A NEW FOSSIL WHALE FROM THE MIOCENE OF PERU

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Volume 83, article 3, pages 195-216, text figures 1-3, plates 11-14, tables 1-4 Accepted for publication November 3, 1943 Issued July 29, 1944 THE AMERICAN MUSEUM OF NATURAL HISTORY was very fortunate to receive, during the summer of 1941, the partial skull and skeleton of a fossil whale from Peru. This specimen was presented to the Museum through the courtesy of Dr. J. A. Broggi of the Sociedad Geologica del Peru, and had been collected by him some years previously near the mouth of the Ica River, in Ica Province, Peru. The fossil came to the Museum in a shipment of invertebrate fossils which had been collected in Peru and sent to this institution by Dr. William F. Jenks, Geologist for the Cerro de Pasco Copper Corporation. After being prepared in the Museum laboratories the fossil was turned over to me for identification and study, and it forms the subject of the present contribution.

As said above, the fossil was found by Dr. Broggi near the mouth of the Ica River, which flows into the Pacific Ocean along the southern coast of Peru, at some distance southwest of Lima. It was discovered in Tertiary beds, the relationships of which will be discussed below, and after its discovery was stored for some years in San Marcos University in Lima. Unfortunately the specimen suffered the effects of an earthquake while it was deposited in the University, so that it was damaged to a certain extent. Nevertheless, it is fairly complete, comprising a portion of the skull and jaws and a considerable part of the post-cranial skeleton, and as such merits careful consideration in the literature of the fossil Cetacea.

The fossil, when it reached the American Museum, was encased for the most part in an unusually hard, consolidated matrix; consequently the preparation of the specimen was a long and arduous process—one that was admirably performed by Mr. Carl Sorensen, Preparator in the Laboratory of Vertebrate Palaeontology at the Museum. As a result of the preparation work, it has been possible to make a fairly detailed study of the structure and relationships of this fossil with interesting results, which will be presented in the following pages of the present contribution.

At this point it may be said that the American Museum of Natural History is greatly indebted to Dr. Broggi and to the Sociedad Geologica del Peru for their great kindness and generosity in presenting the specimen to the Museum and for making arrangements with Dr. Jenks to have the specimen shipped to New York. To Dr. Jenks we are indebted for information regarding the discovery and locality of the specimen.

During the prosecution of the study of this interesting fossil I was greatly aided by constant and experienced advice from the late Mr. Henry C. Raven of the Department of Comparative Anatomy of this Museum, a recognized authority on the Cetacea. Mr. Raven's opinions, based upon a long and intimate knowledge of this order of mammals, formed the basis for many of the conclusions reached in the present work.

The illustrations were made by Mr. John C. Germann.

TAXONOMY

ZIPHIIDAE GRAY, 1865

INCACETUS, NEW GENUS¹

DIAGNOSIS: A small cetacean showing a combination of both delphinid and ziphiid characters. Short, deep rostrum, with an open mesirostral groove. Palate flat and rather broad. A series of well-developed teeth in both maxilla and mandible; these teeth set in well-defined sockets. Skull but slightly assymetrical. Periotic similar to that in the Delphinidae, but tympanic typically ziphioid, with a strong external vertical fold. Small pterygoids, with external reduplication of the bones to form "pterygoid pockets" as in the Delphinidae. Posterior portion of mandibular ramus strongly convex as in the Ziphiidae. Cervicals free. Neural arches of dorsals and lumbars high, and spines inclined backward; centra of vertebrae elongated. Manubrium of sternum strongly bifid as in the Ziphiidae. Number of ribs not certainly determinable. Scapula ziphioid, similar to that of Mesoplodon, with three strong external ridges, including the scapular spine, and large, well-developed acromion and coracoid. Radius and ulna short and distally expanded, as in the Delphinidae. Carpus typically delphinid, with hexagonal bones, particularly the lunar. Digits unknown.

GENERIC TYPE: Incacetus broggii, new genus and species.

Incacetus broggii, new genus and species²

HORIZON AND LOCALITY: From the Pisco formation of Miocene age as exposed at the mouth of the Ica River, Ica Province, Peru.

DIAGNOSIS: Since this is at present a monotypical genus, the specific diagnosis is the same as that given for the genus, above.

TYPE: A.M.N.H. No. 32656, partial skeleton, including the following elements. The rostrum and lower jaws, much of which are

² Named in honor of Dr. J. A. Broggi of the Sociedad Geologica del Peru, who discovered the type specimen and presented it to the American Museum of Natural History. preserved only as an internal mold with the bone surface missing, the basicranium and the floor of the endocranium, the right periotic and tympanic, and the hyoids. The second to seventh cervical vertebrae, inclusive, and following this the first eleven dorsolumbar vertebrae in series. In addition, there are three other vertebrae from a more posterior position in the column. The right scapula, humerus, radius and ulna, and carpus. At least 13 ribs and the manubrium of the sternum.

DESCRIPTION

Size

This new cetacean from the Tertiary of Peru is a small member of the order, possessing a mixture of characters that would seem to relate it to both the Delphinidae and to the Ziphiidae, a point that has been brought out in the diagnosis and which will be elaborated on below. Suffice it to say at this place that there are reasons for considering the present fossil as a primitive and a rather unusual member of the Ziphiidae. In general, it may be said that this specimen is comparable in size to some of the smaller delphinids and thus is much smaller than most of the ziphiids, including the primitive genus Diochotichus. An early and relatively primitive member of the Ziphiidae, such as this genus is thought to be, might be expected to be smaller than the recent genera, although a conclusion such as this does not necessarily follow as applied to cetacean development between Miocene and Recent times.

Skull

The skull of *Incacetus* is at once characterized by its proportions, for the rostrum is seemingly rather short in comparison to the total length of the skull, a feature rather unusual in the earlier members of the Odontoceti. Unfortunately the anterior portion of the rostrum is missing in the fossil, so that truly definitive comparisons cannot be made, but for various reasons it would seem probable that the rostrum did not extend forward to a degree comparable with that typical of the other early members of either the Delphinidae or Ziphiidae.

¹ From Inca, the name of the dominant peoples of ancient Peru, plus $K \tilde{\eta} \tau os$, whale.

For instance, in Diochotichus, a primitive ziphiid with 21 teeth in the upper jaw, the rostral length from the nares to the tip of the premaxilla is about 3.9 times that of the cranial length, from the nares to the occipital condyle. In a like manner, the rostral length of Tasmacetus, a toothed ziphiid of Recent age having 19 teeth in the upper jaw, is about 3.1 times the cranial length, while in Mesoplodon, a specialized ziphiid in which the teeth are suppressed, the rostral length is about 3.6 times the cranial length. Supposing Incacetus to have had about the same number of upper teeth as the toothed ziphiids cited above, that is about 20, the rostral length, upon the basis of the 16 teeth preserved in the specimen at hand, would be only about 1.6 times the cranial length. Thus a comparison such as this indicates a mid-Tertiary ziphiid with a rostral length much less than that either of its contemporaries or of its successors, a rather anomalous situation in view of the fact that evolution among the Ziphiidae has been accompanied by a certain amount of rostral shortening.

The same holds true, only in a more marked degree, when Incacetus is compared with various early or generalized delphinids. The mid-Tertiary Delphinidae are notable for the length of the rostrum. In Eurhinodel*phis*, for instance, a genus characterized by about 60 teeth on either side of the upper jaw, the rostral length, as measured above, is about nine times that of the cranium. In Kentriodon, a much less "extreme" form, the rostral length is about 3.7 times the cranial length. To achieve a ratio similar to that of Kentriodon it would be necessary to suppose that there were something like 60 teeth present in each upper jaw of Incacetus, a figure that is felt to be out of proportion to the probabilities. On the other hand, supposing that there were about 25 to 30 teeth on either side in the skull of Incacetus, a figure based upon a restoration of the rostrum that appears very probable by reason of the manner in which the maxillary borders are converging toward each other anteriorly, the ratio of cranial length to rostral length would be about 1/2.0. This ratio compares fairly closely with the ratio in some of the shortbeaked Delphinidae, such as Tursiops or Lagenorhynchus.

Therefore, it may be seen that the length of the rostrum in the new fossil cetacean would seem to be comparable to the condition in some of the modern forms, especially among the Delphinidae, rather than with the mid-Tertiary odontocetes with which it was contemporaneous. In this respect, *Incacetus* would seem to show a specialized delphinid trait.

The preceding remarks may be illustrated by a table of ratios as follows:

Ratios,	CRANIAL	то	Rostral	Length
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Incacetus	1/1.6	(restored on the basis
		of about 20 teeth)
Diochotichus	1/3.9	21 teeth
Tasmacetus	1/3.1	19 teeth
Mesoplodon	1/3.6	no teeth
Incacetus	1/2.0	(restored on the basis of about 30 teeth)
Eurhinodelphis	1/9.0	60 teeth
Kentriodon	1/3.7	40 teeth
Delphinus	1/2.9	44 teeth
Sotalia	1/2.4	30 teeth
Tursiops	1/2.1	23 teeth
Cephalorhynchus	1/1.4	27 teeth
Lagenorhynchus	1/1.6	30 teeth

Much of the bone of the rostrum in Incacetus is missing, especially that of the upper portion of the rostrum, but fortunately an inner mold of matrix is preserved which is sufficient, together with the preserved bone below it, to give a clear picture of the structure of the skull in this region. This mold and the bones of the maxillaries that are preserved indicate a rather narrow, deep rostrum, as is characteristic of the ziphiids, which offers a decided contrast to the delphinid condition in which the rostrum is flattened. What is particularly interesting about this fossil skull is that the mold shows the premaxillaries to have formed a long, deep trough, open along the top, the vomerine trough, the mesirostral gutter, or the mesirostral trough as variously designated by different authors. This deep trough, bounded on the sides by the comparatively high walls of the premaxillaries, is a very definite ziphiid character, quite in contrast to the mesirostral region of the delphinids which takes the form of a tubular canal, placed internal to the maxillaries (not above them as is the case in this fossil and in the typical ziphiids). It is enclosed on top by the contiguous edges of the premaxillaries. The internal mold of the vomerine trough shows by a rough ridge along its dorsal median line that the trough was open in life, a characteristic of young odontocetes, so it is logical to assume that this was a relatively young individual. With increasing age among these whales the vomerine trough or mesirostral groove is gradually closed by a dorsal expansion and calcification of the vomer, so that in aged individuals the rostrum is a solid,

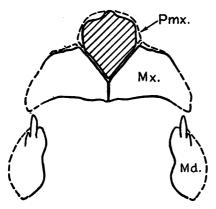


FIG. 1. Incacetus broggii, new genus and species. A.M.N.H. No. 32656. Cross section of rostrum and mandible, near the anterior end of the specimen as preserved. Md., mandibular ramus; Mx., maxilla; Pmx., premaxilla. The lined area indicates the matrix filling of the mesirostral trough. Three-fourths natural size.

bony structure. Nothing much of the maxillaries is preserved posteriorly, but there is a sufficient amount of bone and internal mold present to show that these elements became flat and broad behind the tooth row.

The nasal choanae, preserved by internal molds, are slightly asymmetrical with the right naris somewhat anterior to the left one. Generally speaking, however, the asymmetry in the skull of *Incacetus* is not strong. It might be said that the molds of the nares, and that portion of the septum preserved between them, indicate a rapid upward sweep in this portion of the skull, still another character that would seem to point to ziphiid affinities for *Incacetus*.

Of the cranium, only the cranial floor is preserved. This shows the braincase to have been of characteristic cetacean form, large and rounded and very similar in general aspect to the cranial cavity in Delphinus. The bone of the cranial floor is rather thin, as is typical in the cetaceans, with a certain resultant lack of ossification in some regions. Thus there is a large sphenorbital fissure between the alisphenoid and the orbitosphenoid, as in the modern odontocetes, serving presumably for the passage of the optic nerve as well as for those cranial nerves ordinarily passing through the foramen rotundum. Behind this there is what appears to be the foramen ovale in the alisphenoid and around the tympanic the usual large opening seen in the Cetacea representing in part a confluence of the foramen lacerum medius and the foramen lacerum posterius. In the middle of the basioccipital the bone is thin, tending to form an irregular circular opening, a feature common in many cetaceans.

In spite of the damage to the skull of *Incacetus*, the right periotic and its associated bones were preserved with but little breakage, while the right bulla, although lacking some of its outer surface, is still essentially complete. These elements may be considered in some detail.

The periotic in this genus would seem to resemble that of the delphinids more closely than it does the periotic in the ziphiids. According to Kellogg, the ziphiids are characterized by the fact that "the grooved anterior process of the periotic is lodged in a slender ventrally directed dactyloid process of the squamosal" (Kellogg, 1928, pp. 61-62). In this present specimen the anterior process of the periotic is not grooved but smooth, just as it is in the delphinids. This, together with the fact that the superior portion of the bone above the pars cochlearis is broad as in the delphinids and not narrow as in the ziphiids, that the posterior process is transversely directed as in the delphinids, that the pars cochlearis is delphinid-like in shape, not ziphiid-like, and especially that the large fossa on the internal surface of the pars cochlearis (in which are contained the internal acoustic meatus, the foramen centrale, the foramen singulare, and the entrance to the aqueductus fallopii) is very similar to the same feature in the delphinids and quite different from that in the ziphiids, contributes to make the periotic of *Incacetus* very similar to the same bone in the delphinids and quite definitely dissimilar to that of the ziphiids.

The anatomy of the periotic in Incacetus is shown by the accompanying figures, so that little discussion is needed at this place. On the external surface this bone shows the bulbous pars cochlearis, posterior to which is the fenestra rotunda. Above this fenestra is a long fossa for the stapedial muscle, leading into the region of the middle ear. Luckily, the auditory ossicles are preserved, at least in part, in this fossil whale. Of these, the malleus is the bone most incompletely preserved, since only a portion of it resting in the mallear fossa of the petrosal is present. However, this fragment articulates with the incus, of which the body and the crus longum are preserved. As is characteristic of the cetaceans, this ossicle is broad with two facets for articulation with the malleus. On the side of the crus longum is a facet for articulation with the head of the stapes. The stapes is rather long and flattened, pierced by a small foramen. Its foot is in place in the foramen ovale.

Internally the periotic consists of the large dorsal portion made up of the anterior, superior, and posterior processes, ventrad to which is the pars cochlearis. On the posterior portion of the pars cochlearis are two openings, the cerebral orifice of the aqueductus vestibuli above, and the cerebral orifice of the aqueductus cochleae below. As was mentioned above, much of the internal surface of the pars cochlearis is occupied by the fossa (filled in the fossil with matrix) for the internal acoustic meatus, the foramen centrale, the foramen singulare, and the entrance to the aqueductus fallopii. Since the matrix is so exceedingly hard, it has not been removed from above these several openings, for fear of breaking the periotic bone in the process of such preparation.

Due to the vicissitudes to which the fossil was exposed during the course of its history, the periotic was broken away from the tympanic bulla. It was this breakage that caused the destruction of a great portion of the malleus. Even though broken, the tympanic shows the base of the sigmoid process, which formed one of the attachments of this bone to the periotic. In Incacetus the tympanic is acuminate anteriorly, while posteriorly it is deeply bilobed, a form that is seen among members of both the Delphinidae and the Ziphiidae. The interesting feature of this bone is the strong vertical fold on the anterior portion of its outer surface, a character that is quite typical of the ziphiids but that is absent or but feebly developed in the delphinids. Thus it would seem that the two bones of the acoustic complex in Incacetus show different relationships, the periotic being throughout strongly delphinid in its form and features, and the tympanic, especially because of the well-developed external fold, being of definite ziphiid type.

The palate of *Incacetus* is comparatively broad and flat, particularly in its anterior region. Here we see the retention of a delphinid character in this whale, a character quite at variance with the typical convex palate of the modern ziphiids. It might be pointed out in this connection that in *Diochotichus* the palate is rather flat, although not so much so as in the form now under consideration.

In its posterior portion the palate of Incacetus exhibits two large, elongated depressions, one on either side, separated each from the other by a high, thin, median bony septum or wall. These depressions are in the maxillaries and they represent an invagination of the palatal roof in this region, possibly as an accommodation for diverticulae of the air sacs that are commonly developed in the throat of the Cetacea. The median ridge separating them seems to be also of maxillary origin. Along its broken edge it shows a median dividing line where the thin walls of bones are closely appressed. The effect is as if there had been an upward pushing against the palatal roof forming the depressions, and an inward pushing from either side against the median portion of the maxillaries, pinching them together to form a thin wall. Perhaps the structure in this region is shown to better advantage by a figure (pl. 12) than it can be described.

In this development the palate of *Incacetus* shows a certain amount of similarity to some of the delphinids, in which there is a median ridge in the posterior portion of the palate.

However, in none of the modern types is the lateral compression so extreme as in *Incacetus*, for in them the ridge, though present, is broad, never a thin wall.

This structure in the palate of *Incacetus* is not to be confused with the thin vomerine ridge that is exposed at the back of the palate in *Diochotichus*. In *Incacetus* the ridge, of maxillary origin, is in front of the pterygoids, whereas in *Diochotichus* the ridge, of vomerine origin, was in life enclosed and hidden by the pterygoids.

Behind these depressions are the pterygoids, which seem to show a delphinid rather than a ziphiid type of development. Kellogg has pointed out the fact that the ziphiids are characterized by their very large pterygoids which spread over the palatines, almost completely covering these latter bones, but which nevertheless are simple in that they do not show the external reduplication that is so typical of the delphinids. This is without much doubt a secondary enlargement and simplification from the delphinid condition, in which the pterygoids are small, so that much of the palatines is visible in front of them, and at the same time is reduplicated externally, so that there is formed a bony "pterygoid pocket" to accommodate the air sac.

In *Incacetus* this region is difficult to interpret with complete satisfaction, but it would seem that there are rather typical delphinid pterygoids, each with a posterior wall separating the nasal passages from the buccal region, and anteroventrally to this a folding over to form the "pterygoid pocket." Here again the figure (pl. 12) explains the structure much more satisfactorily than it can be described in words.

The pterygoids of *Incacetus* appear to be rather small, as in the delphinids, but it is possible that these structures may have been large and that their anterior reaches were formed of very thin bone or even were membranous, spreading out to cover the depressions in the maxillaries, which were described above. That such a possibility is to be considered is due to the fact that the anterior edges of the pterygoids, as preserved, seem to indicate the "pterygoid pocket" to have been open anteriorly, not closed as in the delphinids, and this is the reason for supposing the possibility of an extension covering the maxillary depressions. On the other hand, it may be that this appearance is artificial and not real, a point that cannot be satisfactorily determined upon the basis of this specimen. Suffice it to say that if there was a thin, bony or membranous forward extension of the pterygoid we would see here a combination of delphinid and ziphiid characters, delphinid in the folded-over, pocket-like structure of the bones, ziphiid in their great extent.

The hyoids, fortunately partially preserved between the posterior portions of the mandibular rami, are characteristic but not particularly definitive. The basihyal is bilobed on its anterior border, a condition similar to that described by Thorpe for the modern ziphiid *Mesoplodon*. Articulated to its lateral edges were the long thyrohyals, while parallel to these latter bones were the stylohyals, each connected by a cartilage to one of the basihyal lobes or prongs. These bones, restored to their original positional relationships, are shown in plate 12.

In this specimen there are approximately 16 maxillary teeth, shown to a large extent by their alveoli, although the bases of many of the teeth are preserved. These are seemingly simple but large teeth, showing no indication of dental suppression.

Naturally the actual number of teeth present in *Incacetus* is a question of importance which can be answered only in the most tentative fashion. As was shown above, if the rostrum of this cetacean were proportionately as long as in other toothed ziphiids such as Diochotichus or Tasmacetus, there would be an inordinately large number of teeth present in the upper jaw of the new genus. However, as has been shown, there is good reason to suppose that the rostrum and the lower jaw of Incacetus were relatively short as in some of the delphinids, and that the tooth count was probably low, perhaps similar to that of the other toothed ziphiids, with about 20 to 30 teeth in the skull. These teeth are separated from each other by osseous, interdental walls, as is the case in Diochotichus and Tasmacetus. In the more specialized ziphiids, in which the upper teeth are present but nonfunctional, they are lodged in maxillary

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grooves, the interdental bony divisions having been largely broken down.

The presence of large teeth in *Incacetus* and especially the method of their implantation, with the osseous interdental walls retained, indicate the relatively central position of this fossil in odontocete phylogeny. The various ziphiid characters in *Incacetus* are advanced habitus features that indicate pretty well the position of this genus as an early expression of the ziphiid line of adaptive radiation. The delphinid characters are for the most part the retained heritage characters that indicate the origin of the genus.

MANDIBLE

The mandible in this new cetacean is characterized by the strong convexity of its ramus in the posterior region, a ziphiid feature that is shown in Diochotichus. The ramus is rather low in its anterior region and rises gradually to the coronoid, as is the case in Diochotichus and in such recent ziphiids as Mesoplodon europaeus. The symphysis seemingly is far forward, for there are at least 16 teeth, possibly more, in the tooth row behind its posterior border. The short, anteriorly placed symphysis is a condition somewhat similar to that found in some of the modern delphinids and certain ziphiids such as Mesoplodon, and is in decided contrast to Diochotichus, in which the symphysis extends back so that its posterior border is about opposite the fifth tooth from the back of the tooth row. Although the front of the mandible is missing in Incacetus, there is good reason, because of its forward position, to think that the symphysis was relatively short, again a character of similarity between this fossil and some of the recent ziphiids and delphinids and one of decided contrast to the condition in *Diochotichus* in which the symphysis is long. In this connection it might be said that the symphysis of *Tasmacetus* is long, a primitive character carried over into modern times by this very interesting ziphiid.

To indicate the general relationship of symphysis to mandibular length the following data are presented in the table below.

Vertebrae

Of the vertebral column, all cervicals except the atlas, and the first 11 dorsals or dorsolumbars are preserved in series. In addition there are three additional vertebrae from a more posterior portion of the column.

The cervicals are free, a primitive character to be seen in other Miocene cetaceans, both Delphinidae and Ziphiidae, and one retained in variable degrees among the modern members of these two families. Consequently these vertebrae in *Incacetus* are not particularly distinctive.

The dorsolumbars are, however, definitely distinguished by a number of important characters. Thus, in these vertebrae the neural arches are high, their pedicles are strongly notched anteriorly and posteriorly, and the spines project back with a distinct "rake." These are all delphinid characters, to be seen in various genera belonging to this family. In the more posterior elements of the vertebral column of *Incacetus*, there is a marked elongation of the centra, a character that is quite typical of the vertebrae of the Ziphiidae. Consequently this might be thought to be a ziphiid trait in the fossil whale. It should be

	Length of mandible	Length of symphysis	Ratio symphysis/ mandible	
Incacetus	350.0 mm. (est.)	90.0 mm. (est.)	26 (est.)	
Diochotichus	580.0	282.0	49	
Tasmacetus ¹	103.7	42.3	40	
Mesoplodon europaeus²	657.0	160.0	24	
Kentriodon ³	262.0	85.0	32	
Sotalia ⁴	252.0	60.0	24	
Delphinus	373.0	45.0	12	

¹ Measurements from Oliver, 1937.

² Measurements from Raven, 1937.

* Measurements from Kellogg, 1927.

⁴ Measurements from Van Beneden and Gervais, 1880, atlas.

noted, however, that elongation of the centra may be a primitive character in many lines of cetacean development, so that a great deal of care must be exercised in attempting to evaluate this development in *Incacetus*. For instance, in the Miocene delphinid *Kentriodon*, described by Kellogg, the posterior vertebral centra are elongated, so it may be that the very short centra characteristic of many modern delphinids represent a secondary development in the history of this family. Therefore, it is felt that the elongated centra in *Incacetus* carry little weight in the arguments for relationships being presented here, either in one direction or in the other.

The lumbar vertebrae of *Incacetus* show a distinct keel ventrally, along the mid-line of the centrum.

RIBS AND STERNUM

Some of the ribs are preserved in the specimen under consideration, notably a series of seven or eight ribs from the right side. Of these the first member of the series is long and comparatively straight, so there is reason to think that it is not morphologically the first rib. It may have been as far forward as the second or third of the rib series, it may have been as far back as the fifth or sixth. Consequently it is impossible to determine even approximately the number of ribs that were present in this cetacean. In the delphinids there are about 14 ribs, in the ziphiids about 10.

Raven has shown in a recent paper (Raven. 1942) how there are three methods of articulation for the posterior ribs in the Cetacea. In the first place the articular facets of the capitulum and tuberculum coalesce in the more posterior ribs to form a single articulation. This type of rib articulation is found among the Plantanistidae and in certain archaeocetes. Secondly, the capitulum may be lost in the posterior ribs, the articulation with the column being confined to the tubercle. This type of articulation is found among the delphinids and in certain mysticetes. Finally, the tubercle is lost in the posterior ribs with the articulation being confined to the capitulum, a type that seemingly is found only in the ziphiids.

In this last type of development, there is a

sudden "break" in the rib series (noted by Kellogg and other authors) where the change from a double-headed articulation to articulation by means of the capitulum only occurs, and this change is between the seventh and eighth rib. Due to the broken conditions of the ribs in the present specimen, particularly the damaged ends of these ribs, and due to the mutilated condition of the vertebrae, it is impossible to arrive at any conclusions as to relationships as based upon these structures, which if completely preserved would be diagnostic as outlined above.

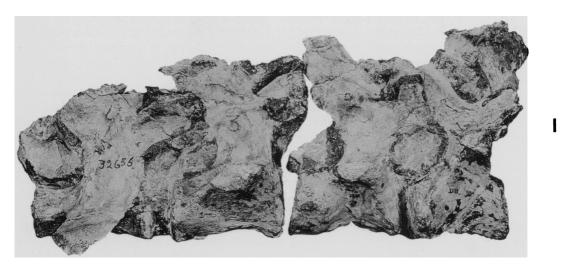
Fortunately, enough is preserved of the sternum to afford a very definite idea as to its characters and relationships. In this specimen only the manubrium is present, but it is sufficiently well preserved to show a distinct and deeply bifid or double-pronged termination anteriorly. This type of manubrium is very characteristic of the Ziphiidae and is in decided contrast to that of the Delphinidae.

Certain delphinids may have a shallow anterior bifid border on the manubrium, but it is never so deeply cut out as in the present specimen or as in the Ziphiidae. Moreover, this fossil shows no traces of lateral processes on the manubrium, again a ziphiid character in contrast to the condition in the delphinids where strong lateral processes are present.

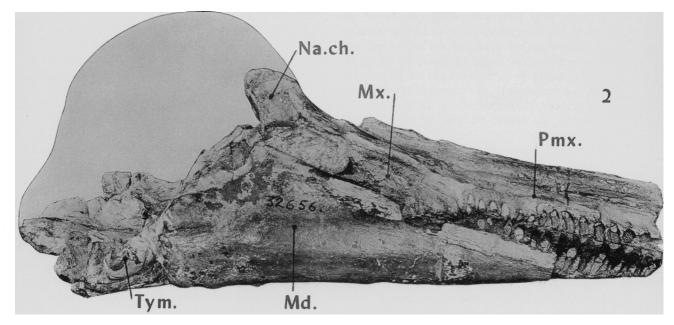
FORELIMB

The scapula of *Incacetus* is well preserved and is very much like the same bone in some of the ziphiids, especially *Mesoplodon*. It is broad, with three strong ridges on its external surface, the anterior one of which is the scapular spine. From the scapular spine there projects forward a long and rather broad acromion process, and ventral to this there is an equally long but thinner coracoid process. The vertebral and cranial borders appear to meet at an acute angle. In all these characters the scapula of *Incacetus* would seem to resemble that of *Mesoplodon* more closely than that of any of the other cetaceans.

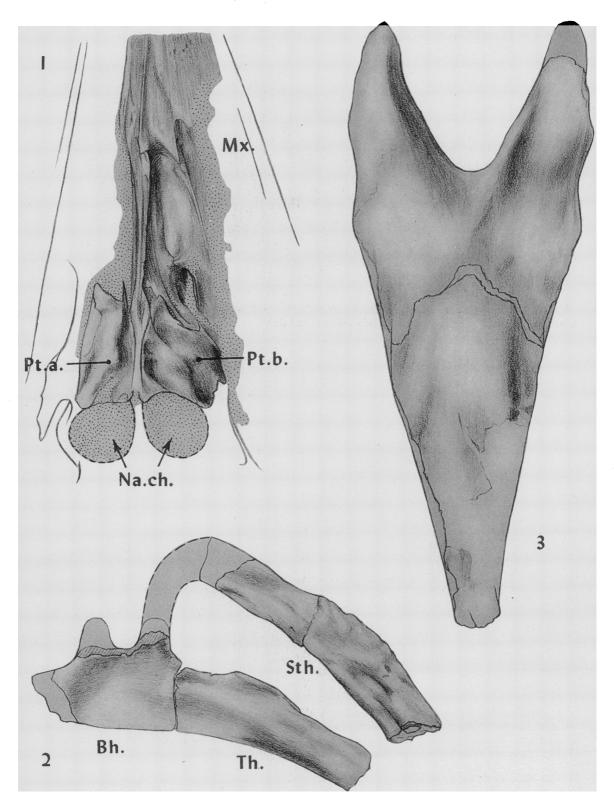
The humerus is a short, stout bone with a rounded head and a greatly expanded lesser tuberosity on the *inner* side of the bone, as is typical of the Cetacea. This bone is comparatively long, being about equal in length to the radius-ulna, in which respect



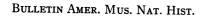
1. Incacetus broggii, new genus and species. A.M.N.H. No. 32656. Eighth to eleventh dorsolumbar vertebrae. Lateral view of right side. One-half natural size.

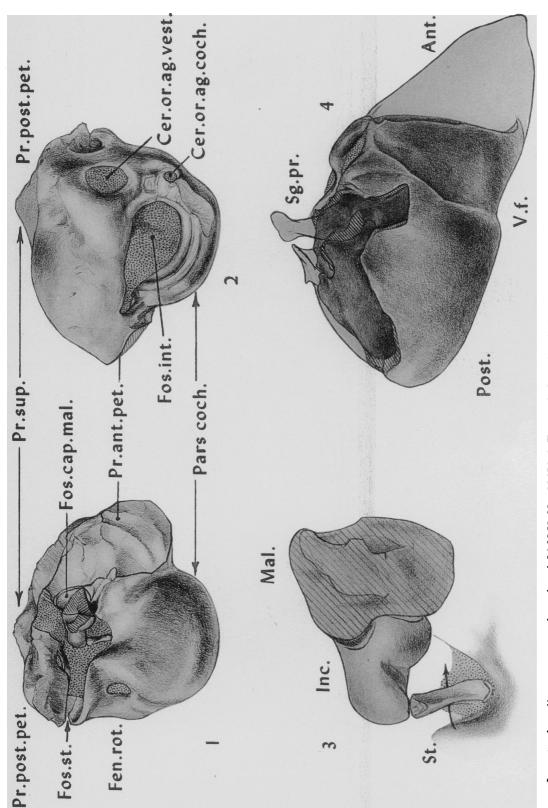


2. Incacetus broggii, new genus and species. A.M.N.H. No. 32645. Rostrum and basicranial region of skull and mandible. Lateral view of right side, with probable outline of the cranium indicated by shaded area. Md., mandible; Mx., maxilla; Na. ch., matrix plugs in nasal choanae; Pmx., premaxilla; Tym., tympanic. One-half natural size.

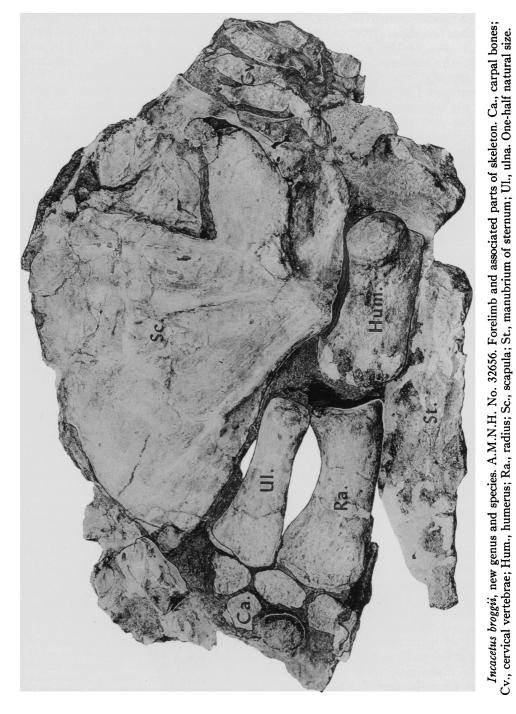


Incacetus broggii, new genus and species. A.M.N.H. No. 32656. 1. Portion of palate. Mx., maxilla; Na.ch., matrix plugs filling the nasal choanae; Pt.a., outer surface of "pterygoid pocket"; Pt.b., inner surface of "pterygoid pocket." 2. Hyoid bones, restored to their presumably natural positions. Bh., basihyal; Sth., stylohyal; Th., thyrohyal. 3. Manubrium of sternum, ventral view. All figures three-fourths natural size.





Incacetus broggii, new genus and species. A.M.N.H. No. 32656. 1. External view of periotic, showing the auditory ossicles in place. 2. Internal view incus; Mal, malleus (restored); St., stapes (arrow shows direction of foramen). 4. External view of tympanic bulla. Ant., anterior portion; Post., posterior portion; Sg. pr., sigmoid process; V.f., vertical fold in outer surface of bulla. All figures three times natural size except 3, which is nine times of periotic. Cer.or.aq.coch., cerebral orifice of aqueductus cochleae; Cer.or.aq.vest., cerebral orifice of aqueductus vestibuli (endolymphatic duct); Fen.rot., fenestra rotunda; Fos.cap.mal., fossa for head of malleus; Fos.int., internal fossa (here filled with matrix), containing the internal acoutic learis; Pr.ant.pet., anterior process (broken); Pr.post.pet., posterior process (broken); Pr.sup., superior process; St., stapes. 3. Auditory ossicles. Inc., meatus, foramen centrale, foramen singulare, entrance to aqueductus falopii; Fos.st., fossa for stapedial muscle; Inc., incus; Pars coch., pars cochnatural size. Bulletin Amer. Mus. Nat. Hist.



it resembles the comparatively long humerus of the ziphiids and differs from the noticeably shorter humerus of the delphinids. Again, in *Incacetus* the humerus is not appreciably expanded distally, a ziphiid character that may be contrasted with the expanded distal portion of the humerus in the delphinids.

The radius and ulna are notable because of their expanded distal ends and their rather constricted medial portions. This causes much of the posterior border of the radius and the anterior border of the ulna to be widely separated from each other, rather than closely appressed, as is common among the cetaceans. The expanded distal extremities of these bones is a distinct delphinid character; in the ziphiids there is little noticeable expansion of the lower arm bones distally.

It is, however, in the construction of the carpus that this fossil cetacean shows especially strong delphinid characters. In the first place, the carpal bones of Incacetus tend to be of hexagonal form, a character that is particularly noticeable in the lunar, and this development is quite characteristic of Delphinus and allied genera. It is in decided contrast to the square or rectangular carpals of the ziphiids, as they are exemplified in Mesoplodon. The resemblance between the carpi of Incacetus and Delphinus does not end with the correspondence in the shapes of the individual elements, for in addition there is a close correlation between the two genera in the positions of the carpal elements, a correlation that must be of considerable significance.

The arrangement of the carpal bones in the cetaceans has been accorded quite a bit of attention by certain authors, notably by Weber in 1888, by Kükenthal in 1889, and by Turner in 1909. From the work of these authorities and from original observations by the present writer it would appear that the carpus of *Delphinus* shows an arrangement of bones quite distinctive from that of *Mesoplodon* and that the carpal arrangement in these two genera is in a broad way more or less characteristic for the two families of which these genera are representative.

In *Delphinus* there has been an inward shift of the outer distal carpal elements from their primitive positions. The magnum, which is co-ossified with the trapezoid, articulates only with the inner portion of the proximal facet on the third metacarpal. The outer portion of this facet, in reality a separate facet, articulates with the unciform, which has likewise shifted inwardly to establish contact with the third and fourth metacarpals. The unciform has, in effect, migrated away from the fifth metacarpal, its original articulation, so that this latter bone has established a new contact with the cuneiform. Finally, this inward pushing of the distal row of carpals has caused the establishment of a broad contact between the magnum-trapezoid and the scaphoid. The trapezium is fused with the first metacarpal.¹

Exactly this same arrangement of carpal elements is to be seen in *Incacetus*, as shown by figure 2.

The above arrangement of the carpals is to be contrasted with that of *Mesoplodon*, in which the square bones are arranged in two rather regular rows. The proximal row consists, of course, of the scaphoid, lunar, and cuneiform in series. In the distal row, the trapezium fused with the first metacarpal is directly beneath the scaphoid, the fused trapezoid and magnum are beneath the lunar, while the unciform is beneath the cuneiform. The fifth metacarpal articulates with the unciform, as does the fourth metacarpal, while the second and third metacarpals articulate with the combined trapezoid-magnum. This arrangement also is shown in figure 2.

In view of the close correspondence between Incacetus and Delphinus in the arrangement and form of the carpals, there is good reason

¹ It has been thought by some authors (see Turner, 1909) that the trapezium is present in the odontocete manus. By others it has been considered to be completely eliminated (Flower, 1870; Weber, 1888), to be occasionally present (Weber, 1888), or to be fused with the scaphoid (Weber, 1928).

In 1937 Raven figured the manus of *Mesoplodon*, indicating a fusion of the trapezium with the first metacarpal. This view was reached particularly because of a study of the carpus in *Monodon* in which a long element occupies the position that would naturally be taken by a fused trapezium and first metacarpal. Moreover, in a recent examination by the author of X-ray photographs of the manus of *Monodon*, taken under the direction of Mr. Raven, there seems to be a reasonably clear indication of a separation in this elongated bone pointing to the presence of trapezium above and metacarpal below, composing the element. (See fig. 2.)

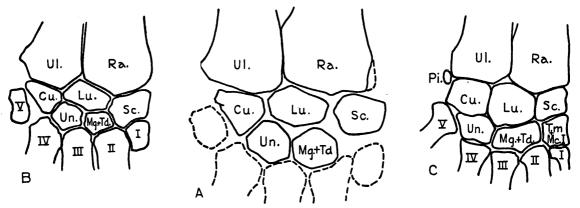
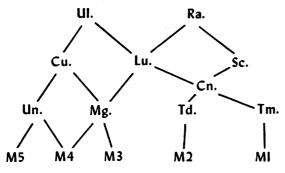


FIG. 2. Comparative figure to show the resemblances and differences among the carpi of (A) *Incacetus* broggii, (B) *Delphinus*, and (C) *Mesoplodon*. Cu., cuneiform; Lu., lunar; Mg. +Td., coalesced magnum and trapezoid; Pi., pisiform; Ra., radius; Sc., scaphoid; Tm. +McI., trapezium coalesced with meta-carpal I; Ul., ulna; Un., unciform; I, II, III, IV, V, metacarpals. Not to scale.

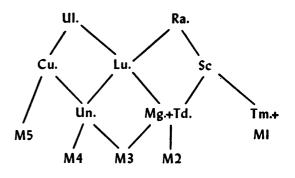
to think that the digits, which unfortunately are missing in the fossil, were developed much as they are in the modern genus. *Delphinus* is characterized by the hypertrophy of the second and third digits and the reduction of the other fingers, which may be contrasted with the more or less equally developed digits in *Mesoplodon* and the other ziphiids.

Considering for a moment the broad implications of the structure of the manus in *Incacetus* and those cetaceans with which it has been compared, we are immediately confronted with certain difficulties. Which type of carpus, delphinid or ziphiid, is the more primitive? The solution of this question may not be possible in the present state of our knowledge, but as a background for the phylogenetic comparisons of the two structures it may be well to attempt an analysis of the archaeocete carpus.

As figured by Kellogg, the archaeocete carpus is built up about as follows:



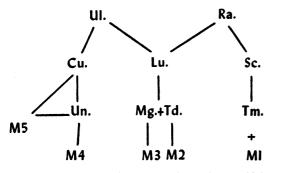
From a form presumably similar to this the central type of delphinid carpus has been derived, a process involving the radial shift of the outer distal carpals, already described.



From these diagrams,¹ in which the positions and the principal articulations of the carpals are shown, it may be seen that the delphinid carpus (which is found in *Incacetus*) has a pattern rather similar to that of the archaeocete carpus, but one that is actually different since there have been shifts of the bones, in the course of which some new articulations have been established.

The ziphiid carpus has arisen in a somewhat different way, as follows:

¹ In these and the following diagrams, the letters indicate the approximate spatial relationships of the carpals and metacarpals to each other. The lines indicate contacts between the bones, with the exception of lateral contacts, which are eliminated for the sake of clarity.



Here there seemingly has been less shifting of the distal carpals and consequently fewer changes in the articular relationships of the carpals and metacarpals to each other than is the case in the delphinids, but due to the "squaring" of all the carpal elements the wrist has become quite unlike that of the archaeocete, perhaps to a degree greater than is the case in the delphinid carpus. For in the ziphiids, the carpus assumes a "serial" arrangement, with two rows of square or rectangular bones, superficially not unlike the condition seen in the Proboscidea. (Of course this comparison is made in a purely descriptive way and does not imply any cetaceanproboscidean relationship.)

Consequently it is hardly possible to say that either type of these two derived forms of cetacean carpi is decidedly primitive, taking the archaeocete wrist as the ancestral form from which both were derived. Each has evolved along its own line of adaptive radiation. But in a general way it might be said that the delphinid carpus is perhaps somewhat less far removed from the archaeocete type in the arrangement and form of the carpal elements than is the ziphiid carpus. Therefore, if the square bones of the ziphiid wrist represent a rather aberrant specialization, it would seem likely that Incacetus represents an early stage in the development of the modern odontocetes, in which carpal specialization had attained the delphinid condition but had not proceeded beyond that stage.

TABLE 1¹

MEASUREMENTS OF THE SKULL AND JAW (Measurements in millimeters)

	Incacetus	Diochoti- chus	Tasmace- tus	Kentriodon	Delphinus	Delphinus
	A.M.N.H. No. 32656	A.M.N.H. No. 9485	Ohawe specimen	U.S.N.M. No. 8060	A.M.N.H. DCA	from Van Beneden and Gervais
Skull, total length	4 25e	634	1148	298.0	396	420.0
Rostrum, length, anterior border nasal choanae to tip	290e	485	884	230.0	270	312.0
Cranium, length, anterior border nasal choanae to occipital condyles	135	150	264	70.0	126	118.0
Rostrum, breadth, palatal suture	90	142	332	68.0	60	78.0
Rostrum, depth, palatal su- ture	33	39			23	30.0
Diameter of orifice of an- terior nares	50	53	95	24.0	42	45.0
Tympanic bulla, length	29	49		29.7	32	30.0
Periotic, length	25e	_		28.8	29	28.5
Mandibular ramus, length	350e	580	1037	262.0	337	375.0
Mandibular ramus, depth	70	70	183	_	56	54.0
Symphysis, length	90e	282	423	85.0	61	45.0
Tooth row, length	210e	363	490	190.0	198	210.0

¹ In tables 1-3, certain measurements of *Incacetus* are estimated, but such estimations are felt to be fairly close approximations. All measurements from Van Beneden and Gervais and a few from Kellogg and from Oliver are taken from plates.

TABLE 2

MEASUREMENTS OF THE SKELETON (Measurements in millimeters)

	Incacetus A.M.N.H. No. 32656	Mesoplodon from Van Beneden and Gervais	Tasmacetus	Kentrio- don U.S.N.M. No. 8060	Delphinus from Van Beneden and Gervais
Manubrium, length	200+		283		72
Manubrium, width	70		243		105
Scapula, length	255 ap.	350			
Scapula, height	168	225			
Scapula, length, acromion	64	85 ap.			
Humerus, length	91	140			60
Humerus, anterior-posterior diameter					
(proximally)	41	87			38
Radius, length, anterior	97	160			70
Ulna, length, anterior	90	150			63
Radius-ulna, anterior-posterior diameter, proximally	59	120			53
Radius-ulna, anterior-posterior diameter, distally	84	91			68
Carpus, breadth	80e	93			67
Carpus, height	37	57	_		25

TABLE 3

MEASUREMENTS OF VERTEBRAE (Measurements in millimeters)

	Incacetus	Diochotichus	Mesoplodon	Kentriodon	Delphinus
	A.M.N.H. No. 32656	A.M.N.H. No. 9485	from Van Beneden and Gervais	U.S.N.M. No. 8060	from Van Beneden and Gervais
4th cervical					
Length, centrum	12		14	61.1	6.6
Height, centrum	30		40	—	25.0
6th dorsal					
Length, centrum	44	50e	62	21.8	29.0
Height, centrum	26	36	50		27.0
Height, neural arch	32	31	20e		15e
Breadth, anterior zyga-					
pophyses	58	50+			
11th dorsal					
Length, centrum	65		86	28.4(10th)	31.0
Height, centrum	32		60	— ` <i>´</i>	28.0
Height, neural arch	36	—	25e		17e
Breadth, metapophyses	15				
Lumbar					
Length, centrum	74		106	36.0	25.0
Height, centrum	42		71	26.0	30.0
Height, neural arch	35		25e		25e
Breadth, transverse process	210e	_			186.0

TABLE 4

RATIOS AND INDICES

	Incacetus	Diochoti- chus	Tasmace- tus (skull) Mesoplodon (skeleton)	Kentrio- don	Delphinus
Skull $\frac{\text{cranial length}}{\text{rostral length}} \times 100$	47	31	30	30	47
Skull $\frac{\text{rostral length}}{\text{skull length}} \times 100$	68	77	77	77	68
Skull $\frac{\text{tooth-row length}}{\text{skull length}} \times 100$	52	57	42	64	50
$Jaw \frac{symphysis \ length}{ramus \ length} imes 100$	26	78	41	32	18
4th cervical $\frac{\text{length}}{\text{height}} \times 100$	40	_	35		26
$\frac{6 \text{th dorsal length}}{11 \text{th dorsal length}} \times 100$	68	_	72	77	93
11th dorsal $\frac{\text{height neural arch}}{\text{length}} \times 100$	56		29		55
Scapula $\frac{\text{height}}{\text{length}} \times 100$	66	_	64	_	_
$\frac{\text{Humerus length}}{\text{Radius length}} \times 100$	93		88		86
Radius-ulna $\frac{\text{proximal breadth}}{\text{distal breadth}} \times 100$	70		132		78
Distal breadth, radius-ulna Length of radius	87		57		97
Carpus $\frac{\text{height}}{\text{breadth}} \times 100$	46		61		37

RELATIONSHIPS AND GEOLOGIC OCCURRENCE

RELATIONSHIPS

THE FOREGOING DESCRIPTION and comparisons have shown that *Incacetus* is a genus possessing both ziphiid and delphinid characters, which may be summarized as follows:

Delphinid Characters

- 1.
- 2. Flat, broad palate
- 3. Small pterygoids, with "pterygoid pocket"
- 4. Periotic-form and topography
- 5.
- 6. Functional teeth in separate sockets
- 7.
- 8. No fusion of cervicals
- 9. High neural arches and inclined spines of dorsals and lumbars
- 10.
- 11.
- ----
- 12.
- 13. Radius-ulna expanded distally
- 14. Carpus with generally hexagonal elements, especially the lunar

The characters typical of the two cetacean families under consideration are about equally balanced in this new fossil form from Peru, a fact that offers considerable complications in any attempt to place the genus taxonomically. If there were a preponderance either of ziphiid or of delphinid characters, the problem would not be so difficult as it is. Moreover, if there were definitely primitive archaeocete characters, the classification of this new genus might conceivably be made clearer, but such truly primitive characters are not to be seen. The characters found in Incacetus, whether delphinid or ziphiid in their expression, are all essentially modern in aspect. With these difficulties in mind, an attempt will be made to evaluate the characters of Incacetus with a view to assigning to the genus its approximate position in the phylogeny of the Cetacea.

In the first place, since *Incacetus* possesses both delphinid and ziphiid characters, the former for the most part primitive, the latter for the most part advanced or specialized, it would seem logical to associate this fossil form with the ziphiids upon the basis of its specialized or habitus features, regarding the primitive characters as persistent heritage traits. Following this line of reasoning, it is neces-

ZIPHIID CHARACTERS

Deepened rostrum with open mesirostral groove (Palate rather flat in *Diochotichus*)

Tympanic with strong anterior fold (Functional teeth in separate sockets in certain primitive genera)

Strong posterior convexity of mandibular ramus (Little fusion in some forms)

Bified manubrium, without lateral processes Scapula, form and development of acromion and coracoid

Humerus heavy but not unduly shortened

sary to regard the delphinids as more primitive, on the whole, than the ziphiids, and such a view is reasonable upon the basis of a comparison of the two families. Certainly most of the characters in the anatomy of the ziphiids, particularly in the skull, are highly specialized, while those of the delphinids are of more generalized cetacean pattern. Indeed, the ziphiids would appear to be the most specialized of the Odontoceti, with the possible exception of the Physeteridae. Of course such general statements are subject to certain qualifications as to detail.

Generally speaking, we may imagine the ziphiids and the delphinids as arising at about the same time, namely, at the beginning of the Miocene epoch. Each of these two groups followed separate lines of adaptation, the delphinids being generally the more conservative group, thereby retaining more of the generalized odontocete characters, the ziphiids being the more aberrant group, developing new heritage characters that supplanted in part the generalized features found in the other family. Naturally, the early members of the Ziphiidae, while showing the beginnings of those specializations that were to become so characteristic of the family, would nevertheless retain many generalized features that are typical of the Delphinidae.

Delphinidae

Ziphiidae

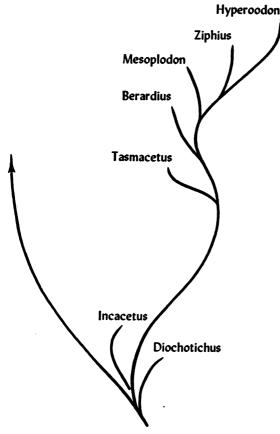


FIG. 3. Diagram to show the supposed relationships of the various genera of Ziphiidae. *Incacetus* is shown as occupying a basal but somewhat intermediate position between the Ziphiidae and the Delphinidae. It is indicated as being possibly more closely related to the former than to the latter family.

Such is the case of *Incacetus*. It has developed the typical ziphiid open rostrum, tympanic, mandibular convexity, sternum, and scapula. It has retained the generally primitive broad palate, pterygoid structure, teeth, and paddles that are found in the delphinids. Consequently this fossil genus may be thought of as occupying a position near the base of the Ziphiidae and close to the point where both this family and the Delphinidae branched from their earlier archaeocete ancestry.

This is a position shared in part with, but nevertheless differently from, two other genera of Ziphiidae, namely, Diochotichus and Tasmacetus. The former, as has been mentioned previously in this paper, is from the Miocene of Patagonia; the latter is a recent form found off the coast of New Zealand. Diochotichus has a relatively primitive cranium (no direct comparison can be made with Incacetus) and an elongated rostrum and symphysis, generally primitive in the odontocetes but not necessarily so among the ziphiids. On the other hand, Diochotichus would seem to have had large pterygoids, probably like those of the typical ziphiids. Whatever its relationships, this fossil genus certainly developed along adaptational lines somewhat different from those followed by Incacetus.

Tasmacetus is a toothed ziphiid that has persisted to Recent times. This genus is, however, of typical ziphiid development except for its retention of functional teeth and concomitantly a rather flattened palate. In the strong vertical growth of the cranial roof and the nasal region, the enlargement and transformation of the pterygoids, and in various developments of the postcranial skeleton the fusion of the cervicals, and the strongly bifid manubrium, for instance—this genus is as completely specialized as other modern members of the Ziphiidae.

The suggested position of this new fossil from Peru in relation to other odontocetes is represented by figure 3.

GEOLOGIC OCCURRENCE

So far in this discussion, little if any attention has been given to the geological relationships of *Incacetus*. However, from the zoological and taxonomic comparisons that have been made, some inferences may have been outlined as to the general position of the new genus in the phylogeny of the modern cetaceans. For instance, since it has been shown that this new form has a mixture of the characters found in both the delphinids and the ziphiids, it has been suggested that *Incacetus* might occupy a position on the ziphiid branch of cetacean phylogeny near the point where it diverged from the delphinid branch. Since the palaeontologic history of the whales shows that the several odontocete families became pretty well defined in early Miocene times, it is logical to assume that *Incacetus*, being near the point where the definition of the families began, might be regarded as of about Miocene age.

This conclusion is borne out by the geological relationships of the fossil. As mentioned above, the specimen was found at the mouth of the Ica River on the southern coast of Peru. The rocks at this locality are marine Tertiary sediments, belonging to the Pisco formation and, according to the latest work of Steinmann, Lissón, and others, may be regarded as ranging from the Eocene through the Miocene. This series of Tertiary beds had been regarded by Adams in his earlier work (1908, p. 416) provisionally as of Pliocene age, but such a late designation for the sediments is denied by Steinmann (1929, pp. 202-203).

"So deuten verschiedene Tatsachen bestimmt darauf hin, dass Eozän und wahrscheinlich auch Miozän in der 'Piscoformation' enhalten sind; ihr pliozänes Alter wird dadurch sehr unwahrscheinlich" (Steinmann, 1929, p. 203).

Since *Incacetus*, being an odontocete, obviously cannot be older than Miocene, it may logically be referred to the Miocene portion of the Pisco formation, as defined by Steinmann, assuming that this author is correct in excluding these beds from the Pliocene.

Both Steinmann and Adams mention the presence of fossil whales as characteristic of the Pisco beds. In fact, it would seem that these fossils are so typical of the Pisco beds as to be recognized by the inhabitants of the region, for Dr. Jenks has informed us that the place where *Incacetus* was discovered is well known because of the abundance of fossil cetaceans discovered there.

Some fossil mollusks were found associated with *Incacetus*, but these have been of no help in determining the age of the fossil, since they are internal molds and thus do not show any truly diagnostic characters. There was also found a mass of small bones associated with the specimen, and it was thought that they might prove to be remains of fish, but Mr. G. Miles Conrad, formerly of the American Museum, after examining this material carefully, informs me that nothing definite can be said concerning it.

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