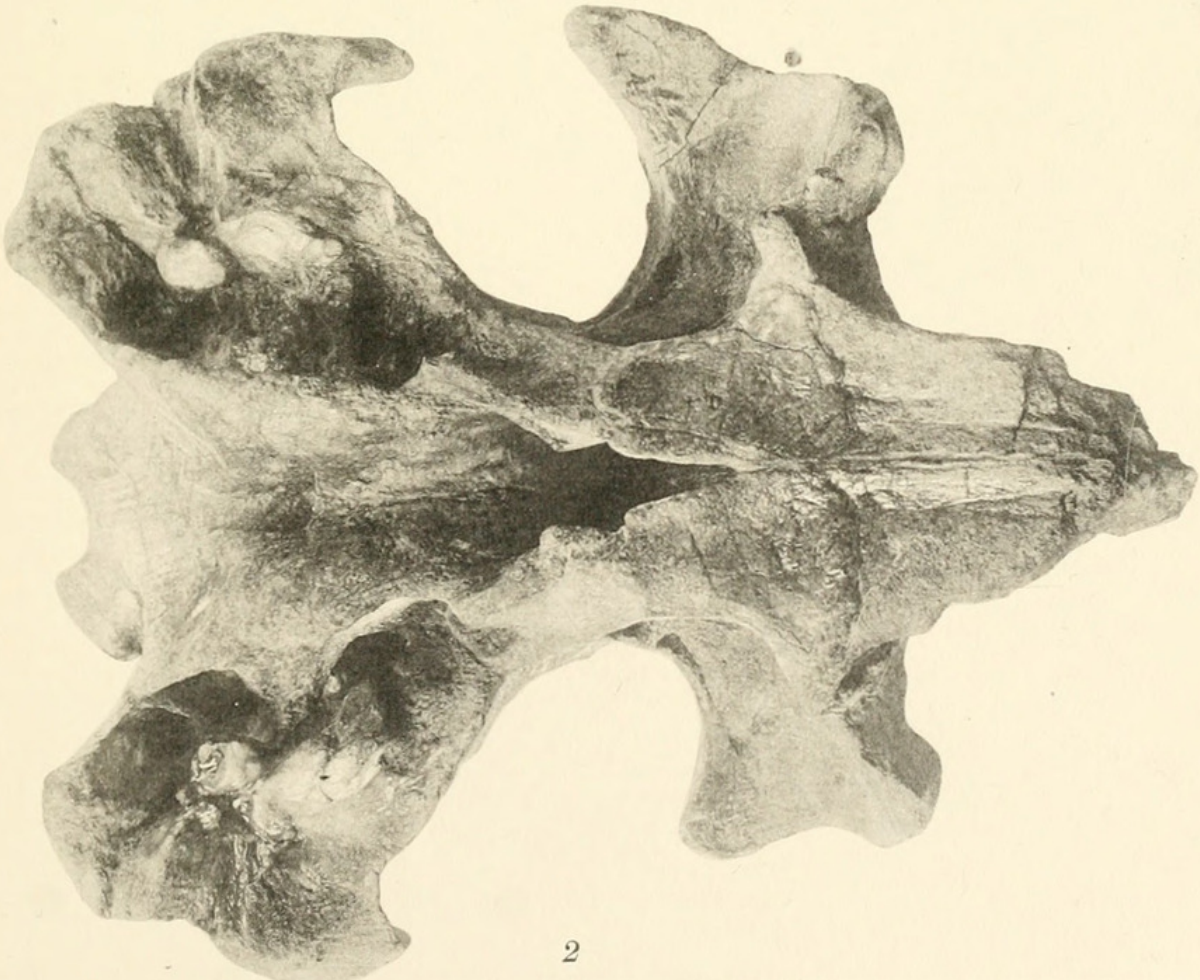

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