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A REVIEW OF THE INTERRELATIONSHIPS
OF THE CETACEA

BY

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[Translated by GERRIT S. MILLER, JR.]



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A REVIEW OF THE INTERRELATIONSHIPS OF THE CETACEA

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In translating Doctor Winge's "Udsigt over Hvalernes indbyrdes Slægtskab" (Vidensk. Medd. fra Dansk naturh. Foren., vol. 70, pp. 59-142, 1918) my aim has been to give the author's ideas as clearly and exactly as possible rather than to make smooth English sentences. I have been much aided by the kindness of Dr. Leonhard Stejneger, who has compared the entire MS with the original, making himself responsible in particular for the rendering of the adverbs *ret*, *sikkert*, *vel*, and *vist*, whose idiomatic shades of meaning present many difficulties to one whose acquaintance with Danish is limited to the printed language. Doctor Winge has also examined the translation, expressed his approval of it, and made some useful suggestions for its improvement. I have added an index, a few bibliographical references, and in some instances the generic names which are correct according to the International Code of Nomenclature. Brackets are used to distinguish all additions to the original text.—G. S. M., Jr.

The Cetacea¹ originated² from the *Hyænodontidæ*, the most primitive family of the Carnivora, by way of the most typically carnivorous members of the group such as *Pterodon* and *Hyænodon*. The oldest known whales have such a great likeness to *Hyænodon* and its nearest relatives that there can be no doubt about the relationship. Aquatic habits have given the cetaceans their special peculiarities and have caused their differentiation from the Hyænodonts.

As an inheritance from the highest Hyænodonts, and as an indication of relationship with exactly these animals, the most primitive whales retained a series of special peculiarities which the Hyænodonts had developed in the course of their differentiation from the insectivorous stage. They still had about the same dentition as the Hyænodonts. All the teeth were fitted for flesh eating; the incisors and canines were strong and hooked, the anterior cheekteeth strong, elongated, compressed, smooth-edged; the molariform cheekteeth, especially those of the upper jaw, had a peculiar form and all of them were nearly alike. In the upper molars the 4th and 5th cusps [paracone and metacone] were coalesced to form a trenchant longitudinal ridge, the 1st and 2d cusps [parastyle and mesostyle] were reduced, the 3d cusp [metastyle] was a compressed ridge, and the

¹ Notes are at end of paper, pages 47-93.

6th cusp [protocone] was reduced or absent. All of the upper molari-form teeth including the third premolar still had the inner root, though this was in process of reduction. All the teeth of the typical [eutherian] dentition were present, 11 in each jaw [44 in all]. The jaws were elongated in harmony with the long, well-developed tooth-rows. The temporal fossa was very large, widened out by a powerful temporal muscle. It was bounded by a high sagittal crest, by a strong, backward-projecting occipital crest, and by an abruptly outstanding, posteriorly heavy *processus zygomaticus squamæ*.

In addition to these peculiarities the most primitive whales had two high characters which were perhaps inherited from the Hyænodonts; at any rate they are to be found in the latter group, though less pronounced: a rather large supraorbital process, and a bony palate lengthened backward far under the posterior nares.

Radical alterations have taken place during the change from Hyænodont-like carnivores to true whales. In many of the mammalian groups there have arisen forms modified for life in the water; but no other aquatic mammals are modified to the same degree as the cetaceans, nor has any other become so exclusively aquatic; only to breathe do they raise the nose above the water in which they otherwise are hidden.

The cetacea have used the tail as the chief implement of locomotion; the hind limbs are put wholly out of service; the fore limbs are scarcely used for much else than steering and balancing.

The tail becomes enormous, long and thick, powerfully muscled. It is formed in agreement with the manner in which it is wielded: with strokes from side to side, or up and down, or with a sculling motion. Throughout most of its extent it becomes compressed, but at the tip it acquires a powerful, horizontal, caudal fin constructed of skin folds (not present in quite young embryos of recent cetaceans). At the front of its upper margin, in the region where the tail joins the back, there may occur a special erect skin fold in the form of a longitudinal crest, a dorsal fin. Most of the caudal vertebræ lose the atrophied appearance which they have in primitive mammals; they acquire powerful centra, heavy, flat-outspread transverse processes, high dorsal arches with large, compressed spinous process, and articular processes which are distinct though not mutually fitting together. The ventral arches with the inferior spinous processes become so large that they approach the upper arches in size. Only the outermost caudal vertebræ, which lie almost inclosed in the caudal fin, retain the degenerate character. The tail has an influence on the

dorsal vertebræ also. Its powerful muscles, which have their origin in part on the sacral and dorsal vertebræ, and are also in connection with the muscles of the back, widen their place along the spinal column and stimulate the vertebræ to increase in bulk. The sacral and lumbar vertebræ come to resemble the largest, most anterior caudal vertebræ exactly, apart from the lower arches. On a few of the hindmost thoracic vertebræ, which in the ancestral forms are without, or as good as without, transverse processes, there grow out powerful transverse processes on a line with and similar to those of the lumbar vertebræ (parapophyses, apparently corresponding to the lower section of the double, rib-bearing "transverse process" of the anterior thoracic vertebræ, which supports the rib's capitulum; but in reality they most probably correspond to the upper and lower sections combined), and on their tip they eventually bear the attachment surface for the rib. Apparently this surface may be either for the attachment of the tuberculum or of the capitulum or of the two coalesced, but in reality it is perhaps always for the two combined (or, more correctly, not separated). The transverse processes of the anterior thoracic vertebræ (diapophyses, the upper portion of the double "transverse processes"), which in the beginning are quite short, may eventually grow long, pushing far out to the side the articular surface for the rib's tuberculum which they bear at their extremity. On all the thoracic vertebræ the spinous processes finally become high and strong.

The hind limb atrophies completely, and disappears. At length only quite insignificant parts of its skeleton are found, hidden deep under the skin, finally in the form of a mere little rod-shaped bone, a remnant of the pelvis.³ In small embryos the hind limb can, however, still be distinguished externally.

The disappearance of the hind limb has a great influence on the vertebral column. No longer does a pelvic bone come in contact with any of the vertebræ. In consequence the sacral vertebræ completely lose their peculiarities: their characteristic strength, their mutual firm connection, their robust transverse processes with flattened areas for the hip bones. They are formed exactly like the adjacent dorsal and caudal vertebræ. The movements of the spinal column become changed in character. Bending of the column in the vertical plane, which depends especially on the movements of the hind legs, is reduced or abandoned, and as a result the differences in slant—forward or backward—of the spinous processes as good as disappear,

so that all the processes alike are directed upward. The zygapophyses become reduced and in large part lose their mutual articulations.

The fore limb, which no longer comes in contact with the earth or bears any load, is changed into a flipper whose single function is that of striking against the water. The entire arm becomes an oar blade. Of the fore limb's articulations the shoulder joint only is used; it retains its ball-and-socket structure. All the other articulations are held stiff. They degenerate, become flat and immovable, or are wholly effaced. Practically the only function of the upper arm is to support the forearm and hand. It becomes short and heavy. Its middle portion retains its terete form, but its lower end is compressed in agreement with the bones of the forearm. The radius and ulna become very simply-formed, compressed bones, losing muscle crests, sinew furrows and all pronounced articular surfaces; even the olecranon may wholly disappear. The mutual position of the two bones is somewhat altered, so that they eventually lie exactly fore and aft of each other. The hand is set somewhat supine, fore edge downward. The carpal bones become compressed, or more correctly flattened, pieces [like sections of a mosaic]. They are rather indifferent as to form and number, and are immovable. The folds of skin between the fingers are lengthened out to the finger tips; and the hand stiffens. The claws disappear. The first and fifth fingers are somewhat inclined to be stunted, but the other fingers, particularly the second, tend to lengthen and to form new joints at their tips, so that the number of phalanges may increase far beyond the typical three. The metacarpals and phalanges are shaped almost alike, as more or less flattened pieces of bone.⁴ The shoulder blade degenerates only slightly. In the most primitive whales it already has the form which, with few exceptions, is found among the highest. It is broadly fan-shaped, with a prominent, antrorse acromion, and a large coracoid, but on the other hand almost without *crista scapulae*. Rarely it becomes narrower or lacks both acromion and coracoid.

The fact that the fore limb does not act as a support for the body results in lessening the limb's pressure on the chest. Another result is that the spinous processes on the anterior thoracic vertebræ lose their special height. Still another result is that the connections between the ribs and both the thoracic vertebræ and the sternum have a tendency to become loose or to disappear. Perhaps this tendency is also brought out by the fact that the water pressure on the chest during diving changes strongly. The ribs may lose the capitulum, and the costal cartilage may practically disappear. When this happens

the sternum loses an essential stimulus and becomes reduced and atrophied.

The head, during swimming, is held directed as firmly as possible forward. The neck is not moved, and for this reason it becomes short and stiff. During motion through the water the head is pressed from the front; it is forced backward against the cervical vertebræ, which thereby are squeezed excessively together and pressed back against the anterior dorsal vertebræ, with the ribs of which they may even come in connection. Most of the cervical vertebræ may become almost as thin as paper. The odontoid process of the axis becomes short and blunt; the articular surface between the bodies of the atlas and axis becomes almost flat. And there arises a strong tendency to coalescence of the cervicals.⁵ The occipital condyles lose their projecting form and become almost flat, only quite weakly convex, pressed in against the wall of the braincase; and the concave surface of the atlas likewise becomes flattened out. The occipital crest in its capacity as an attachment for the upper neck muscles is restricted; the points of attachment for the lower neck muscles on the basal part of the occipital bone are effaced, and the under side of the occipital bone is formed more as a sheath around the gullet and windpipe.

The pressure of the water on the head when the cetacean swims has a highly modifying effect on the skull.

From above the water presses especially during the animal's constant rising to the surface to breathe. This gives the skull a tendency to acquire a flat and broad upper surface, with thick bones. The size of the horizontally outspread supraorbital process of the frontal, which pushes itself far out over the orbit, becomes particularly noticeable. The facial part of the cheek bone may likewise become peculiarly flattened out.

From in front the water presses during forward motion, the more strongly as the motion is faster. Its effect is to develop an unusual strength in those bones of the face which project furthest forward, the intermaxillary, maxillary, and vomer, as well as in the cartilaginous nasal partition which the vomer embraces. This strengthening may show itself in different ways: in the noticeable lengthening forward of the bones in question, in their solid ossification, in their tendency to coalesce. It also appears in the backward spreading of the intermaxillary and especially of the maxillary. The latter may extend itself out over the facial part of the zygoma and over the frontal, which it almost entirely covers to the hinder margin, so that the supra-orbital foramen may pierce not only the frontal as in other mammals.

but the maxillary as well. The cartilaginous nasal partition, the mesethmoid, has a tendency to ossify. The incisive foramen is narrowed and closed. In the palate the maxillary pushes itself far backward, forcing the palatine behind it; the palatal surface of the palatine is thus shortened. But at the same time the maxillary acts on the palatine in such a way that it also increases in thickness. The braincase is acted on from the front by the pressure of the water against the forehead; from behind it is pressed by the cervical vertebræ and the neck muscles. In this manner it becomes so squeezed that it acquires a short, broad form. Pressure is exercised especially on the frontal and on the supraoccipital and interparietal. These bones widen out at the expense of the parietal, whose innermost part is squeezed quite narrow and eventually obliterated. The exoccipital also grows, especially noticeably downward, where it broadens out shield-like behind the mastoid and the tympanic. The mastoid is compressed inward between the exoccipital and the squamosal, by both of which it is so overgrown that at last it is no longer visible on the outer surface of the braincase.

The water pressure on the head from in front has also a great influence on the soft parts of the face and through them on the skull. It assists in shifting the nasal apertures. The cetacean has tried, with the help of the nose muscles, to draw the apertures as high as possible up on the head's upper side, in order to be able easily to get them raised above the water. The result has been that the nasal cartilage has caused resorption of the anterior border of the nasal bones and has forced them further and further back. The cartilage has also worked itself back between the anterior median part of the frontals, pushing the plates of the ethmoid behind it. Thus at last the nares have acquired a position which appears to be on the forehead but which in reality is close in front of the anterior wall of the braincase. The moving of the nasal cartilage has been accelerated in those cases where the facial adipose cushion which originally lay in front of the nares and which in the first place was merely a little filling out of fatty connective tissue has been stimulated to growth by the pressure of the water, becoming very large, pushing the nasal cartilage backward, pressing it against the front wall of the braincase and disintegrating the nasal bones and the plates of the ethmoid. The nasals then become tuberformed and are pressed into the frontals. The adipose cushion together with the nasal muscles and other neighboring structures may exercise an enormous influence on the skull, the anterior and upper sides of which it modifies to form its bed, the "facial depression."

The water acts in a very special way where the whale lets it stream into the mouth for the purpose of catching the small animals which it carries in with it. In such cases it brings about huge increase in the size of the jaws together with many other remarkable peculiarities.

For smelling there comes to be no use; this sense is not exercised, and the nose is therefore formed in accordance with the needs of breathing only. The ethmoid degenerates. The numerous folded laminae of which it originally consisted disappear, while the cribriform plate loses its nerve perforations and becomes a solid lamina of bone on the front wall of the braincase. The nose becomes a simple passage for air. The air, which is exposed to strongly varying pressure and temperature, has a tendency to provide itself with greater space by widening out the nasal passage and Eustachian tube wherever it meets with least resistance. It may form air-sacs, partly on the upper side of the skull over the facial bones, partly on the under side behind the palate. Here an air-sac may spread itself forward along the outer side of the pterygoid and palatine and backward along the outer margins of the body of the sphenoid and the basal part of the occipital, pushing itself out under the *ala parva*, *ala magna* and the squamosal, and bounded more or less by plate-like outgrowths from all the bones mentioned. The bony palate is lengthened backward still more by the pushing out from the pterygoids of laminae which extend into the soft palate beneath the nasal passages. This clearly takes place partly under the action of the tongue, but doubtless still more under the influence of the larynx. The fact that the two original outer nostrils finally coalesce into one is an indication of the nose's degeneration.

The lacrimal bone is reduced and eliminated, or it fuses with the cheek bone as in many other aquatic mammals, probably because the bone is no longer acted upon by a lacrimal duct.

The outer ear disappears from lack of use; the outer auditory aperture is so strongly contracted that it may be difficult to find. The bones of the inner ear acquire a peculiarity which is found again in several other mammals that live in the sea, and which certainly in some manner or other must be dependent on aquatic life. They are formed of unusually thick, stony-hard masses of bone; this is especially remarkable as regards the tympanic, the inner wall of which is thickened in a peculiar way.⁶

The dentition degenerates because the chewing of food is given up as not easy to carry on satisfactorily under water. Most animals chew with open mouth; under water the chewed food would be

washed away from between the teeth. The dentition is therefore chiefly used for grasping the food and holding it fast. In the most primitive whales the mouth did service as an implement for catching fish. The jaws were used in exactly the same manner as in the shell-drakes, *Mergus*, and they were produced forward as a long slim beak, a kind of tweezers, influenced not only by the use to which they were put, but also by the pressure of the water during swimming forward. The *Hyænodon*-like dentition which the most primitive whales inherited, with teeth of considerable size, diversified form, and of typical number, at first becomes more simple. The upper molariform teeth lose the inner cusp and the inner root, and the crown undergoes compression. A further step in the reduction is that the crowns of the cheekteeth, or at least of most of them, acquire a serrated anterior and posterior margin. Next the two remaining roots, foremost and hindmost, of the cheekteeth fuse into one, and the serrations of the crowns are reduced and obliterated. The size at the same time is reduced, and the form becomes simply conical so as to resemble that of the incisors and canine, which in their turn undergo reduction. While this is happening the number of teeth in the long jaws is increased, no doubt because in the place of the few quite large teeth there spring up many smaller ones; scarcely by the actual splitting up of the few. Perhaps also in the beginning some of the milk teeth came to take a place in the series with the permanent ones, without, however, the entire milk dentition's intercalation in the permanent set. The number of teeth grows greater and greater, far beyond the typical, while the individual teeth become smaller and smaller. Those at the front and back of the series become especially stunted, frequently disappearing from the intermaxillary. The enamel covering of the teeth becomes thin or disappears entirely. What later happens to the dentition depends on the use to which it is put. It may happen that there comes to be no use whatever for it, and that it consequently disappears. Or it may, wholly or in part, be once more put to heavy use and be modified to this end; or a single tooth may take on power while all the others atrophy.

The succession of teeth, which in the most primitive whales took place in the ordinary way, ceases. It is not clear how this happens. Judging from investigations of the teeth in embryos of the higher cetaceans it might appear, at least sometimes, as if it were retained milk teeth that are found in the adult animal's dentition—as if the successors to the milk teeth had disappeared. Such, however, is scarcely the explanation. Most probably it is really the actual perma-

ment set that is found in the adult, while those that precede and follow (both of which have been demonstrated) disappear.⁷

The fact that mastication ceases and that the teeth become stunted has a great influence on the chewing muscles and the jaws. It was necessary for the first whales as fish catchers to be able to open the mouth wide. The masseter muscle which has the tendency to limit the opening of the mouth was therefore little used, and it became restricted; together with the muscle the region of its origin became shrunken. This region is the anterior and median part of the zygoma; it is transformed into a slender bridge of bone. The temporal muscle has been more used, but it also shows the tendency to be reduced by lack of vigorous use, and it draws itself backward quite low on the side of the braincase, losing its influence on the zygomatic process of the squamosal. This process shrivels up like the coronoid process of the mandible, the muscle's point of insertion. In cases where the under jaw becomes very large the temporal muscle may acquire renewed strength and may spread its region of origin out over its surroundings in an unaccustomed manner. With the atrophy of the teeth they cease to influence the body of the mandible, which consequently loses its original height. The alveoli become less defined and the partition walls between them may disappear so that there arises a common dental furrow. The articular condyle of the mandible weakens, loses its cylindrical form, and the articular surface becomes an almost flat area pointing backward at the similarly formed glenoid fossa on the squamosal, which as good as loses its postglenoid process and is otherwise inclined to suffer reduction. It may happen, however, that the lower jaw becomes huge and that its articular condyle acquires corresponding heaviness. In such cases the condyle is curiously modified, losing the true articular surface. This is grown over by articular ligament, and the lower jaw stimulates the squamosal to grow out in prodigious size, bearing, instead of the true articular surface, an area of attachment on a projecting foot. The symphysis menti, long in the most primitive whales, is restricted. The under jaw's degeneration is also no doubt indicated by the huge gaping posterior entrance to the mandibular canal, which is mostly filled with loose connective tissue. It is not clear what the reason is for this peculiarity, which was already present in the most primitive cetacea and is found in all the later ones though sometimes in a rather disguised form; possibly it might in some way depend on the air-sacs of the nasal passages which lie exactly internal to this part of the lower jaw.

Whales lose their hair covering because it ceases to be of use; at most some few degenerated vibrissæ remain.⁸

It holds good for the cetacea as for other groups of mammals that the most primitive forms have much less brain than the later ones; in the highest whales the brain is extremely well developed.

It likewise holds good for the cetacea as for others that the earlier forms are smaller than the later, though dwarfs may at any time be developed. Ordinarily whales increase noticeably in size as they become more highly developed; the highest forms have reached gigantic proportions.

Judging by their greater or less resemblance to the Hyænodonts the cetacea are mutually related essentially as follows:⁹

Cetacea.

- I. The number of teeth is not more than typical [44]. Braincase not telescoped, not shortened.

Archæoceti.

Zeuglodontidæ.

Protocetus, Prozeuglodon, Zeuglodon.

- II. The number of teeth is or has been more than typical. Braincase telescoped, shortened.

- A. Nasal bones forming a roof over hinder part of nasal cavity. Maxillary not covering frontal.

Mystacoceti.

Balænidæ.

BALÆNINI: *Balæna, Neobalæna.*

BALÆNOPTERINI: *Rhachionectes, Plesiocetus, Cetotherium, Balænoptera, Megaptera.*

- B. Nasal bones pressed into fore wall of braincase, not or scarcely forming a roof over any part of nasal cavity. Maxillary covering frontal.

Odontoceti.

1. Teeth not alike, the most posterior less simply formed than the most anterior.

Squalodontidæ.

Agorophius, Squalodon, Neosqualodon, Prosqualodon.

2. Teeth now or formerly alike, simple in form.

- a. Temporal fossa large, not covered over by frontal and maxillary; zygomatic process of the squamosal heavy, primitive in form.

Platanistidæ.

Pontistes, Pontoporia, Lipotes, Inia, Saurodelphis, Platanista.

b. Temporal fossa relatively small, covered anteriorly by the widened frontal and maxillary; zygomatic process of the squamosal reduced, losing its primitive form.

a. Occipital wall not especially elevated.

Delphinidæ.

Delphinodon, Champsodelphis, Schizodelphis, Heterodelphis, Eurhinodelphis, Argyrocetus, Delphinapterus, Monodon, Steno, Prodelphinus, Delphinus, Tursiops, Tursio, Lagenorhynchus, Orca, Orcaella, "Grampus," Pseudorca, Globiceps, Phocæna, Neomeris.

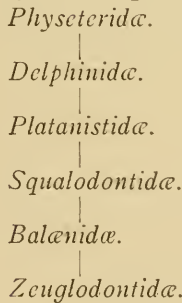
β. Occipital wall highly elevated.

Physeteridæ.

XIPHIINI: *Argyrodelphis, Mesoplodon, Xiphirostrum, Chonoxiphius, Xiphius, "Berardius," Hyperoodon.*

PHYSETERINI: *Hoplocetus, Physeterula, "Cogia," Physeter.*

In the form of a genealogical tree [see pp. 45-46]:



Zeuglodontidæ [Basilosauridæ].—Of all known cetacea the Eocene Egyptian *Protocetus* of the family *Zeuglodontidæ* is the most primitive. It is known from a rather complete skull without the

lower jaw, and from a few vertebræ and ribs. In all that is known it stands so near to the *Hyænodontidæ* that there would scarcely have been any reason to separate it from them had it not been evident that it was one of the first members of the cetacean series. The number of teeth in the upper jaw is, as in *Stypolophus* and *Pterodon*, the typical 11, since m^3 is present, while it has disappeared in *Hyænodon*, the highest genus of *Hyænodontidæ*. But the form of the teeth is most nearly as in *Hyænodon*, more shearing than in other members of the family. The difference from *Hyænodon* is chiefly a result of the fact that heavier use has been made of that part of the toothrow which serves for grasping the food and that consequently the incisors and anterior cheekteeth have increased in size. The incisors have become about as heavy as the canine, the premolars have become heavier and more elongated than formerly, while the molars are weakened and m^2 has lost its predominance. The mouth was already used mostly as a pair of forceps; the long, narrow, but strong, beak-shaped jaw, in which the teeth have abundant space, bears witness to the fact. The anterior nasal aperture is already forced considerably backward; but it has, however, only reached a point scarcely half way to the anterior margin of the orbit, and it has kept a rather primitive form. The nasal bone is long and narrow, roofing over a large part of the nasal cavity. The intermaxillary is strengthened anteriorly, its body is lengthened, likewise its nasal process, though this process does not reach to the frontal. Otherwise the intermaxillary does not show much deviation from the conditions ordinarily found in carnivores. The maxillary also is lengthened and thickened, but is not otherwise modified to any noticeable degree. Posteriorly it does not push itself out over the facial part of the zygoma or over the frontal, which it merely forces slightly backward. On the palatal surface it has not crowded the palatine bone, which has retained its original length. The incisive foramina seem to have disappeared. The forehead is pressed quite flat, and the supraorbital process of the frontal has become very broad; otherwise the forehead is unmodified. The anterior and median part of the zygoma is already well on its way to become slender, but the zygomatic process of the squamosal is still robust. It bears a considerable postglenoid process, though the articular surface for the lower jaw has begun to assume the peculiar vertical position that it has in the higher whales. The temporal fossa has on the whole remained primitive in size and form. It is bounded by high crests. The braincase is not compressed antero-posteriorly; the frontal and supraoccipital are

not widened so as to encroach on the parietal. The mastoid is still visible on the outer wall of the braincase. Occipital crest well developed, projecting. Occipital condyles not pressed flat. On the basal part of the occipital the impressions where the lower neck muscles were attached are essentially unmodified in character, and the under side of the occipital bone's basal part is not shaped for sheathing the gullet and larynx. On the other hand the exoccipital has already acquired a noticeable widening out to the side. The hinder part of the nasal cavity appears to be wholly undisturbed; it must contain a well-developed ethmoid. The bony palate is already prolonged backward by plate-like outgrowths from the lower margin of both the palatine and the pterygoid. No doubt an air-sac formed by an enlargement of the nasal passage lay on the outer side of the pterygoid, but whether it was enclosed by outgrowths from the adjacent bones is doubtful. The tympanic bone had already acquired the characteristic cetacean thickening of the inner wall. The cervical vertebræ are mutually free, not strongly compressed. The odontoid process of the axis is strong, projecting. The spinous processes of the dorsal vertebræ differ noticeably among themselves as to their slant, some of them sloping strongly backward, others upright or directed a little forward; those on the hindmost dorsal vertebræ are rather low. Zygapophyses apparently well developed. No projecting transverse processes on the hindmost thoracic vertebræ. Centra of ordinary size. On the tip of the transverse process of a sacral vertebra there is present a rather large area of attachment for the ilium, although the process has otherwise already lost much of its original character. On such ribs as are present in the fossil there is a well-developed capitulum; the hindmost ribs lack the tuberculum and are articulated with the corresponding vertebræ by the capitulum.

Prozeuglodon (*Zeuglodon osiris*, *Prozeuglodon atrox partim*³⁰), also Eocene, Egyptian, has departed in dental characters not a little from *Protocetus*. In the number of teeth the difference is only that m^3 , small in *Protocetus*, is here absent. The form of the teeth has undergone greater change: pm^1 has lost the compressed form of the crown and has become simply conical with a single root like the incisors and canine; pm^2 has acquired a serrate posterior margin; pm^3 , pm^4 , m^1 and m^2 are strongly serrated on both the anterior and posterior margins of the crown; in pm^3 and pm^4 the inner heel is much reduced and in the two molars it has entirely disappeared. The lower jaw is also known; it contains the typical II teeth. Incisors, canine, and pm_1 approximately uniform, simply conical; pm_2 , pm_3

and pm_4 with compressed crown and serrated anterior and posterior margins; m_1 , m_2 and m_3 also with compressed crown, its anterior margin smooth, its posterior margin serrate. Tooth succession occurred in the ordinary way as it assuredly did in *Protocetus* also. In all characters the skull agrees essentially with that of *Protocetus*. The basal part of the occipital appears, however, to be more adapted to the larynx and gullet. A few peculiarities of *Prozeuglodon* which are not clearly demonstrated in *Protocetus* are: the presence of an elongated, compressed incisive foramen on each side; the presence of a distinct lacrimal bone; and the presence to the outside of the pterygoid and in front of the tympanic of a considerable pit bounded by high ridges springing from the surrounding bones, evidently the impression of an air-sac. The under jaw already has nearly the same peculiar form as in many highly developed cetaceans with long symphysis menti; it has, however, a relatively large coronoid process. But the mandibular condyle is placed low and is turned backward, and the strange gaping hinder entrance to the mandibular canal is present. Of the rest of the skeleton rather more is known than of *Protocetus*, among other parts most of the vertebral column and the fore limb down to the hand. There is a great similarity to *Protocetus*. A difference from this genus is that no sacral vertebra is found with the transverse process plainly acted upon by the ilium. The skeleton of *Prozeuglodon* throws light on certain conditions that are not understood in *Protocetus*. The sternum is of considerable size, with several joints. The shoulder blade is essentially as in the higher whales. The humerus has retained relatively much of the original form: distinctly separated greater and lesser tubercles, a distinct deltoid crest, and a well-developed hinge-shaped lower articular surface. Radius and ulna have correspondingly well-developed articular surfaces for the humerus, are relatively only a little compressed, and have distinct articular surfaces for the carpal bones; the ulna has a rather large olecranon.

Zeuglodon [*Basilosaurus*] (*Z. cetoides*, *Z. isis*), known rather completely as to the skeleton, occurs in Eocene strata of both the Old and New Worlds. In most respects it resembles *Prozeuglodon*. But it has acquired a highly remarkable peculiarity in the vertebral column. While the centra in *Prozeuglodon* are not in any direction strikingly altered in form, in *Zeuglodon* the centra of most of the hinder thoracic vertebræ, of the lumbar vertebræ, sacral vertebræ and all but the outermost of the caudal vertebræ, have become remarkably large and especially greatly elongated, while the vertebral arches have remained short, standing about midway on the centra, the arches.

in common with the spinous processes, widely separated from each other. Thus in *Zeuglodon* the body has acquired an altogether peculiar length, putting one in mind of the snakes. The posterior thoracic vertebræ seem to have developed considerable transverse processes which bore the ribs on their extremities. In size also *Zeuglodon* went further than its relatives. Of the hind limb there is known a small, quite atrophied pelvic bone with articular surface for the femur, and an even more degenerated little rod-shaped femur.²¹

The genera of Zeuglodonts together form the section Archæoceti, the source from which all the higher cetaceans have originated. *Protocetus* has scarcely a single peculiarity, apart from its large size, that one would not expect to find in an ancestral stock for the higher whales. The same is true of *Prozeuglodon*. On the other hand *Zeuglodon*, a descendant of *Prozeuglodon*, has followed its own line away from the starting point of the other whales, deviating particularly in its remarkable vertebræ.

The peculiarities which especially place the Zeuglodonts lower than all other cetaceans are that the teeth are still present in the typical number, and that the braincase is not telescoped and shortened. Of all other whales it holds good that they, so far as they are known, have the number of teeth raised above the typical (or that they are descended from cetacea in which it had been raised), and that they have the braincase more or less compressed antero-posteriorly. As regards the form of the teeth *Protocetus* no doubt stands lower than all other cetaceans; but *Prozeuglodon* and *Zeuglodon* are in this respect scarcely more primitive than the lowest members of the higher families. Of all the many other primitive characters that are found in the Zeuglodonts some are, it is true, no longer to be found in the higher families, not even among the extinct lowest forms; but for most of them this does not hold good.

*Zeuglodontidæ*²² [*Basilosauridæ*].

I. Crowns of cheekteeth with smooth, not serrate, margins.

Protocetus.

II. Most of the cheekteeth have serrate anterior and posterior margins to the crowns.

A. Centra of thoracic, lumbar, and caudal vertebræ not elongated.

Prozeuglodon.

B. Centra of posterior thoracic, of lumbar and caudal vertebræ elongated.

Zeuglodon [*Basilosaurus*].

Balænidæ.—The group *Mystacoceti* with the single known family *Balænidæ* includes whales that stand near to the *Zeuglodonts*; but the most primitive members of the group had already advanced a step further than the *Zeuglodonts*. They presumably had the number of cheekteeth raised above the typical. With that change there followed others. The most primitive *Mystacoceti* must have already had the nasal aperture pushed further back than in the *Zeuglodonts*. The intermaxillary probably extended further back. The maxillary must have been somewhat more broadened out posteriorly. The parietal was slightly encroached upon, and the braincase was a little telescoped. The spinous processes of the dorsal vertebræ presumably slanted to a less degree in different directions. The joints at the elbow and wrist must have almost wholly lost their primitive structure, etc. Taken all in all, however, the most primitive *Mystacoceti* must have been in general like the most primitive *Zeuglodonts*.

Of the many forms which the group *Mystacoceti* must have included no others are known than a little circle of highly developed genera very specially modified in their own direction; but in spite of their remarkable development they have retained many primitive features which are no longer found in the other, higher families. This holds good especially in the structure of the face. Although the nasal aperture is drawn backward into proximity with the anterior wall of the braincase the nasal bone is not wholly misshapen. It retains part of its long, narrow form and it still roofs over the hind part of the nasal cavity which may yet inclose very considerable remnants of the ethmoid plates. The anterior part of the nasal cavity, bounded by the intermaxillary, maxillary and vomer, is also relatively primitive in structure, more open than usual, with less tendency to closing together of the bones. And the maxillary, although it has expanded backward, and shoved itself somewhat back both above and beneath the frontal, has nevertheless not in any way covered the frontal's broad supraorbital process. A distinct lacrimal is present, but this is not unknown among higher cetacea. The zygomatic arch has retained more of its primitive form and strength than elsewhere. Two outer nasal apertures are still found; they are not mutually united. The basal part of the occipital is also to a somewhat less degree modified than in other recent cetacea, being less specialized to accommodate larynx and gullet.

That which more than anything else has left its impress on the known *Balænidæ*s is their habit of not hunting after single large fish, but of swimming with open mouth into shoals of small fish, crus-

taceans, or other small creatures, which they allow to stream into the mouth in multitudes along with the water. They seek to retain the edible contents when they close the mouth and the water flows out again between the lips. The water has thereby acquired great power to act upon the mouth cavity from within; it distends the opening enormously; the jaws grow and acquire a disproportionately large size in comparison with the braincase; the branches of the mandible are bowed strongly outward to the sides and are widely divergent from each other behind, while the connection between them in front becomes quite loose. The gigantic lower jaw wears so upon the ligaments which bind its articular head to the squamosal that the ligaments are incited to growth. They become uncommonly strong and spread themselves over the original gristle-covered articular surfaces on the jaw and the squamosal, both of which surfaces they entirely cover. They cause the squamosal to grow out as a huge process which bears the attachment surface for the lower jaw on its free margin. By the enlargement of the mouth cavity the squamosal together with the articular head of the lower jaw is pushed far out to the side and so far back that at last its free postero-external extremity comes to lie further back than the occipital condyles. The squamosal in its turn presses strongly on the parts which lie behind it: on the mastoid which is squeezed inward, and on the exoccipital which is pushed backward. In proportion to the size of the under jaw the temporal muscle increases and pushes its region of origin forward over the supraorbital process. There has been no use whatever for the teeth; they atrophy so completely that finally they are to be found only in the embryo as a long series of insignificant, small, pin-shaped teeth, hidden under the skin and soon resorbed. On the other hand the inflowing and outflowing water acted as a stimulant on the corneous papillæ of the roof of the mouth. The papillæ along the margin of the upper jaw are so stimulated that they have grown out as a close-set series of "whale-bones": high, crosswise-placed, corneous plates, the inner margin of which is frayed out into threads. The entire set of whale-bones functions as an excellent instrument for catching the solid material that flows with the water into the open mouth. The palate is strongly acted upon by the instreaming water, by the larynx, and by the tongue, which is pressed against it when the water is to be expelled. The palatine bone grows and forces itself backward, pushing back the pterygoid behind it; and the pterygoid pushes and presses that which lies still further back; namely, the tympanic bulla and the region of attachment of the neck

muscles on the basal part of the occipital. The palatine may push itself wholly back under the base of the occipital, and the muscle attachment may come to lie about on a line with the posterior margin of the occipital condyle.

In other respects also the known Balænidæ have reached particularly high. The supraorbital process of the frontal acquires an unusual breadth, no doubt for the special reason that it follows the eye, which, by the widening of the mouth cavity, is pushed out to the side. The supraoccipital becomes very large and strongly slanting forward under the influence of pressure by the water and by the muscles of the neck. The transverse processes of the thoracic vertebræ become widely projecting; this is especially noticeable as regards the hindmost thoracic vertebræ (where the processes are parapophyses, while on the anterior vertebræ they are diapophyses). The ribs have a strong tendency to lose the capitulum and to restrict their connection with the sternum. In most of the recent members of the family the capitulum is absent from all the ribs, even the more anterior, although an evident collum is present (it is, however, doubtful whether it is really the capitulum that is absent from the hindmost ribs; more likely the single articular head which appears to be the tuberculum is in reality either the capitulum alone or the capitulum and tuberculum undifferentiated). The sternum is so reduced that it consists of the manubrium alone. The first finger has a tendency to atrophy. Etc.

In the section Balænini are found the most primitive of the family's known genera: *Balæna* and *Neobalæna*. With them the anterior facial part of the skull has kept relatively much of the form ordinarily present in mammals. This is especially true of the intermaxillary and still more of the maxillary, which is quite slender in front and not depressed. Body and tail are rather short, not quite so well fitted for rapid swimming as in the others. The hand is more primitive. Of the hind limb's skeleton there are present, at least in *Balæna*, relatively quite considerable remnants, among other parts a stunted femur and the upper end of the tibia. The mouth is shaped somewhat differently than in the others; it is formed as an enormous barrel or bag, bowed outward on all sides. Not only are the rami of the lower jaw bent outward, but the upper jaw with the whole facial part of the skull is also bent, arched highly upward. Both the upper jaw and the branches of the lower jaw assume the structure of stays in the walls of the pouch-like mouth cavity. The whale-bone plates acquire a remarkable length. Finally the head becomes more pre-

ponderant as regards the body than in other whales. The cervical vertebræ are pressed together unusually strongly; they coalesce.

Balæna appears in some respects to stand on a lower level than *Neobalæna*. Its slender under jaw seems better to agree with the condition primitive to the cetacea than does the strikingly massive, strongly compressed under jaw of *Neobalæna* in which the mandible presumably must be especially influenced by the large under lip. Its relatively few, ordinarily formed, slender ribs, and its correspondingly rather long series of lumbar vertebræ are also undoubtedly primitive characters; in *Neobalæna* the ribs have become unusually numerous and the number of lumbar vertebræ is reduced to a few bones, while the ribs, or at least most of them, have become remarkably broad and have to a remarkable degree lost connection with the vertebræ so that they lie loose among the muscles. *Balæna* is no doubt the more primitive also in the short, broad form of the hand. The first finger is either (in *B. australis*) rather well developed, containing two phalanges in addition to the metacarpal, or (in *B. mysticetus*) reduced, though still retaining the metacarpal.²³ The other fingers are not much lengthened; in the median digits, however, especially in the third, the number of phalanges may be increased to four or five. The form of the phalanges is terete, not compressed. In *Neobalæna*, the hand appears to have essentially the same structure as in *Balæna*, but the first metacarpal is said to be absent, and the entire hand has become narrower. The lack of a dorsal fin in *Balæna*, in contrast with *Neobalæna*, is, presumably, also a primitive character; though the fin may have been lost. But in the adaptation of the head as a pouch for catching small animals *Balæna* has reached far beyond *Neobalæna*. In the more primitive of the two certainly known species of *Balæna*, *B. australis*, the modification is a little less noticeable than in the higher species, *B. mysticetus*; the head is slightly smaller, the upper jaw is somewhat less bowed upward, etc. In *B. mysticetus* the head becomes so huge that in full grown individuals it reaches a third or more of the animal's total length, the upper jaw is thrown upward in an enormous arch, the palatine and pterygoid are forced backward under the hindmost part of the basioccipital, etc. The coracoid process of the scapula may be absent (in *B. australis*).

Neobalæna must assuredly have originated from *Balæna*, but from one of the most primitive species of the genus, in which the head was only a little increased in size; but since then it has gone its own way, developing peculiarities in the form of the lower jaw, in the ribs, vertebral column and hand.

In the genera of the section *Balænopterini* the intermaxillary and also the maxillary are rather strongly flattened anteriorly so that the facial part of the skull has lost its primitive pointed form. Body and tail are uncommonly long, adapted to more rapid swimming with stronger muscles. Among the alterations produced by these muscles are the higher spinous processes on the dorsal and caudal vertebræ. The hand is shaped more like an oar blade. The fingers are laid more closely together and the third and fourth may have the number of phalanges increased; the first digit has completely disappeared. The skeleton of the hind limb is more reduced. The mouth is modified in its own way; its outbowing in the upward direction is slight or absent, that to the sides and downward is conspicuous. The floor of the mouth cavity has become to a high degree expansible, and the intermaxillary and maxillary, like a broad, more or less flattened lid, cover over the pouch which it forms. The Balænopterines stand lower than the known Balænines in the condition of the cervical vertebræ: the bones retain their freedom.

Among the known Balænopterines, *Rhachionectes* is one of the most primitive. Its nasal bone is still relatively very well developed. The breadth of the intermaxillary and maxillary in front is rather slight. The supraorbital process is relatively weak and not strongly flattened. The braincase is relatively only slightly telescoped so that on the middle of its upper side there can be seen not a little of the frontal. The supraoccipital is not especially large or forward-slanting. The articular surface for the lower jaw on the squamosal is not pushed out especially far downward and backward, and, when seen from beneath, has not entirely covered the mastoid or pushed the exoccipital very far backward. Bony palate relatively not strongly lengthened behind. The point of attachment for the neck muscles on the basal part of the occipital is still tubercular, and the basioccipital on the whole is only to a slight degree shaped to accommodate the larynx and gullet. In contrast with its nearest recent allies *Rhachionectes* stands lower in a few other respects also: an evident capitulum is still found on some of its anterior ribs; the skin beneath its mouth cavity is not thrown into longitudinal folds; the dorsal fin is not present; the hand is relatively short, and the number of phalanges is only a little increased. It has perhaps high specializations in its decidedly heavy under jaw, which slightly suggests *Neobalæna*, and in its somewhat upwardly arched facial portion of the skull.

Plesiocetus from the Tertiary of Europe, and presumably from that of North America also, is best known from the skull. To a high

degree it resembles *Rhachionectes*, but appears to differ in having a considerably more reduced nasal, like the higher Balænopterines.

Cetotherium, also from the Tertiary of Europe and presumably of America, which is likewise known from scarcely anything else than the skull, is a very near relative to *Plesiocetus*. It is slightly more specialized, with the articular surface for the lower jaw on the squamosal pushed somewhat further backward, pressing more against its surroundings, and covering the mastoid; but otherwise it scarcely differs except in trifles.

As a pronounced contrast to *Rhachionectes* the genus *Balænoptera*, on the other hand, stands much higher: with much smaller nasal; with intermaxillary and maxillary more broadened in front; with broader and flatter supraorbital process; with more telescoped braincase in the median upper part of which there shows itself only a little of the frontal; with larger, more forward-slanting supraoccipital; with the articular surface for the lower jaw on the squamosal pushed much further backward, wholly covering the mastoid and shoving the exoccipital more to the rear; with bony palate strongly lengthened backward; with point of attachment for the neck muscles on basal part of occipital compressed, flattened; with the basioccipital more shaped to the larynx and gullet; with the skin under the floor of the mouth cavity thrown into longitudinal folds; with a dorsal fin; with the hand more lengthened; with frequently more phalanges in the median fingers.

Magaptera stands yet higher than *Balænoptera*. Its body is relatively not much elongated, a fact which points to its origin among the most primitive species of *Balænoptera*. But in the structure of the fore limb it has reached far beyond its relatives. On account of some special use or other, perhaps most likely from rapid turning about in the water, the arm has grown to an enormous length. The forearm has become very much stretched out, and the hand is yet more conspicuously lengthened, the number of phalanges in the third and fourth finger increased in addition. The scapula has lost both the coracoid process and the crest.

Balænidæ.¹⁴

I. Intermaxillary and maxillary narrow anteriorly, not flattened.

Balænini.

A. Mandible slender. Ribs not broad. First metacarpal present.

Balæna.

B. Mandible robust. Most of the ribs broad. First metacarpal absent.

Neobalæna.

II. Intermaxillary and maxillary broad anteriorly, flattened.

Balaenopterini.

A. Nasal relatively well developed.

Rhachionectes.

B. Nasal reduced.

1. Area of insertion of neck muscles on basal part of occipital tubercular.

a. Articular surface for lower jaw on squamosal not strongly pushed backward, not covering the mastoid when seen from below.

Plesiocetus.

b. Articular surface for lower jaw on squamosal more pushed backward, covering the mastoid.

Cetotherium.

2. Area of insertion of neck muscles on basal part of occipital compressed.

a. Hand not especially elongated. Shoulder blade with crest.

Balaenoptera.

b. Hand greatly elongated. Shoulder blade without crest.

Megaptera.

Squalodontidæ.—The Squalodonts must have originated from among the most primitive Balænidæ which still had the teeth shaped like those of the Zeuglodonts but increased in number, and which had not yet begun to get the mouth refashioned into a catching-bag. Their differences from the most primitive Balænidæ are due especially to stronger pressure of the water on the facial part of the skull; most likely the Squalodonts were from the beginning more rapid swimmers than the Balænidæ. The nasal passage is pushed much further back, not by muscle action alone, but probably especially by the influence of the facial adipose cushion. The water both stimulates the cushion to growth and presses it against the nasal passage. The nasal bone is completely atrophied, almost tubercular in form, and pressed into the frontal in the fore wall of the braincase, not or almost not covering over any part of the nasal cavity. The plates of the ethmoid are probably pushed wholly away and the lamina cribrosa has probably become a solid bone-plate without perforations or almost so. The nose muscles, the pneumatic diverticulum from the nasal passage, the adipose cushion of the snout, in short all that covers the skeleton of

the face, is pressed by the water in against the bones and has moulded the upper side of the whole face as its bed, especially hollowed out posteriorly. This bed, the "facial depression," extends backward along the sides of the nasals on the forehead. The beginning is traceable of a remarkable peculiarity which, in the more advanced cetaceans may become conspicuous to a high degree: an asymmetry in the structure of the face. The head must no doubt be so held during motion that the water comes to press not quite equally on both sides, but more strongly on the right side than on the left. The facial cushion therefore becomes larger on the right side than on the left, extends its bed most on the right side, forces the nasal passage to bend over to the left, and causes the bones of the face to develop somewhat dissimilarly on the two sides.²⁵ The maxillary has pushed itself posteriorly up over the frontal to such an extent that it almost wholly covers it, also spreading out over the supraorbital process. The zygoma appears to have been quite slender. The two nasal apertures were presumably united into one. In all of these points of difference from the Balænidids the Squalodonts agree with the higher cetacea, of whose most primitive forms they remind one in nearly everything, so far as they are known, except in the condition of the teeth.

The Tertiary North American *Agorophius*, which is only known from a very incomplete skull, almost without teeth, appears to be the most primitive member of the family. The number of teeth is not known, but certainly, to judge by the other peculiarities of the genus, it must have been greater than typical. Its braincase is much less telescoped than in the other Squalodonts, also less than in any of the known Balænidids, somewhat suggesting the Zeuglodonts in being relatively strongly constricted anteriorly between the large temporal fossæ, and in having the parietal form a considerable part of its roof. In the other Squalodonts the braincase, so far as it is known, is so telescoped and so broadened out to the sides that there is a wide area between the temporal fossæ although these are relatively large; also the parietal in the middle of the roof of the braincase shows itself at most as a narrow band. In other respects *Agorophius* appears to agree well with *Squalodon*.

Squalodon is known rather completely from skulls from Tertiary strata in both the Old and New Worlds. Almost nothing is known of other parts of the skeleton. The teeth are well developed, heterodont. In each jaw there are three incisors with conical crown and single root, a canine of similar form and size, and 11, or sometimes

in the upper jaw 12, cheekteeth. Of these last the four or five anterior have conical crown and single or bifid root, and the seven posterior have compressed crown with more or less serrate anterior and posterior margin (or only the posterior margin serrate), and two roots, an anterior and posterior. The fact that the number of cheekteeth is most often 11 might indicate that the increase above the typical number, seven, was produced by the intercalation of four milkteeth in the series with the seven permanent teeth; but there is no decisive evidence either for or against this explanation, as the tooth succession is not known. If the number exceeds 11 a true increase must have taken place. As in the most primitive of the higher whales the jaws are very elongate, narrow; the intermaxillary and maxillary are not especially closed together, and the mesethmoid is not ossified in front; the symphysis menti is long (the rami of the mandible may have grown together); the facial depression does not extend very far backward, the braincase is relatively only a little telescoped, the temporal fossa is considerable, the zygomatic process of the squamosal strong, the occipital condyle projecting.

The Tertiary European *Neosqualodon* is only known from pieces of jaws. It has the number of serrate cheekteeth raised to at least 11; otherwise the characters of the dentition are not known.

The Tertiary Argentinian *Prosqualodon*, known from the more essential parts of the skull, differs from *Squalodon* in having a much shortened face, with the facial depression relatively strongly broadened behind. The number of teeth appears to be somewhat reduced. It is no doubt a little more primitive than *Squalodon* in the less strongly telescoped form of the braincase proper.

Squalodontidæ.³⁶

I. Braincase only slightly telescoped.

Agorophius.

II. Braincase strongly telescoped.

A. Face long.

1. Number of cheekteeth relatively little increased above the typical [44].

Squalodon.

2. Number of cheekteeth increased above the typical 44.

Neosqualodon.

B. Face shortened.

Prosqualodon.

Platanistidæ.—The Platanistids no doubt originated from the most typically defined Squalodonts such as *Squalodon*. The most important and perhaps in the first place the only distinction between the Platanistids and their precursors among the Squalodonts is that the teeth in the Platanistids are to a higher degree structurally degenerated. They have lost their heterodonty, have become smaller but more numerous, all of them nearly simply conical with a single root. On the other hand the Platanistids have retained most of the other peculiarities in which the Squalodonts show themselves to be relatively primitive. Especially noticeable in comparison with higher cetacea are the following characters: facial depression rather narrow, not much widened laterally behind, so that its outer margin covers over the temporal fossa to a slight degree only; temporal fossa rather large; zygomatic process of the squamosal robust; all these peculiarities are no longer or scarcely ever found among cetacea of the higher families. The braincase appears to be rather small and not very much compressed antero-posteriorly, this also in contrast with the higher whales. In common with the most primitive forms of the higher cetacean families the Platanistids have, so far as they are known, such peculiarities: as the mutual independence and rather considerable size of the cervical vertebræ; as the conspicuous lack of uniformity in the shape of the dorsal vertebræ (for instance the long, broad transverse processes of the lumbar vertebræ in contrast with the rather short processes of most of the thoracic vertebræ; only on a few of the hindmost thoracic vertebræ do there occur robust transverse processes, parapophyses, which bear ribs at their tips in the Platanistids that are known in this respect); as the well-developed heads to the anterior ribs, and probably also the coalescence, or more correctly the non-separation, of the tuberculum and capitulum on the hinder ribs; as the rather large, ossified costal cartilages; as the rather well-developed sternum; as the presence of the first finger, the metacarpal at least of which is found; as the rather slight lengthening of the middle fingers, etc.

In one single direction the known Platanistids have developed themselves highly. They have used the jaws as a kind of delicate forceps to seize and hold prey that did not make very strong resistance. The jaws grow to an unusual length but become noticeably slender, fine, though solid. The intermaxillary and maxillary press close together, covering over the anterior part of the mesethmoid, and they have a tendency to coalesce. The maxillary has pushed itself forward anteriorly beyond the tip of the intermaxillary. In the lower

jaw the symphysis menti becomes very long, and the rami of the mandible are inclined to grow together. The teeth that lie at the front of the jaws are inclined to increase in size, probably because the tips of the jaws come to be the most used part of the forceps. In another respect also the known Platanistids stand high: the sides of the facial depression are inclined to grow upward. Perhaps they also stand high in the tendency of the pterygoid to widen itself out unusually far backward in the outer wall of the air-sac behind the palate, reaching back to the squamosal; a circumstance that may call to mind both lower and higher whales, *Balænid*s and *Physeterid*s.¹⁸

The genus of Platanistids which has removed itself least from *Squalodon* appears to be the Tertiary South American *Pontistes*, which is known from most of the skull. In relation to one or another of its nearest allies it has the following primitive characters: the teeth, judging from the alveoli, were small, simply formed, the anterior not enlarged; the toothrows stand rather distant from each other, as the palate is relatively broad; the outer margin of the facial depression, especially the longitudinal crest on the maxillary above the orbit, is relatively low. A character which must be considered advanced in comparison with the nearest relatives is the specially large number of teeth, about 40 in each jaw if one judges rightly from the fragments of toothrows that have been found.

Near to *Pontistes* but on a slightly higher level is *Pontoporia* (*Stenodelphis*). The teeth have become smaller but more numerous, about 55 in each jaw. Those in front have a slight tendency to be enlarged. The toothrows are placed nearer together and the palate is narrower. A high specialization, which also holds good for the other recent members of the family, is the complete absence of the olecranon.

Lipotes (known from external characters, skull, and cervical vertebrae) and *Inia* are near relatives of *Pontoporia*. Their face is shorter, the number of teeth is less (about 30 in each jaw in the former, about 26 in the latter), the anterior teeth show scarcely any tendency to be enlarged. It might appear as if the two genera were, in these characters, less specialized; but the explanation is presumably another. The two genera most likely originated from forms that more nearly resembled *Pontoporia*, and that had the strongly narrowed palate and numerous small simply conical teeth, although not so many as in *Pontoporia*. *Lipotes* and *Inia* appear to have used the teeth in a special manner, most probably for the crushing of food, and the teeth have therefore regained some of their earlier strength, have grown

and become massive, with wrinkled enamel. In compensation, however, they have become less numerous and the most posterior in the jaws have acquired a form which is anything but primitive: the base of the crown is more or less tubercularly widened out inward. The narrow palate is retained. The lateral margin of the facial depression is considerably more upturned than in *Pontoporia*, and the posterior border, especially in the median region formed by the frontal, is far more elevated.

Lipotes as compared with *Inia* is surely the more primitive in the greater slenderness of the teeth; on the contrary it is the less primitive in having the facial depression relatively strongly widened behind.

Saurodelphis (*Saurocetus*, *Pontoplanodes*), Tertiary, Argentinian, known from most of the skull, appears to have also originated from *Pontoporia*-like animals, but it has gone in another direction than *Inia*. It has retained the slender face with the narrow palate, but the number of teeth is reduced to about 20 in each jaw. At the same time the teeth are enlarged; in any event they have acquired roots that are more widened antero-posteriorly; this is especially true of a number of the anterior teeth in each jaw. In these teeth the root appears to be in process of dividing in two, so that in cross-section it is almost 8-shaped, a form which, especially as regards the anterior teeth, is quite the opposite to primitive. The lateral margin of the facial depression is trenchant and highly upraised, even more than in *Inia*. The hinder margin of the depression is not only elevated in the middle as in *Inia*, but is also pushed further back.

Platanista also probably traces its origin back to *Pontoporia*-like creatures. It has gone further than any other member of the family in the direction of making over the jaws into delicate forceps. The face is so slender and the palate so narrowed that the right and left tooththrows in the upper jaw lie closely side by side; they may even, especially at the extreme rear, where the teeth are undergoing atrophy, be pushed into each other. Somewhat similar conditions obtain in the lower jaw. The number of teeth is about 30 in each jaw. Several teeth at the front of each jaw have acquired high, pointed crown and compressed, enlarged root. The outer margin of the facial depression has grown upward, higher than in any other genus, especially that part of it which runs along the outer margin of the maxillary over the orbit and front of the temporal fossa. This part has shaped itself quite fantastically as a huge plate which rises high upward and bends in over the posterior part of the face, which it covers like a mask, since each plate nearly meets its fellow from the

opposite side. On the other hand the posterior margin of the depression is not particularly highly elevated. The eye is atrophied; touch more than vision probably guides in the capture of prey. The hand's unusually broad, rounded-off outline, with the especially short, uniform, well-developed and wide apart fingers, might appear more primitive than in other members of the family; but possibly it may be the story of a partial reversal from an earlier more flipper-like condition.

Platanistidæ.¹⁷

I. Upper tooththrows well separated throughout. Maxillary with longitudinal crest not excessively large.

A. All the teeth with terete or scarcely compressed root.

1. Longitudinal crest on maxillary relatively low. Frontal behind nasal only a little elevated.

a. Palate relatively broad. About 40 teeth in each jaw.

Pontistes.

b. Palate relatively narrow. About 55 teeth in each jaw.

Pontoporia [*Stenodelphis*].

2. Longitudinal crest on maxillary relatively high. Frontal behind nasal rather strongly elevated.

a. Teeth relatively slender.

Lipotes.

b. Teeth relatively robust.

Inia.

B. Teeth with compressed root; in some of the anterior teeth the cross-section of the root is almost 8-shaped.

Saurodelphis.

II. Upper tooththrows placed close together, especially behind, so that teeth from the right and left sides may be pushed in among each other. Maxillary with longitudinal crest excessively large, completely covering over the face.

Platanista.

Delphinidæ.—The most important character—perhaps in the beginning the only one—which has separated the Delphinids from the most primitive Platanistids from which they sprang is the widening out of the facial depression. This broadens posteriorly to such an extent that its floor wholly covers over the temporal fossa like a roof formed by the frontal and maxillary together. A second

peculiarity, which in any event soon showed itself, is the reduction of the temporal muscle through lack of use; its fossa becomes smaller and the zygomatic process of the squamosal becomes less projecting and less robust, losing, moreover, its primitive arched form. In the more advanced members of the family many other modifications may appear. The facial part of the skull, which begins by being long and narrow, almost compressed, used as forceps, may become still longer. Or the use as forceps may grow less and be exchanged for service as an implement for rooting in the sea bottom; followed by alteration in the form of the face. Or the mouth is used merely to clap together around the prey; followed by flattening and shortening of the face. In each instance the facial cushion contributes to the flattening of the facial part of the skull. The extreme tip of the intermaxillary has the tendency to be restricted, to be grown over by the maxillary and to lose the teeth which at first were implanted in it. Its upper margin may extend in over the anterior part of the mesethmoid and coalesce with its fellow of the opposite side. The symphysis menti has a tendency to be weakened and shortened. The teeth are inclined to a further reduction, and they may disappear; but they may also be again applied to special work and be modified in various ways. The braincase increases in size and is more subject to pressure from in front and from behind. The nasal passage may be pushed further back. The nasal bone, which in the most primitive Delphinids retained a slight trace of its earlier function as a cover for the nasal cavity, becomes in most cases quite sunk into the frontal. The occipital condyle, which at first is rather projecting in the usual manner, becomes flattened out and pressed in against the wall of the braincase. The cervical vertebræ may coalesce. The thoracic vertebræ acquire unusually long transverse processes which are especially noticeable on the hindmost of the series. Most of them are diapophyses except the most posterior ones; these are parapophyses. Only the anterior ribs retain the capitulum. On the hindmost ribs the capitulum disappears entirely, and the rib is articulated with the tip of the long transverse process by the tuberculum only. (As in the Platanistids the single articular head on the very hindermost ribs is presumably formed by the capitulum or by the capitulum and tuberculum undivided.) The flippers may be lengthened. Etc. The pterygoid varies capriciously. It is true that it always spreads inward under the posterior nares; but it is sometimes rather widely separated from its fellow of the opposite side, sometimes almost in contact with it, while probably after having been in the latter condition it may

withdraw. The number of vertebræ also varies in a quite capricious manner.

One of the most primitive Delphinids is no doubt the Tertiary North American *Delphinodon*, the skeleton of which is known rather completely. In comparison with its various relatives it has the following primitive peculiarities. The teeth are present in large numbers. They are small and nearly simply conical, some of them, however, with wrinkles or small projections on the base of the crown, probably mementos of the crown's formerly serrate margins and of its also otherwise less simple form. The facial part of the skull is rather long and narrow. As in the related forms which are lowest in this respect the anterior end of the intermaxillary was probably freely projecting, tooth bearing, and not grown over by the maxillary. The upper margin of the intermaxillary does not come in contact with its fellow. The symphysis menti is long; nasal slightly projecting; cervical vertebræ distinct. It shows a peculiarity of its own in having a longitudinal crest on the projecting lateral part of the basioccipital.

The Tertiary European *Champsodelphis* (judging chiefly from *Ch. ombonii*, *Acrodclphis*) presumably stands near to *Delphinodon*. It is known from scarcely anything else than scanty remains of the skull. It shows high specialization in the modification of the rostrum to serve as an implement for boring or rooting in the sea bottom. The facial part of the skull has acquired an unusual length and slenderness; the teeth have probably disappeared from the intermaxillary, and the upper margin of this bone was probably in contact with its fellow through a considerable part of its extent.

The Tertiary European *Schizodelphis* (judging from *S. sulcatus*, *Cyrtodelphis*), also known practically from the skull only, must be a near relative of *Champsodelphis* with which it appears to have most of its peculiarities in common, both the primitive characters and the special modifications. Its most important difference appears to be that its teeth have gone still further in the direction of simplicity; the only reminders of earlier, less reduced form that have remained behind are a slight widening out of the crown's base, which may be found on some of the teeth, and the trenchant character of its anterior and posterior margins.

The Tertiary European *Heterodelphis*, which is known from rather considerable parts of the skeleton, undoubtedly stands close to *Schizodelphis*. Its teeth have become still more simple, with purely conical crowns.

In the Tertiary European *Eurhinodelphis*, which is known from most of the skull and from parts of the rest of the skeleton, the transformation of the snout into a rooting implement has reached the highest limit. The rostrum, both upper jaw and lower jaw, has grown forward anteriorly as a long slender point, still more noticeably than in any of the other genera. The intermaxillary has extended itself, awl-shaped and toothless, far forward beyond the maxillary. The tip of the lower jaw appears to be formed in a corresponding manner. The teeth are simply conical.

No doubt the Tertiary South American *Argyrosetus* is very nearly related to *Eurhinodelphis*. It is known from a defective skull, and appears to differ in trifles only.

The genera just mentioned of the group Eurhinodelphini form a contrast with the group Monodontes. The latter includes the genera *Delphinapterus* and *Monodon*, which must have originated from the oldest Eurhinodelphines in which the tip of the snout had not been remodeled as a rooting implement. In common with the Eurhinodelphines (at least with *Delphinodon*, *Heterodelphis*, *Eurhinodelphis*, and *Argyrosetus*, which are known in this respect) the Monodonts alone among the Delphinids have the primitive character that the cervical vertebræ are mutually independent. Other indications of low origin seem to be shown by the Monodonts in the form of the teeth (in which one of the genera may recall *Delphinodon* and others), in the decidedly short spinous and transverse processes of the thoracic vertebræ, in the relatively short fingers, and perhaps also in the absence of the dorsal fin. But in the flat and broad form of the face, probably resulting from their habit of not using the jaws for much else than to clap together on tender cuttlefish, the Monodonts are more highly developed than their progenitors among the Eurhinodelphines. The same is true of their lack of the olecranon.²⁸

The most primitive of the known Monodonts is *Delphinapterus*. It shows its primitiveness in relation to its nearest ally by its rather ordinary dentition: the teeth are present in relatively considerable numbers, about 10 in each jaw; they are small and conical, but in the upper jaw they are directed forward in a peculiar manner. The teeth have disappeared from the intermaxillary.

In *Monodon* the teeth, with a single exception, are in process of atrophy and disappearance; only a few of them are present in the young. One of the foremost teeth in each maxilla has had its peculiar destiny: it has grown forward as a "ramming-tooth," at first no doubt uniformly in the right and left jaw and in the male and female,

probably used, in a similar manner to the upper canine in the walrus or to the tip of the snout itself in the Eurhinodelphines, for rooting in the sea bottom. Such a function might be initiated by forward-slanting anterior teeth like those in *Delphinapterus*, but later it must have been restricted to the ramming-tooth in the left jaw of males. The work of the males may possibly be of service to the females because the species is gregarious. The ramming-tooth has become a kind of male secondary sexual character and has grown to an exaggerated size as the well-known "unicorn horn." As a memento of an earlier condition the ramming-tooth is still found in a reduced form in the right upper jaw of the male, and in both upper jaws of the female; in rare instances it may even now be found in the male well developed on both sides [when the spiral of the two tusks is parallel].

All the other Delphinids are contrasted with the Eurhinodelphines and Monodonts by the partial or complete coalescence of the cervical vertebræ, the atlas and axis being always united. The genera in question constitute a compact group, rich in forms, which traces its origin back to low Eurhinodelphines.

Lowest of all stands the section Delphini, whose most primitive known genus is undoubtedly *Steno*. This has still the primitive Eurhinodelphines' long, but not exaggeratedly long, narrow, scarcely flattened fore-face, with long tooththrows and long symphysis menti. It is indeed scarcely distinguishable from the primitive Eurhinodelphines except by its partly ankylosed cervical vertebræ. The circumstances which place it low among its nearest relatives are the facts that the teeth have fluted enamel, and that the symphysis menti is long. The peculiarity of the enamel is presumably a slight reminiscence of an earlier, less-reduced condition.

Very near *Steno* comes *Prodelphinus* (probably including "*Sotalia*"), not differing in much else than that the enamel is smooth, not fluted, and that the symphysis menti is shortened.

Delphinus differs from *Prodelphinus* in scarcely anything else than a peculiar palate form: at the inner side of the tooththrow the bony palate is hollowed out into a long longitudinal furrow which is especially deep behind. The intermaxillaries have a relatively strong tendency to coalesce and to cover over the mesethmoid. A few small teeth may be found in the intermaxillary as in *Steno* and *Prodelphinus*; in most of the Delphinids the teeth have wholly disappeared therefrom.

In contrast to the Delphinines the other higher Delphinids have the skull's fore-face shorter and more depressed. As a beginning the

difference is only slight, but it finally increases so as to become very noticeable. At the same time that the anterior facial part of the skull is shortened, because the mouth is no longer used as a pair of forceps but as a "clap-trap," it becomes flatter and broader, while its upper side is more pressed upon by the facial cushion. The cushion becomes larger, especially widening itself out anteriorly and pushing into the originally slender "beak." The intermaxillaries, in their anterior portion particularly, together lose their structure as an upstanding roof-ridge, and finally become quite flat, each of the bones widened out.

The genera of the section *Legenorhynchi* depart so slightly from the more primitive members of the section *Delphini*, such as *Prodelphinus*, that there would scarcely be any reason to set them apart in a special group were it not evident that they represent the beginning of new series of forms.

Doubtless *Tursiops* occupies the lowest position. The anterior facial part of the skull is indeed broader than in *Prodelphinus*, but it has, however, not lost its form as a roof-ridge, and it has still a considerable length.

Near *Tursiops* probably belongs *Tursio* [*Lissodelphis*], which also has the fore-face rather long, though more flattened. Another difference is that it lacks the dorsal fin, either because it has lost it or has never acquired it.

Lagenorhynchus (to which should probably be joined *Cephalorhynchus* and *Sagmatias*, and perhaps "*Feresa*") has gone a step further than *Tursiops* and *Tursio* in the direction of shortening and flattening the rostrum.

Among the *Delphinids* in which the process of shortening and flattening the rostrum has been more perfected the members of the section *Globicipites* are contrasted with those of the section *Phocænæ* by reason of their greater primitiveness. In them the crowns of the teeth have retained their primitive conical form, while in the *Phocæans* the crowns have become entirely peculiar.

Orca [*Orcinus*] is the one among the *Globicipites* which has retained most of the ordinary dolphin type in the structure of the rostrum, particularly as regards the narrowness of the intermaxillary. The rather short, rounded-off form of the hand might appear to be primitive also, but various circumstances strongly indicate that it has arisen through the shortening of an ordinary, pointed, porpoise flipper: the number of phalanges in the second finger is rather large; the finger is merely more strongly arcuate than usual. In the transformation of the dentition to a conspicuously powerful biting imple-

ment *Orca* has gone further than any other genus of the family. It has habituated itself to living on large prey such as seals and the smaller cetaceans, and it even slashes into the largest. The teeth are, it is true, relatively few, about 12 in each jaw, but in compensation they are massive.

Orcella has reached higher than *Orca* in the great breadth of the intermaxillary, but it must have originated at a level lower than that on which *Orca* stands, since its teeth are small and rather more numerous, while its hand is essentially like an ordinary porpoise hand. The genus gives the impression of being a dwarf form with noticeably large braincase in proportion to the face.

The following genera of Globicipites must have originated from Delphinids that were essentially like *Orcella* but without the dwarfing. Each has gone its own way. There is, however, one peculiarity that unites them: the hand has acquired an uncommon length and narrowness, though in different degrees, at last with an unusual number of phalanges in the second finger.

In "*Grampus*" the intermaxillary has retained a breadth similar to that in *Orcella*. Although the hand is long and narrow there are only about eight phalanges in the second finger. The chief peculiarity of the genus lies in the atrophy of the dentition: only a few and rather small teeth remain. These are at the front of the mandible, and with age they may entirely disappear.

In *Pseudorca* the hand is essentially as in *Grampus*. But the intermaxillary has acquired a very noticeable breadth anteriorly, and the dentition is developed in a similar manner as in *Orca*.

The intermaxillary is conspicuously wide in *Globiceps* [*Globicephala*] also; it may be even wider than in *Pseudorca*. Peculiarities of *Globiceps* are: that the nostril is pushed unusually far backward, that the dentition is atrophied so that only a few, about 10, small teeth remain, situated at the front of the jaws, and that the hand is conspicuously long, with as many as 14 or more phalanges in the second finger.

The section *Phocænæ* presumably originated among the most primitive Globicipites or perhaps *Lagenorhynchi*. That which places this group in contrast not only with the *Lagenorhynchi* but also with all other Delphinids is the peculiar form of the teeth. The teeth are present in large number and are of small size. Some of the foremost and hindmost may have about the usual conical crown, and all of them are single rooted. Most of the teeth, however, have the crown compressed, widened out fan-wise or leaf-wise, and often with notches in

the margin; a form which is not only unique among the cetacea, but the contrary to the forms found among the most primitive cetacean genera.¹⁹

Phocæna is, besides, a little broad-snouted porpoise, rather evenly developed in all directions. A few small teeth may be present in the intermaxillary.

Neomeris (*Neophocæna*) is nearly related to *Phocæna*. It differs in having acquired a yet shorter and broader face, in having a noticeably spacious braincase, and in lacking the dorsal fin, which it doubtless has lost.

Delphinidæ.²⁰

I. Atlas and axis mutually free.

A. Face long and narrow, not flattened.

EURHINODELPHINI.

I. Intermaxillary (undoubtedly) not specially elongated in front of maxillary.

1. Face not noticeably elongated.

Delphinodon.

2. Face noticeably elongated.

a. Teeth with slight traces of less simple forms.

a. Crowns of teeth partly with remains of lateral cusps.

Champsodelphis.

β. Crowns of teeth without lateral cusps.

Schizodelphis.

b. Teeth purely conical.

Heterodelphis.

2. Intermaxillary with tip produced far forward in front of maxillary.

Eurhinodelphis, Argyrocetus.

B. Face relatively short, broad and flat.

MONODONTES.

I. Several teeth present in each jaw, none of them especially enlarged.

Delphinapterus.

2. Almost toothless, a single tooth in the upper jaw of males a gigantic ramming-tooth.

Monodon.

II. Atlas and axis coalesced.

- A. Anterior facial region, formed mostly of intermaxillary and maxillary, long and narrow, not or scarcely flat, nearly roof-shaped; intermaxillary in particular relatively narrow.

DELPHINI.

1. Crowns of teeth rough; symphysis menti long.

Steno.

2. Crowns of teeth smooth; symphysis menti short.

a. Palate without grooves.

Prodelphinus.

b. Palate with a longitudinal groove on each side.

Delphinus.

- B. Anterior facial region, formed mostly of intermaxillary and maxillary, becoming relatively short, broad and flat; intermaxillary in particular broad.

1. Face relatively only a little shortened.

LAGENORHYNCHI.

- a. Fore-face, beak, relatively long.

a. Rostrum not wholly flattened. Dorsal fin present.

Tursiops.

β. Rostrum more flattened. Dorsal fin absent.

Tursio [*Lissodelphis*].

- b. Fore-face relatively shorter.

Lagenorhynchus.

2. Face more strongly shortened.

- a. Crowns of teeth conical, terete, pointed.

GLOBICIPITES.

- a. Intermaxillary not especially broad proportionally.

Orca [*Orcinus*].

- β. Intermaxillary more or less noticeably broad.

1. Flippers not or scarcely lengthened and pointed.

Orcella.

2. Flippers lengthened, pointed.

a. Intermaxillary not conspicuously broad anteriorly.

"Grampus."

β . Intermaxillary strongly broadened anteriorly.

(1) Nostril not pushed especially far back. Teeth not atrophied. Flippers quite short.

Pseudorca.

(2) Nostril pushed unusually far back. Teeth somewhat atrophied. Flippers very long.

Globiceps [*Globicephala*].

b. Crowns of teeth in part compressed, widened out leaf-wise.

PHOCÆNÆ.

a. Face relatively long and narrow. Brain-case relatively small.

Phocæna.

β . Face relatively short and broad. Brain-case large.

Neomeris [*Neophocæna*].

Physeteridæ.—The *Physeteridæ* probably originated from the most primitive Delphinids, from Delphinids in which the margin of the facial depression must have been so widened that it covered the temporal fossa, but which at the same time retained these primitive features: zygomatic process of the squamosal relatively large and somewhat arcuate; teeth small and conical, but still with traces of notching on the margin of the crown; teeth in the intermaxillary well developed; anterior part of mesethmoid free, not covered over by the intermaxillaries; free though stunted lacrimal; separate cervical vertebræ; rather short transverse processes on the thoracic vertebræ; a well-developed capitulum on all the ribs, etc. The character that already places even the most primitive Physeterids on a higher plane than the Delphinids is a result of stronger action of the facial cushion. It appears as if the *Physeteridæ* had from the very first trained themselves to swifter, more violent swimming than other whales, and that the fat-pad in front of the nose had therefore been pressed in with greater force against the facial part of the skull. The pad, together with the nasal muscles, etc., has modified the face to an unusual degree. Especially the posterior margin of the facial depression is transformed, more or less conspicuously elevated. The crookedness

in the posterior nasal passage and in the facial bones becomes more conspicuous than in other whales. The resistance of the water has acted upon the skull in other ways also, different in the different groups; there is a tendency toward strengthening and coalescence of the bones of the face, toward the appearance of projecting osseous protuberances, etc.

The members of the family, so far as they are known in this respect, show a peculiarity in the relation between the ribs and the transverse processes on the posterior thoracic vertebræ, in which they form a contrast to at least the living forms of Delphinids. While in the Delphinids the hinder ribs apparently lose the capitulum and retain the tuberculum (the most posterior, probably having their own history, have never had more than a single head), in the *Physeterids* it is the tuberculum that disappears, while the capitulum remains. On one or two of the hindmost ribs it may happen that the capitulum and tuberculum can be seen at the same time, each in contact with its "transverse process"; but the tuberculum with its corresponding process, a diapophysis, is in course of atrophy.²¹

The genera of the section *Xiphiini* stand lowest. In them the occipital wall, which forms the posterior margin of the facial depression, is highly elevated in a section at the middle only, behind the nares, and is not pushed very far back in relation to the nares. In the contrasted *Physeterini* the occipital wall is heightened through its whole extent and more pushed backward. Likewise a primitive feature of those *Xiphiines* that are known in this respect is that a more or less distinct lacrimal bone is present, though in an atrophied condition, spreading out especially in the roof of the orbit.

The essentially most primitive genus of the *Xiphiines* is no doubt the Tertiary South American *Argyrodelphis* (*Notocetus*, *Diochotichus*), of the group *Argyrodelphini*, not known from much else than the skull. It stands lower than all other known *Physeterids* in having a relatively robust and arcuate zygomatic process of the squamosal and in the character of the dentition. There is a long row of small, well-developed, conical teeth in both upper and lower jaw, some of them bearing notches on the margin of the crown. On the contrary, as compared with one or another of the other genera, it is advanced in having the occipital wall pushed rather far back, in having a rather large cushion-shaped outgrowth on the maxillary above the orbit, and in having the intermaxillaries spread inward over the mesethmoid and coming into mutual contact with age. The cervical vertebræ were free.

In all other Xiphiines the zygomatic process of the squamosal is smaller and more atrophied, the teeth in the upper jaw disappear, while of those in the lower jaw one or two only remain in each ramus and these are particularly modified. A peculiarity of at least the living forms of the section is the unusual size of the air-sac at the outer side of the pterygoid, which is shaped to fit it. Somewhat of a peculiarity likewise is partly the height of the spinous processes on the dorsal and caudal vertebræ (while the transverse processes are relatively rather short), and partly the small size of the hand. The former character indicates unusually heavy dorsal and caudal muscles, or perhaps a widening out of the muscles in a different direction—more upward than sideways—than in the Delphinids with specially long transverse processes. The latter makes it appear that the hand is somewhat disused. The cervical vertebræ are inclined to coalesce as in the Physterines.

In the members of the group Xiphii, as contrasted with the Hyperoodontes, the bones of the face have remained primitive to the extent that no raised longitudinal crest is present on the maxillary in front of and above the orbit; at most there is found in the corresponding place a weak cushion-shaped elevation. But in other ways the bones of the face have increased in strength and have permitted themselves to be moulded by the pressure of the water.

In a few respects *Mesoplodon* is the most primitive among the Xiphii. To be sure, the facial cushion, by pressing back against the occipital wall, has caused the median part of the wall, formed for the most part of projecting outgrowths of the intermaxillaries, to be abruptly elevated. But the cushion has not acted on the wall to such a degree that the upper margin together with the nasal bones has been either very strongly forced back or caused to bend forward in any noteworthy manner; neither has it formed for itself any distinct pit around the nares. Moreover the intermaxillaries have retained their original relation to the mesethmoid, which they do not grow over. On the other hand the rostrum acquires increased strength by the ossification, as age advances, of the mesethmoid, and its coalescence with the surrounding bones into a stony-hard mass. Of the teeth in the upper jaw there is found in *Mesoplodon* at most a series of quite small remnants, more or less hidden in the skin and scarcely leaving any traces in the bones. In the lower jaw there is found only one well-developed tooth. This is situated at the front of the mandible and is peculiarly modified, having a large, compressed crown and a big root which sometimes, presumably in the male especially, may

grow to a disproportionate size and to a high degree affect the form of the jaw.

The Tertiary European *Xiphrostrum* ("Ziphrostrum," "Miozi-phius"), which is known from parts of the skull, has in a single respect gone further than *Mesoplodon*, near to which it otherwise stands: the intermaxillaries have grown over the mesethmoid and come in contact with each other along their upper margins. But *Xiphrostrum* must have taken its origin from whales that were less far advanced than the known species of *Mesoplodon*; as the mesethmoid is not ossified anteriorly; the teeth in the upper jaw are slightly less atrophied, leaving traces behind them in the maxillary; and at the front of the lower jaw there are two well-developed teeth on each side.

Chonoxiphius ("Choneziphius"), likewise Tertiary European and known from parts of the skull, stands near to *Xiphrostrum*. It has gone further in the modification of the face. The facial cushion has begun to modify a special area around the nares for its bed. Here the lateral margins of the premaxillaries are caused to grow slightly upward, so that they together, and the bones that lie between, form a special pit, a structure the first traits of which, more or less evident, are found in many other toothed cetaceans. In the middle of the pit there has arisen an erect longitudinal crest, evidently formed from the posterior part of the mesethmoid. (The under jaw is probably not known.)

Xiphius ("Ziphius") appears to have originated from whales which stood on about the same level as *Mesoplodon*. Its deviations are of two principal kinds: (1) the median part of the occipital wall is forced further back and raised higher upward, so that the nasal bones, which are even more modified than in other Xiphiines and are widened out plate-wise in front, once more come to form a forward-bent roof over the nasal cavity, and (2) the lateral margins of the intermaxillaries have grown upward as in *Chonoxiphius*, but much more conspicuously, bounding a deep pit. As in *Mesoplodon* the anterior part of the mesethmoid becomes ossified with age.

In the genera of the group Hyperoodontes, which must have originated from the lowest Xiphii, the bony crest, a faint indication of which is found in many toothed cetaceans running along the upper surface of the maxillary in front of and over the orbit, becomes so stimulated to growth by resistance of the water that it gradually swells up to a huge hump which spreads itself over most of the face in front of the nares. Each hump is closely appressed to its fellow

of the opposite side, leaning inward over the intermaxillary and mesethmoid so as to turn a broad shock-receiving surface forward. The nares and middle part of the occipital wall are forced unusually far backward toward the posterior boundary of the braincase.

The most primitive genus of the group is "*Berardius*." The longitudinal crest on the upper surface of the maxillary is well developed and erect, but the face, however, has retained essentially its ordinary form. At the front of the lower jaw are found two rather well-developed teeth.

In *Hyperoodon* the face becomes with age wholly abnormal, since the longitudinal crest on the maxillary elevates itself to a height which exceeds even the highest part of the occipital wall. In the lower jaw at the front is found only a single tooth (apart from embryonic conditions).

The genera of the section Physeterini must have originated among the most primitive Xiphiines, from Xiphiines in which the dentition was still rather well developed, with teeth in the intermaxillary as well as the maxillary; in which the intermaxillaries were free from each other and from the surrounding bones; in which the mesethmoid was not ossified, etc. Their peculiarity is that the pressure of the facial cushion on its surroundings acts differently than in the Xiphiines, and even more strongly. The facial cushion, especially that part of it which is formed by the adipose mass, widens out still more, particularly outside of and behind the nasal passages. It pushes the median part of the occipital wall far back behind the nares, while at the same time the margins of the facial depression, at the back and at the sides, grow high upward. The bones which form the bottom of the facial cushion's bed are strongly acted upon by the stimulating mass of the cushion. They widen out. This holds good especially of the bones in the rostrum, and chiefly of the anterior part of the maxillary. The lower jaw on the contrary retains its primitive narrowness.

The genera of the group Hoploceti are extinct, Tertiary, and are only incompletely known, chiefly from fragments of skulls. It may be concluded that the skull in essential respects is modified in the same manner as in the highest group of Physeterids, the Physeteres, but to a distinctly less noticeable degree. They are also less advanced than the Physeteres in the development of the dentition, there being a long row of well-developed teeth in both upper and lower jaws, while the upper teeth of the Physeteres have atrophied.

In the European and American *Hoplocetus* (*Balænodon*, *Physodon*, "*Scaldicetus*," etc.) the teeth are covered with enamel.

The European *Physcterula* has lost the enamel, it appears.

In the genera of the group *Physeteres* the influence of the facial cushion on the skull has led to fantastic results. The dentition also is modified in a strange manner. In the lower jaw the teeth continue to be well developed; but in the upper jaw they atrophy and disappear either wholly or essentially so. It is not clear what the reason can be for this difference between the upper and lower jaws. Perhaps the difference is connected with the great lateral broadening out of the maxillary whereby the upper tooththrows are so pushed outward that they lose their interaction with the lower tooththrows which retain their ancestral position in the closely appressed mandibular rami. There has been no hard work for the upper teeth which might have maintained them in spite of all; the lower teeth together with the palate must have proved sufficient, as the task is indeed scarcely anything else than to grasp the cuttlefish which appear to be the favorite food for this whole family as well as for various other cetaceans, especially for those with more or less degenerate dentition.

"*Cogia*" is in some respects the most primitive of the genera. In the upper jaw there is still found, or may be found, a tolerably well-developed tooth. In the skull there remains a rather considerable, curved remnant (although very narrow and compressed) of the heightened osseous ridge which elsewhere in the toothed whales lies between the nares and the occipital wall; the adipose cushion has not yet wholly destroyed it. Neither has the cushion so grown around the outer nasal passage that it has pushed the orifice away from its accustomed place, nor has it to any noticeable degree pressed the roof of the braincase down. The anterior part of the face has become broader than usual, but it is still rather short, or, more strictly speaking, has been further shortened. On the other hand the lateral margin of the facial depression, over the braincase, is pushed unusually far out to the side and raised conspicuously high upward; it has also acquired a unique thickness.

In *Physeter* nothing has remained of the upper teeth except small vestiges hidden in the skin. The fat-cushion, which has grown gigantically, has caused the bones of the rostrum to grow far forward and to broaden themselves strongly at the side. The posterior margin of the facial depression is more abruptly elevated than in any other whale and is pushed further back. The fat-cushion has completely overgrown and leveled off the bony wall which elsewhere lies be-

tween the nares and the occipital wall. The soft outer nasal passage is pushed forward so that the blow-hole lies far to the front. The adipose cushion has forced the roof of the braincase down by its weight, and the whole braincase has sunk down below its original level, so that the spinal marrow, or medulla oblongata, has to bend down in an S-shaped curve to connect with the brain. The skull has acquired a noticeably large size in proportion to the body, and most of its bones have become conspicuously ponderous; this is especially noticeable as concerns the zygoma. Just as *Physeter* is the largest of all the toothed whales and pushes through the water with greater force than any other, it is the one on which the resistance of the water has had the most powerful influence. But it is a question whether this high development is not a menace to the creature's life. Irresistibly the water's pressure has caused the facial cushion to grow to a disproportionate degree and in its turn to call forth a skull the size of which is without relation to brain and body. The fate of *Physeter*, the most highly developed toothed whale, is much like that of *Balana*, the strangest whale-bone whale; the difference is that the pressure of the water in the one has acted most strongly on the outer side of the head, in the other most strongly on the inner walls of the mouth. Both animals are developed with such extravagant one-sidedness that they appear to be in danger of certain extinction even if their extirpation were not being worked at by man.

Physeteridæ.²²

I. Occipital wall highly elevated in middle only, its position close behind the nares.

XIPHIINI.

A. Dentition primitive: a long row of rather uniform small teeth in both upper and lower jaw. Zygomatic process of the squamosal well developed.

ARGYRODELPHINI.

Argyrodelfhis.

B. Dentition atrophied: most of the teeth disappear, leaving one or two in each lower jaw specially modified. Zygomatic process of the squamosal somewhat reduced.

I. Longitudinal crest on maxillary above and in front of orbit absent or slight.

XIPHII.

a. Intermaxillaries not or scarcely forming a cup-shaped depression around nares.

a. Intermaxillaries not covering mesethmoid in front.

Mesoplodon.

β. Intermaxillaries mutually in contact, covering mesethmoid in front.

(1) No pit formation around nares.

Xiphrostrum.

(2) Indication of pit formation around nares.

Chonoxiphius.

b. Intermaxillaries with an elevated outer margin forming a deep cup around nares.

Xiphius.

2. Longitudinal crest on maxillary above and in front of orbit well developed, swollen.

HYPEROODONTES.

a. Longitudinal crest on maxillary relatively weak.

"Berardius."

β. Longitudinal crest on maxillary huge.

Hyperoodon.

II. Occipital wall spreading itself, highly elevated, across entire braincase, and pushed far back behind nares.

PHYSETERINI.

A. Upper tooththrow well developed.

HOPLOCETI.

1. Teeth with enamel.

Hoplocetus.

2. Teeth without enamel.

Physcterula.

B. Upper tooththrow atrophied.

PHYSETERES.

1. Distinct remains of the longitudinal crest that originally extended from the nares to the occipital crest.

"Cogia."

2. Longitudinal crest behind nares wholly flattened out, obliterated.

Physcter.

The Hyænodonts, the nearest stock-forms of the cetacea among terrestrial mammals, lived at the beginning of Tertiary times in the northern parts of both the Old and New Worlds. They had spread over Europe and North America and were found in northern Africa as well. The whales must have made their appearance somewhere within the territory occupied by the Hyænodonts, and probably in the oldest part of the Tertiary; in agreement with this the most primitive cetacean that is yet known, the Hyænodont-like *Protocetus* of the family **Zeuglodontidæ**, is found in Egypt in Eocene strata. Likewise one of the next links in the chain of cetacean development, *Prozeuglodon*, was Egyptian, from the Eocene. But soon the members of the family must have spread widely; in any event the highest genus, the almost fantastic, snake-like *Zeuglodon* [*Basilosaurus*], appears to have found its way during the Eocene to all oceans.

The Zeuglodonts died out early in the Tertiary. Their highest forms left no descendants; but from the more primitive genera of the family sprang the new family **Balænidæ**. The oldest, tooth-bearing forms of Balænidæ are as yet scarcely known. In Miocene times, however, the family had already produced the specialized whalebone-bearing forms, a side branch on the cetacean genealogical tree, and they soon spread themselves to all the seas of the globe, where they still are found. Some of the recent genera are essentially cosmopolitan, even in the sense that individual species occur in all seas. This holds good in part only of *Balæna*, one of whose species, the more primitive, *B. australis*, is almost cosmopolitan, while the second, the more specialized, *B. mysticetus*, is confined to the northern polar oceans. It is literally true of *Balænoptera* and *Megaptera*. Two of the recent genera are confined to a smaller range: *Neobalæna* a relatively high genus that lives in the South Sea, where it likely originated, and *Rhachionectes* a relatively low genus, in many respects recalling extinct Miocene forms. It lives in the northern part of the Pacific, perhaps as a kind of last remnant from an early day. The reason why the Balænidæ, in spite of their rather primitive structure, are not wholly extinct, supplanted by the more specialized cetacea, is probably because they have chosen a peculiar food supply: the small creatures of the sea. Therefore they do not have very many competitors among their kind.

From the most primitive, tooth-bearing Balænidæ the family **Squalodontidæ** branched off in Tertiary times. It had its flourishing period in the Miocene, widely distributed in the oceans. The whole family disappeared before the end of the Tertiary, chiefly, it would appear, because it passed onward into its successors.

The descendants of the primitive Squalodonts are the members of the family **Platanistidæ** which appeared early in the Tertiary and was soon widely distributed. Most of the genera have died out again; only four, *Pontoporia* [*Stenodelphis*], *Lipotes*, *Inia* and *Platanista*, have come down to the present time. These have doubtless avoided being crowded out by higher cetaceans purely because they have chosen a peculiar habitat, rivers and estuaries, which they have been almost alone in utilizing.

Early in the Tertiary the family **Delphinidæ** branched off from primitive Platanistids. Extinct genera, especially in the Miocene, are known from localities that were even then far apart; at present the family is universally distributed, many of the genera and species being nearly cosmopolitan. The family seems to be having its flourishing period now. Only a few of the recent genera have ranges that are somewhat restricted, as *Delphinapterus* and *Monodon* in the Arctic Ocean, *Tursio* [*Lissodelphis*] in the Pacific, *Orcella* in the rivers of Southeast Asia and in the neighboring sea, *Neomeris* [*Neophocæna*] on the eastern and southern coast of Asia and the east coast of Africa.

Early in the Tertiary the family **Physeteridæ** originated from the most primitive Delphinids. It had already reached its climax in the Pliocene, widely distributed. Only rather few genera, but these very highly developed, have come down to the present day. They are widely distributed, essentially cosmopolitan.

NOTES

¹ (P. I.) The present treatise on Cetacea is a continuation of the series of memoirs on the other orders of mammals which have appeared in *E Museo Lundii*, vols. 1-3, 1887-1915, and in the *Vidensk. Medd. Dansk Naturhist. Foren.*, vol. 68, 1917. Part of the opinions that are here expressed have been previously published in the *Vidensk. Medd. Dansk Naturhist. Foren.* for 1882, pp. 29-31, 40 and 53-55; *ibid.*, for 1909, pp. 5-9; *Meddelelser om Grønland*, pt. 21, 1902, pp. 364-368; *Danmarks Fauna*, Pattedyr, 1908, pp. 9-10, 200-209.

² (P. I.) On the origin of the Cetacea very different opinions have been put forward. The idea of Brandt and others that the Cetacea are the lowest, most reptilian mammals is now shared by scarcely any one. Likewise the old idea of the relationship with sea-cows was long ago laid aside. Flower's early opinion that the whales originated from seals, an opinion which he shared with others, was disputed by Winge (*Vidensk. Medd.*, 1882, pp. 53-55) and almost abandoned by Flower himself. It was not taken up by others except in a way by D'Arcy Thompson. D'Arcy Thompson's opinion (*On the Systematic Position of Zeuglodon*; *Studies from the Museum of Zoology in University College, Dundee*, vol. 9, 1890, pp. 1-8, with illustrations) that the Zeuglodonts, really the most primitive whales, are not Cetacea, but near relatives of the seals, is disproved by Lydekker (*Proc. Zool. Soc. London*, 1892, pp. 560-561) and Dames (*Ueber Zeuglodonten aus Aegypten, etc.*; *Palaeont. Abhandl., herausgeg. von Dames u. Kayser*, vol. 5, pt. 5, 1894, section pp. 204-210). Flower's ideas about the whale's relationship to particular ungulates proper other than sea-cows have also shown themselves to be incorrect. The author who has most extensively examined the question in earlier times is Max Weber in his book: *Studien über Säugethiere, ein Beitrag zur Frage nach dem Ursprung der Cetaceen*, 1886, which contains a review of earlier work on the subject. His own conception of the history of the Cetacea was then "dass sie einem generalisirten Säugethiertypus im mesozoischen Zeitalter entstammen, der zwischen Carnivora und Ungulata mitten inne steht, wohl aber nähere Beziehungen zu Carnivora hatte" (*l. c.*, p. 241). In his work *Die Säugethiere*, 1904 (p. 581), Max Weber sets forth the idea that "primitive Condylarthrer" were perhaps most nearly the precursors of the whales.

Solid ground was first reached with the discovery of *Protocetus atavus* described by Fraas (Neue Zeuglodonten aus dem unteren Mitteleocän von Mokattam bei Cairo; Geol. u. Palæont. Abhandl., herausgeg. von Koken, vol. 10, pt. 3, 1904. There could be no doubt that *Protocetus* came from Hyænodonts and that it was itself a forerunner of the Zeuglodonts. Curiously, however, Fraas thought that the origin of the Cetacea was not thereby explained. He considered both *Protocetus* and with it the other Zeuglodonts as a side branch from the carnivores which did not lead in the direction of the true whales. There seems now, however, to be unanimity of opinion that *Protocetus*, *Prozeuglodon*, etc., are some of the long sought progenitors of the whales. In spite of all differences from the higher Cetacea there is a multitude of resemblances to them which it would be impossible to explain except on the basis of relationship. One has only to think of the striking likeness in such peculiarly formed bones as the tympanic and scapula; their characters in the fossils are exactly those that one would expect to find in ancestral Cetacea.

It has been said that the whalebone whales and the toothed whales might have separate "diphyletic" origins; Kükenthal in particular has spoken for this view (Ueber die Anpassung von Säugethieren an das Leben im Wasser; Zool. Jahrbücher, Abth. für Systematik, etc., vol. 5, 1891, pp. 373-399, especially p. 384, and elsewhere). In face of the host of agreements in numerous structural relationships which are found in the two groups this idea is an impossibility. Just one little bone like the tympanic, with its thickened inner wall, its mussel-shaped outgrowth around the outer auditory aperture, its petrous process which reaches out under the mastoid, and other details, all of the most peculiar form, and all essentially identical in all Cetacea, is sufficient evidence of the near relationship of all whales.

Kükenthal has put forward a "Versuch, den Bau des Walkörpers von biologischen Gesichtspunkten aus zu erklären," most elaborately in Die Wale der Arktis, Fauna Arctica, vol. 1, pt. 2, 1900, section pp. 181-203.

³ (P. 3.) We owe to Abel a special treatise on the skeleton of the hind limb in Cetacea: Die Morphologie der Hüftbeinrudimente der Cetaceen; Denkschr. d. math. -naturw. Klasse d. k. Akad. d. Wissensch. Wien, vol. 81, 1907, pp. 139-195, with illustrations. A supplement is given by Lönnberg: The Pelvic Bones of Some Cetacea; Arkiv för Zoologi, vol. 7, No. 10, 1910, pp. 1-15, with illustrations.

* (P. 4.) Much information about the structure of the hand in the Cetacea has been collected by Kükenthal (Die Hand der Cetaceen; Denkschr. d. med. naturw. Ges. zu Jena, vol. 3, pt. 1, 1889, pp. 23-69, pl. 3, and the section "Die Brustflosse," in Vergl. -anat. u. entwicklungsgesch. Unters. an Walthieren, *ibid.*, pt. 2, 1893, pp. 267-312, with illustrations) and Kunze (Ueber die Brustflosse der Wale; Zoologische Jahrbücher, Abt. für Anatomie, etc., vol. 32, pt. 4, 1912, pp. 577-651, pls. 33-35), both of whom give references to earlier works.

Kükenthal regards it as most probable that the large number of phalanges in the Cetacea has originated as follows: That the diaphyses and epiphyses in an ordinary hand whose fingers had mostly three phalanges have loosened themselves from each other, and have become independent and uniform, all of them ossified. This explanation cannot possibly be right. It is immediately contradicted by the fact that in cetacean hands with many-jointed fingers there can be found both diaphyses and epiphyses, ossified, in the larger of the phalanges that are present, as Kükenthal himself has observed. If one examines series of adult cetaceans' hands or of embryo hands, it is quite impossible to detect anything that could point in this direction. It certainly should be possible to find, somewhere or other, transition forms which would show indication that the phalanges were of unlike origin, some of them diaphyses, others epiphyses; but of this there is not the slightest evidence. Neither is it probable that the forerunners of the whales among terrestrial animals, had, even when young, epiphyses at both ends of all the phalanges, as would be needed in order to explain even tolerably the large number of joints in the Cetacea. It is true that in the Cetacea there have arisen supernumerary ossified epiphyses, more epiphyses than in their ancestors. But let it be noted that this has only happened in those Cetacea that already had acquired many-jointed fingers. (The objection to the "epiphysis-hypothesis" that it could at most explain the presence of only 12 joints in the fingers, including the metacarpal, and that it therefore cannot hold good where the number of joints is more than 12, is met by Kükenthal with the admission that in such instances the number of joints is actually increased out beyond the finger tips. *l. c.*, 1893, p. 311.)

Another explanation which is more probable Kükenthal himself sets forth but regards as less happy: "Würde man die Entwicklungsgeschichte allein zur Lösung der Frage heranziehen, so würde sich der Schluss ergeben, dass ausser den vier typischen Finger-

elementen sich immer neue anlegen, indem sie sich, in distaler Richtung aufeinander folgend, in dem sich immer weiter vorschiebenden embryonalen Bindegewebe entwickeln, so dass die letzte Phalanx die jüngste ist" (*l. c.*, 1893, p. 311). Kükenthal finds a reason to reject this opinion in the fact that Leboucq and he have occasionally found something on the outermost tip of one of the digits of a long-fingered porpoise hand which might be interpreted as the weakest remnant of a nail. Should it prove that remnants of a nail are found on the extreme tip of the finger, says Kükenthal, this "hypothesis" concerning the origin of the many phalanges cannot be correct, "denn dann entspricht die Spitze der Walflosse und damit die Spitze von deren Fingern auch der Spitze der Finger der typischen Vorderextremität" (*l. c.*, 1893, p. 312). This objection cannot hold; there is certainly nothing to prevent that the atrophied remnant of a nail should constantly retain its position on the finger tip as this pushes outward further and further, whatever the method by which the finger is elongated.

⁵ (P. 5.) A special treatise on the cervical vertebræ of the Cetacea is due to Reche: *Ueber Form und Funktion der Halswirbelsäule der Wale*; Inaugural-Diss., 1904, with illustrations. See also De Burlet: *Beitrag zur Entwicklungsgeschichte der Wirbelsäule der Cetaceen*; *Morphol. Jahrb.*, vol. 50, pt. 3, 1917, pp. 373-402, with illustrations.

⁶ (P. 7.) On the tympanic bone and its surroundings in the Cetacea, see especially: Van Kampen, *De Tympanaalstreek van den Zoogdierschedel*, 1904, pp. 299-316. Contains references to earlier papers on the subject. On the ear-bones themselves, see especially: Doran, *Morphology of the Mammalian Ossicula Auditus*; *Trans. Linn. Soc. London*, ser. 2, Zoology, vol. 1, 1878, pp. 450-464, pls. 62, 63.

⁷ (P. 9.) The opinion that the increase in the number of teeth in the Cetacea above the typical eutherian number was perhaps initiated by the intercalation of milk teeth in the permanent set was expressed in 1882 (*Vidensk. Medd. for 1882*, pp. 31 and 40) at a time when no trace of tooth succession had yet been detected in whales. The same opinion was maintained by Max Weber (*Urspr. der Cetaceen*, 1886, pp. 195 and 199), but he abandoned it (*Die Säugethiere*, 1904, p. 567) after Kükenthal had demonstrated indications of the tooth succession. Kükenthal had found traces of germs of both forerunners and successors to the teeth which stand in the Cetacea as the permanent set (but which he considered as milk teeth). Perhaps the idea is wrong; but there is nothing in that which has thus far been discovered which

makes its abandonment necessary, inasmuch as only a part of the milk dentition, only four cheekteeth, were ever supposed to be intercalated in the permanent set (it was expressly said that an increase in the number of cheekteeth by other means, by division or by the formation of new elements, was necessary as an explanation when the number exceeded 11 in each jaw); and the milk dentition could perhaps be made whole again after having given up some of its contents. In any event it is impossible to trace in detail the destiny of the tooth-germs through their erratic course during atrophy; there are many possibilities.

In spite of all investigations during recent years into the development of cetacean dentition both embryologically and phylogenetically, no certain conception has been reached. Only this is certain, that the cetacean dentition is derived from the typical carnivore's, that the teeth are increased in number while their size is decreased and their form made more simple, and that the tooth succession has essentially ceased, although in embryos there can still be detected traces of several sets of teeth, as in many other mammals, faint mementos of their forefathers among the reptiles. But of how the changes have in detail come about we can only partly guess.

Abel is the author who has most recently reviewed the present question. He believes that he can more nearly show how the high number of teeth has arisen in the Cetacea; in the whalebone whales he thinks it came about in one way, and in the toothed whales, or at least in the Physeterine series, in another. But his arguments are not irrefutable.

As regards the whalebone whales Abel starts from Kükenthal's investigations. As has long been known from observations by Geoffroy Saint-Hillaire and especially by Eschricht, there is found in embryos of all recent whalebone whales, hidden in each jaw, a long row of small atrophied teeth with conical or knob-shaped crowns, which are resorbed without ever erupting. Frequently some of these small teeth are seen to be mutually united; most often it is two that come together but in rare instances as many as four may unite. A part of his observations on the embryonic teeth of *Balaenoptera musculus*, the species which he has had especially good opportunity to investigate, Kükenthal summarizes in the following words: "Die Zahl der Zähne im Oberkiefer des letzteren Embryos (that is, the largest of those examined) ist 53; sie liegen sämmtlich in gleich weiten Abständen von einander. Bei den kleineren Embryonen beträgt die Zahl der Oberkieferzähne, wenn wir die mit zwei resp.

drei Höckern versehenen Zähne als je einen Zahn rechnen, etwas weniger, und zwar haben alsdann die kleinsten Embryonen die geringste Zahnzahl. Zählen wir jedoch in jedem Oberkiefer die einzelnen Höcker, so erhalten wir gleichzeitig für jeden Kiefer die Zahl 53, dieselbe Zahl, welche wir auch bei dem grössten untersuchten Embryo, der keine Doppelzähne besass, aufgefunden haben. Ich habe aus dieser Thatsache bereits den Schluss gezogen, dass sich im Laufe der individuellen Entwicklung der Bartenwale die Zähne theilen, und dass somit aus den verhältnismässig wenigen, aber mehrhöckerigen Zähnen der jüngsten Stadien viele, aber einspitzige Zähne werden. Aus den ursprünglichen Backzähnen entwickelte sich also durch Theilung derselben ein anscheinend homodontes Gebiss. (Unters. an Walthieren; Denkschr. med. naturw. Ges. Jena, 1893, p. 431). On this Abel builds further. He considers that *Patriocetus* (see pp. 70-72), a Tertiary whale with rather well-developed dentition, with unicuspid incisors and canines, and with serrate margins to the cheekteeth, is an ancestral form of the true whalebone whales—their immediate precursor. In passing to the whalebone whales its teeth would be split up and the marginal cusps would be transformed into independent teeth: “Wie wir gesehen haben, besteht das Gebiss von *Patriocetus ehrlichi* aus sieben zweiwurzigen und siebenspitzigen Backenzähnen, von denen die drei hinteren als Molaren und die vier vorderen als Praemolaren zu deuten sind. Daran schliessen sich vorne ein einspitziger Eckzahn und die drei einspitzigen Schneidezähne an. Im ganzen stehen also 11 Zähne in jedem Kiefer.—Wenn wir die Spitzen der Zähne zusammenzählen, so dass wir nicht nur die Kronenspitzen der vier vorderen Zähne, sondern auch die sieben Zacken der sieben zweiwurzigen Backenzähne als Einzelspitzen rechnen, so ergibt sich eine Gesamtsumme von 53 Spitzen, also genau derselben Zahl, die wir bei dem in Einzelzähne aufgelösten Gebiss des Finwalembryos wiederfinden.—Nach diesem Befunde kann es keinem Zweifel mehr unterliegen, dass das *Patriocetus*-Gebiss mit elf Zahnindividuen und zusammen 53 Schmelzspitzen den Ausgangspunkt des Bartenwalgebisses darstellt und dass die Entstehung des letzteren in der Weise erfolgt, dass die elf Zähne sich im Verlaufe der ontogenetischen Entwicklung in 53 Teile spalten, so dass also schliesslich aus einem siebenspitzigen Backzahn sieben einzelne Spitzen durch Teilung und fortschreitenden Zerfall hervorgehen. (Die Vorfahren der Bartenwale; Denkschr. Akad. Wissensch. Wien, mathem. naturw. Kl., Bd. 90, 1914, pp. 186-187).—Several objections must be raised to Abel's presentation of the subject.

Everyone who has had to do with counting the teeth of cetaceans knows how variable the numbers may be. It is almost a miracle that Kükenthal should have been able to find five or six embryos, or perhaps more, of *Balænoptera musculus*, each of which had 53 teeth or tooth cusps in the upper jaw (see Kükenthal's more special account in *Jenaische Zeitschrift für Naturwissenschaft*, vol. 26, 1892, p. 481, together with his paper of 1893, *l. c.*; in three other jaws the numbers were less, a circumstance said to be accounted for by the fact that some of the teeth had been resorbed). But even if it should prove that *B. musculus* always had 53 teeth in each jaw of the embryo this fact would be without bearing on the question of the original dentition in the whalebone whales. It will occur to nobody to regard *B. musculus* as one of the most primitive species of the genus; on the contrary it is one of the highest, being one of the largest and most elongated. Other species are found in the genus that stand on a lower level; this holds good especially of *B. rostrata*, and in this species Eschricht has found the number of teeth in two embryos to

be respectively $\frac{40}{40} \pm$ and $\frac{44}{40}$ (Unders. over Hvaldyrene, pt. 3, 1845, pp. 314 and 316-317). In two embryos of the same species Kükenthal found 41 in the lower jaw (*Jen. Zeitschr.*, 1892, pp. 485-486). In two embryos of one of the highest species of the genus, *B. gigas (sibbaldii)* Kükenthal found 50 in the upper jaw (*l. c.*, p. 486). In several embryos of *Megaptera boops* Eschricht has found from 46 to 51 teeth in each side of the upper jaw, and in the lower jaw rather fewer, the least number 42 (*l. c.*, pp. 311 and 316). Abel says, it is true: "Bei jenen Bartenwalen, deren Kiefer eine geringere Zahl als 53 Zahnindividuen aufweisen, handelt es sich entweder um frühere Embryonalstadien, wie bei dem von C. Julin beschriebenen Embryo von *Balænoptera rostrata* von etwa 48 cm. Länge (41 Zähne), oder um Reduktionserscheinungen" (*l. c.*, p. 188); but this assumption is entirely inadmissible. Abel himself probably had an inkling of it; he adds: "In dieser Frage müssten noch eingehendere Untersuchungen auf breiterer Grundlage angestellt werden, um unsere bisherigen Kenntnisse in dieser Richtung zu erweitern."

Neither can all of what Abel says about the number of teeth or cusps in *Patriocetus* stand before a closer examination. It is not certain that *Patriocetus* had 11 teeth in each jaw; none of the skulls that have been found has entire jaws, the anterior part is lacking in them all. The number 11 is therefore only a guess, and scarcely very likely; judging from the rest of the cranial characters one would

expect a departure from the typical dentition—more teeth. Of the cheekteeth there are only known a few that are tolerably complete; that every one of them had seven marginal cusps is mere conjecture and not probable; in other cetacea with serrate teeth, both Zeuglodonts and Squalodonts, the number of cusps varies strongly; no cetacean is known in which the same number of cusps is found on all the cheekteeth. Some dissociated teeth that probably are correctly referred to *Patriocetus* (*Squalodon chrlichii*), figured by Suess (Neue Reste von Squalodon aus Linz; Jahrb. d. k. k. geol. Reichsanstalt, vol. 18, 1868, pp. 287-290, pl. 10, figs. 1-3) and reproduced by Brandt (Unters. foss. u. subfoss. Cetaceen Europa's; Mém. Acad. Imp. Sci. St. Pétersbourg, ser. 7, vol. 20, No. 1, 1873, pl. 31, figs. 11-13), also show other numbers, one of them 9, another 10. Moreover it is doubtful whether *Patriocetus* can be regarded as an ancestor of the whalebone whales; it is not precluded that with more exact acquaintance it will show itself to stand on a higher level, nearer to the typical Squalodonts, closely connected with *Agorophius* (see note, p. 72). In short the whole calculation about the 53 teeth in the whalebone whales and the 53-tooth cusps in *Patriocetus* rests on the weakest foundation.

It is also a question whether Kükenthal and Abel are on the whole right in their conception of the many small teeth of the whalebone whales as having originated by the division of fewer, larger, serrate teeth. There is indeed scarcely any doubt that a division of the tooth germ might be able to take place at an early stage of a tooth's development; but that a tooth which had already acquired serrate margins should be able to divide is not probable; in the case of the whalebone whales at any rate there is nothing convincing in this respect—quite the contrary; and other cases are not known. The "double-teeth" of the embryo whalebone whales are the ones that are conceived to be serrate teeth in course of division; but they could be better explained in another manner. Their position in the toothrow is quite erratic—sometimes far to the front, sometimes in the middle or far back. The number of cusps is most often two, only in rare instances as many as four. The cusps have the appearance of being of equal rank, none can be called the chief cusp. In short, the cusps in the double teeth appear to be small, atrophied, unicuspid teeth which have quite casually come near each other and grown together, something which might be able to take place with special ease in the youngest stages of the embryo when the tooth germs are crowded together in relatively short jaws. That double teeth were produced

by the fusion of single teeth was already supposed by Eschricht (*l. c.*, p. 312). Should it be the case that there has taken place in the whalebone whales a splitting up of serrate teeth, the corresponding ancestral forms must probably have had teeth in which the cusps on the fore and hind margins of the crown had great independence and a size very nearly the same as in the principal cusp. In that event it would not be easy to regard *Patriocetus* as an ancestor; since in it the cusps on the fore and hind margins particularly are weak in proportion to the main cusp, and apparently in course of atrophy.

Abel gives the following as his conception of the manner in which the many small teeth of the Odontoceti, or at least of the Physeterids, have arisen: "Dieser Spezialisationsweg des Gebisses (in the whalebone whales) ist fundamental von jenem verschieden, den wir in der Phylognese des Physeteridengebisses finden. Wie ich 1905 gezeigt habe, tritt auf dem Wege zur Entstehung der Squalodontiden zunächst eine starke Vermehrung der mehrwurzeligen, vorn und hinten gezackten Backenzähne ein, so dass sich das primitive Archaeocetengebiss durch Vermehrung der Backenzähne im Prämolarenabschnitt zu dem polyodonten Squalodontidengebiss umformt. Aus den Squalodontiden sind die Physeteriden hervorgegangen, bei welchen das Gebiss eine Reduktion erfährt; dieser Spezialisationsweg führt aber zu einer Vereinfachung der Krone, Verschmelzung der bifiden Wurzeln, Reduktion der Zackenreihen am Vorder- und Hinterrande der Kronen zu einer krenelierten Leiste und endlich zum ganzlichen Verlust der Schmelzkappen" (*l. c.*, p. 187). Here Abel is no doubt right in the main. It can only be objected that it cannot exactly be said that Abel in his more special account (*Die phylogenetische Entwicklung des Cetaceengebisses und die systematische Stellung der Physeteriden*; Verhandl. Deutsch. Zool. Gesellsch., 1905, pp. 84-96, and *Les Odontocètes du Boldérien*; Mém. Mus. Roy. d'Hist. Nat. de Belgique, vol. 3, 1905) has demonstrated that it is precisely in the premolar region that the number of teeth has been increased in the Squalodonts; neither is it probable that the Physeterids originated directly from the Squalodonts. They appear to have branched off at a higher level; probably they had their root in common with the Delphinids.

There is no reason at the present stage for believing that the increase in the number of teeth beyond the typical formula should have had a different origin in the Mystacoceti and Odontoceti. In view of the great resemblances that are everywhere found between the two groups it is not likely that in this respect there would be a

difference. The method by which the increase has come about in the Odontoceti no doubt holds good for the Mystacoceti as well; the most primitive forms of probably both groups had serrate teeth in augmented numbers.

⁸ (P. 10.) It has become usual to believe that the precursors of the cetaceans were armored mammals with well-developed osseous dermal plates. Heated support for this idea is brought forward by Kükenthal (especially in the section "Ueber Rudimente eines Hautpanzers bei Zahnwalen," in *Vergl. -anat. u. entwicklungsgesch. Unters. an Walthieren*, part 2, *Denkschr. d. med. naturw. Ges. zu Jena*, vol. 3, pt. 2, pp. 251-258, pl. 16) and by Abel (especially in the section "L'armure dermique," in *Les Dauphins Longirostres du Boldérien*, *Mém. Mus. Roy. d'Hist. Nat. de Belgique*, vol. 1, 1901, pp. 17-32, with illustrations). Kükenthal has investigated recent cetaceans; Abel more particularly the extinct forms. (In Abel is found reference to previous literature on the subject.) Kükenthal imagines that the Cetacea originated from armored land-mammals with armor suggesting that of the Dasypodids, and that as sea dwellers they have lost the armor more or less completely; Abel thinks, in agreement with Dollo, that the armature did not occur in the terrestrial precursors of the cetaceans, but that it arose in the first whales as part of their adaptation to aquatic life along the coast, and that afterwards it was lost in the more strictly marine members of the group.

What we have to build upon is the following:

Together with the first lot of *Zeuglodon* bones found in Alabama came a few pieces of limestone containing some plate-like, very irregular bones of various sizes. Accounts of these bones are due especially to Joh. Müller (*Ueber die fossilen Reste der Zeuglodonten von Nordamerika*, 1849, p. 34, pl. 27, fig. 7), Carus (*Das Kopfskelet des Zeuglodon hydrarchus*; *Nova Acta Acad. Caes. Leop. Carol.*, vol. 22, pt. 2, 1850, pp. 382-383, pl. 39A, fig. 5), Dames und Jaekel (section *Ueber den Hautpanzer der Zeuglodonten*, in *Dames, Ueber Zeuglodonten aus Aegypten*, *Palaeontol. Abhandl., herausgeg. v. Dames u. Kayser*, vol. 5, pt. 5, 1894, pp. 219-221, with illustration) and Abel (1901, *l. c.*, pp. 24-27). From the beginning the possibility has been thought of that the plates were dermal bones of *Zeuglodon*. They have, however, most often been regarded as doubtful; perhaps they were bones from the carapace of a sea turtle like *Psephophorus* or something of the sort; usually no one has dared to say anything positive. Abel was the first to consider it as proved that they were dermal bones of *Zeuglodon*; of one of the specimens in question he

thinks that it can be nothing else than a piece of armor from the fore angle of a dorsal fin, because the plates are bent toward each other like a roof, in a manner and form that is not possible on any part of a turtle's carapace. As a not unessential ground for believing in the occurrence of armor in *Zeuglodon* he reckons the occurrence in the recent Delphinids *Neomeris* and *Phocæna* of structures which Kükenthal explains as remnants of armor.

At Radoboj in Croatia some remains have been found of a small dolphin-like cetacean, *Delphinopsis freyerii*, established and described by Joh. Müller (Bericht über ein neu entdecktes Cetaceum aus Radoboy, *Delphinopsis Freyerii*; Sitzungsber. k. Akad. Wissensch. Wien, math. naturwiss. Cl., vol. 10, 1853, pp. 1-6 of separate), and again fully discussed and figured by H. v. Meyer (*Delphinopsis Freyerii* Müll. aus dem Tertiär-Gebilde von Radoboj in Croatien; *Palaeontographica*, vol. 11, 1863, pp. 226-231, pl. 34) whose illustration is reproduced by Abel (*l. c.*), who also has personally examined the remains. It was only imperfect remains that were found, not much more than pieces of a flipper lying in a slab of stone; around the bones of the hand lie numerous small disk-shaped bodies a millimeter or less in diameter, the underside of which is covered with minute projecting granules arranged in parallel lines. Joh. Müller seems to have left undecided the question whether these bodies were of organic or inorganic origin, although he leaned mostly to the opinion that they were osseous scales from the skin. But H. v. Meyer maintained that they were inorganic. His reason for this opinion was especially that scattered among them there lie bodies of entirely similar appearance only without markings, and these bodies are undoubtedly inorganic. Abel on the contrary is convinced that the small, striated disks are dermal ossicles.

In *Neomeris*, which lacks or as good as lacks the dorsal fin, the skin of the back in the place where the fin is found in its relatives, and also somewhat further forward and backward, is divided into small, rather regularly placed plates, each bearing a small elevation. Similar small knobs are found, though not always, in the nearly related genus *Phocæna*, along the anterior surface of the dorsal fin and sometimes also scattered in other regions. Kükenthal, who has closely examined these structures, thinks that they are a kind of scale, although they have in their intimate formation only to a slight degree the characters that are found in scales. The explanation given is that they are

scales which are in process of atrophy—on the way to disappearing. A concurrent reason to regard them as scales is that traces of a scaly covering are found in some extinct whales, *Zeuglodon* and *Delphinopsis*.

But to Kükenthal's and Abel's conception there is something to oppose.

It has been shown that the Hyænodonts, the most primitive carnivores, are the precursors of the Cetacea among terrestrial mammals. Remains of Hyænodonts are found in great numbers in many localities; but there has never been discovered the slightest indication that any Hyænodont or any other carnivore has been armored. Remains of Zeuglodonts are found in various parts of the world, but nowhere except in the case of the specimens from Alabama have dermal ossicles been demonstrated in connection with the skeletons. If there had been a dermal armature it certainly would have been found somewhere or other. Besides, it cannot be said to be proved that the plates from Alabama are not those of some kind of turtle. Anyone who has seen the roof-shaped keel on a *Psephophorus* carapace, and has seen the fragments of the carapace mixed up together, will not allow himself to be persuaded by Abel's word in this connection. Finally it is improbable that *Zeuglodon* had a dorsal fin, since this fin may be absent (probably not-developed rather than lost) in diverse recent cetaceans, both Balænid and Delphinid.

The minute plates in *Delphinopsis* are altogether too uncertain to give any evidence. Their characters are, besides, so far from recalling what is otherwise known of dermal bones that one is tempted rather to regard as an error their determination as such structures.

The small callosities in the skin of *Neomeris* and *Phocæna* are scarcely the remains of a dermal armature, they are rather entirely new structures. It is too suspicious that nothing of the sort should be present in lower Cetacea, but that it should be in exactly some of the very highest that it is found. The structure of the callosities, moreover, gives no real support to the idea that they are scales.

Altogether there is no proof that the Cetacea or their ancestors among the mammals ever have had dermal armature.

° (P. 10.) For comparison a few of the most important and most independent synopses of the groups of Cetacea are here given.

A fundamental work in the direction of throwing light on the mutual relationships of the Cetacea is due to Flower, who, however, took into consideration the recent forms only. In 1866 (69), in his

paper on *Inia* and *Pontoporia* (Trans. Zool. Soc. London, vol. 6, p. 115), he gave the following synopsis:

Cetacea.

I. *Mystacoceti* or *Balaenoidea*.

Balaenida.

Balaeninae: Balaena, Eubalaena.

Balaenopterida.

Megapterinae: Megaptera.

Balaenopterinae: Physalus, Sibbaldius, Balaenoptera.

II. *Odontoceti* or *Delphinoidea*.

Physeterida.

Physeterinae: Physeter, Kogia.

Ziphiinae: Hyperoodon, Berardius, Ziphius, Dioplodon,
Micropteron.

Platanistida.

Platanistinae: Platanista.

Iniinae: Pontoporia?, Inia.

Delphinida.

Beluginae: Monodon, Beluga (=Delphinapterus).

Delphininae?: Phocaena, Neomeris, Grampus, Orca, Pseudorca, Lagenorhynchus, Delphinus, Delphinapterus
(=Tursio), Globicephalus.

His conception of the relations between the genera in the family *Delphinida* Flower developed more fully in 1883 (Proc. Zool. Soc. London). His arrangement there was as follows:

A.

a. Monodon, Delphinapterus (Beluga).

b.

a. Phocaena, Neomeris.

β. Cephalorhynchus, Orcella, Orca, Pseudorca, Globiceps,
Grampus, Feresia, Lagenorhynchus.

B.

a.

a. Delphinus.

β. Tursiops, Clymenia, Steno.

b. Sotalia.

Flower followed essentially the same arrangement as that of 1866 and '83, but with greater clearness as to the genera, in 1891, in "An Introduction to the Study of Mammals Living and Extinct" which

be published in association with Lydekker. The arrangement is as follows:

Cetacea.

Mystacoceti, Balænoidea.

Balænidæ: Balæna, Neobalæna, Rhachianectes, Megaptera, Balænoptera. Extinct Genera: Cetotherium, Herpetocetus.

Archæoceti.

Zeuglodontidæ: Zeuglodon.

Odontoceti, Delphinoidea.

Physeteridæ.

Physeterinae: Physeter, Cogia. Extinct: Physeterula, Eucetus, Physetodon, Scaldicetus, Physodon, Hoplocetus.

Ziphiinae: Hyperoodon, Ziphius, Mesoplodon, Berardius. Extinct: Choneziphius.

Squalodontidæ: Squalodon.

Platanistidæ: Platanista, Inia, Pontoporia. Extinct: Palæopontoporia (Pontistes), Champsodelphis, Schizodelphis, Priscodelphinus, Lophocetus, Ixacanthus, Rhabdosteus, Agabelus.

Delphinidæ.

Group A. Monodon, Delphinapterus, Phocæna, Neomeris, Cephalorhynchus, Orcella, Orca, Pseudorca, Globicephalus, Grampus, Feresia, Lagorhynchus.

Group B. Delphinus, Tursiops, Prodelphinus, Steno, Sotalia.

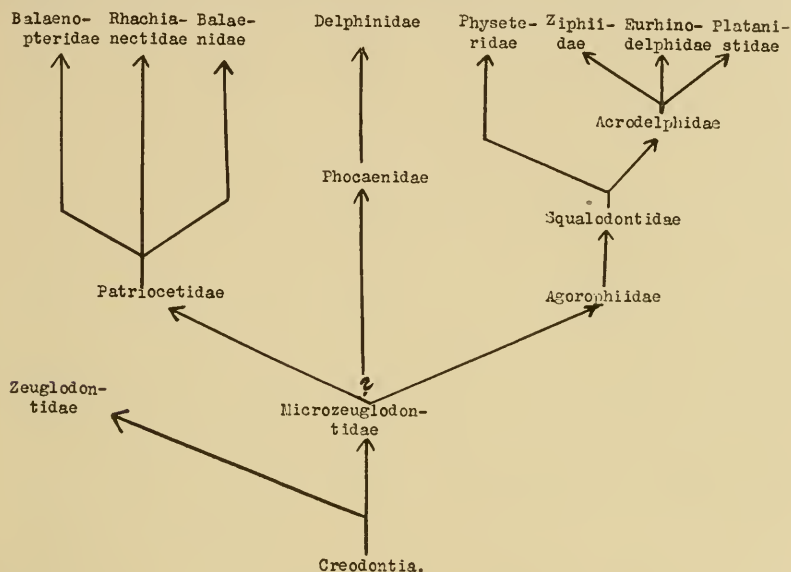
Max Weber (Die Säugethiere, 1904) agrees closely with the conception of Flower and Lydekker. One of the greatest differences is that a special family, *Rhachianectidæ* is established for *Rhachionectes* and also a family *Delphinapteridæ* for *Delphinapterus* and *Monodon*.

Abel has made special researches on the fossil Cetacea, and he has tried to determine their positions in relation to the recent forms. Besides what he has said on the subject in his special monographs, he has more or less completely set forth his ideas in the papers: Die Stammesgeschichte der Meeressäugetiere; Meereskunde, Sammlung volkstümlicher Vorträge, 1907; Grundzüge der Palaentologie der Wirbeltiere, 1912; and Die vorzeitlichen Säugetiere, 1914. He has not given any general synopsis except in the following genealogical tree, published in his work Die Vorfahren der Bartenwale, 1914

(Denkschr. k. Akad. Wissensch. Wien, math. -naturw. Kl., vol. 90, p. 221):

Die Stämme der Wale.

I. Mystacoceti (auct.) II. Delphinoceti (nov.) III. Squaloceti (nov.)
(Blütezeit im Pliocän.) (Blütezeit in der Gegenwart.) (Blütezeit im Miocän.)



(To the *Acrodelphidae* are referred, among the living genera, *Delphinapterus* and *Monodon*, *Inia* and *Pontoporia*.)

True's paper On the Classification of the Cetacea (Proc. Amer. Philos. Soc., Philadelphia, vol. 47, 1908, pp. 384-391) is mostly an account of the opinions which Abel had expressed in 1905, with some objections and some assent.

To cetaceans both recent and fossil have been given various generic names in addition to those which appear in the present article. These names are partly well known as synonyms of others; but partly the corresponding animals are so slightly known that no certain opinion can be had about them. References to all the names theretofore used for cetaceans are found in Trouessart, *Catalogus Mammalium tam viventium quam fossilium*, 1897-99, with supplement, 1904-5, and in Palmer, *Index Generum Mammalium*, 1904; many names are also to be found in Beddard, *A Book of Whales*, 1900; detailed references to the North American fossil genera are due to Hay, *Bibliogr. and Catal. of the fossil Vertebrata of North America*, Bull. U. S. Geol.

Surv., No. 179, 1902. Incorrectly formed names which cannot be accepted as finally settled are, in the present treatise, marked with “ ”.

¹⁰ (P. 13.) The backbones of the Egyptian “*Zeuglodon*” *osiris* with its short vertebræ (especially Stromer, Beitr. Paläontol. u. Geol. Oesterreich-Ungarns, etc., vol. 21, 1908, pl. 4, fig. 1), and those of the American *Z. cetoides* with its long vertebræ (especially Gidley, Proc. U. S. Nat. Mus., vol. 44, 1913, p. 81) differ to such a degree that according to ordinary standards the placing of these animals in the same genus, as has hitherto been done, is certainly out of the question. *Z. cetoides* is the type of the genus *Zeuglodon*. By accident no special name has been proposed that can with full right be used for the genus to which “*Zeuglodon*” *osiris* belongs. But the name *Prozeuglodon* seems to have become vacant and may therefore with some propriety be used. It was proposed by Andrews (especially Tert. Vertebr. of the Fayûm, Egypt, 1906) for a lot of Eocene cetacean remains from Egypt which he united under the name *P. atrox*. But according to Stromer, the type of the species, a skull, and some of the other remains belong to the previously described *Zeuglodon isis*, which is probably correctly called *Zeuglodon*, while still others are referable to “*Z.*” *osiris*. In a way therefore “*Z.*” *osiris* has also been called *Prozeuglodon*. Possibly the name *Doryodon* (“*Dorudon*”) might be used for the genus in question with short vertebræ, or, if there are several genera with short vertebræ, for one of them (see, among others, Leidy, Journ. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 7, 1869, pp. 428, 431, and Lucas, Proc. U. S. Nat. Mus., vol. 23, 1900, p. 331). But *Doryodon* is still not sufficiently known, not even after True (Bull. Mus. Comp. Zool., vol. 52, 1908, pp. 65-78, pls. 1-3) has examined the fragments on which Gibbes founded the genus; the remains in question are altogether too incomplete. For the American “*Zeuglodon brachyspondylus minor*” Joh. Müller and Stromer, also with short vertebræ, which True compares with *Doryodon* and finds different, True (*l. c.*) proposes to erect a new genus, *Zygorhiza*; but the relationship between it and “*Zeuglodon*” *osiris* is not at all clear.

¹¹ (P. 15.) The pelvis and femur of *Zeuglodon cetoides* are described and figured by Lucas (Proc. U. S. Nat. Mus., vol. 23, 1900, pp. 327-331, pls. 5-7). Both right and left innominates were found associated with a backbone lying in the position relative to the vertebræ in which one would expect to find them. In spite of this circumstance Abel explained the bones in question as the coracoid of

a gigantic bird which he called "*Alabamornis*" *gigantea* (Ueber den als Beckengürtel von Zeuglodon beschriebenen Schultergürtel eines Vogels aus dem Eocän von Alabama, Centralblatt für Mineralogie, Geologie und Paläontologie, 1906, pp. 450-458, with illustrations). Stromer (Beitr. z. Paläont. u. Geol. Oesterreich-Ungarns, etc., vol. 21, 1908, p. 146) has expressed doubts as to the correctness of Abel's interpretation, and Gidley (Proc. U. S. Nat. Mus., vol. 44, 1913, pp. 649-654, with illustrations) who has re-examined the specimens, has entirely thrown it over. It can hardly be doubted that Lucas and Gidley are correct.

¹² (P. 15.) On the Zeuglodontidæ [Basilosauridæ] see especially: Joh. Müller: Ueber die fossilen Reste der Zeuglodonten von Nordamerika mit Rücksicht auf die europäischen Reste aus dieser Familie, 1849, pp. 1-38, pls. 1-27.

Carus: Das Kopfskelet des Zeuglodon hydrarchus; Nova Acta Acad. Cæs. Leop. Carol., vol. 22, pt. 2, 1850, pp. 373-390, pls. 39A & B.

Brandt: Untersuchungen über die fossilen und subfossilen Cetaceen Europa's; Mém. Acad. Imp. Sci. St. Pétersbourg, ser. 7, vol. 20, No. 1, 1873, pp. 291-313, 334-340, pl. 34. *Zeuglodon*.

Hector: Notes on New Zealand Cetacea, recent and fossil; Trans. and Proc. New Zealand Inst., 1880, vol. 13, 1881, pp. 434-436, pl. 18. "*Kekenodon*."

Lydekker: On Zeuglodont and other Cetacean Remains from the Tertiary of the Caucasus; Proc. Zool. Soc. London, 1892, pp. 558-561, pl. 36. *Zeuglodon*=in part *Microzeuglodon*.

Dames: Ueber Zeuglodonten aus Aegypten und die Beziehungen der Archæoceten zu den übrigen Cetaceen; Palaeontologische Abhandlungen, herausgeg. von Dames und Kayser, vol. 5, pt. 5, 1894, pp. 1-36, pls. 1-7.

Lucas: The Pelvic Girdle of Zeuglodon, Basilosaurus cetoides (Owen), with notes on other portions of the skeleton; Proc. U. S. Nat. Mus., vol. 23, 1900, pp. 327-331, pls. 5-7.

Abel: Les Dauphins Longirostres du Boldérien des Environs d'Anvers; Mém. Mus. Roy. d'Hist. Nat. de Belgique, vol. 1, 1901, pp. 8-9, 24-32. On the dentition and dermal armature in *Zeuglodon*.

Stromer: Zeuglodon-Reste aus dem oberen Mitteleocän des Fajûm; Beiträge zur Paläontologie und Geologie Oesterreich-Ungarns und des Orients, vol. 15, pts. 2 and 3, 1903, pp. 65-100, pls. 8-11. *Zeuglodon*=in part *Prozeuglodon*.

- E. Fraas: Neue Zeuglodonten aus dem unteren Mitteleocän von Mokattam bei Cairo; Geologische und Paläontologische Abhandlungen, herausgeg. von Koken, vol. 10, pt. 3, 1904, pp. 199-220, pls. 10-12. *Protocetus* and *Mesocetus*, later called *Eocetus*.
- Abel: Les Odontocètes du Boldérien d'Anvers; Mém. Mus. Roy. d'Hist. Nat. de Belgique, vol. 3, 1905, pp. 21-25. On the dentition in the Zeuglodonts.
- Andrews: A descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt, 1906, pp. 235-357, pls. 20-21. *Zeuglodon*, *Prozeuglodon*.
- Stromer: Die Urwale (Archaeoceti); Anatomischer Anzeiger, vol. 33, 1908, pp. 81-88, pl. 1. A short synopsis of the most important part of the contents of the next paper. In the explanation of plates the name *Zeuglodon* (*Dorudon*) *osiris* is used; in the succeeding paper this use of "*Dorudon*" is abandoned.
- Stromer: Die Archaeoceti des Aegyptischen Eozäns; Beitr. Paläontol. u. Geol. Oesterreich-Ungarns u. des Orients, vol. 21, 1908, pp. 106-178, pls. 4-7. *Protocetus*, *Eocetus*, *Zeuglodon*, *Prozeuglodon*.
- True: The fossil Cetacean, *Dorudon serratus* Gibbs; Bull. Mus. Comp. Zool., vol. 52, 1908, pp. 65-78, pls. 1-3. *Dorudon* (= *Doryodon*) and *Zygorhiza*.
- Gidley: A recently mounted Zeuglodon skeleton in the United States National Museum; Proc. U. S. Nat. Mus., vol. 44, 1913, pp. 649-654, pls. 81, 82 and text figures.

Kekcnodon was established by Hector (1881, *l. c.*) on remains from Eocene strata in New Zealand. That which has been found is not much else than a lot of loose teeth which show strong similarity to *Zeuglodon*; but it is impossible to get any certain idea of the exact generic relationships. Hall (Proc. Roy. Soc. Victoria, n. s., vol. 23, pt. 2, 1911, p. 262) refers it to the *Squalodontidae* but gives no reasons.

Microzeuglodon was established by Stromer (Beitr. Paläont. u. Geol. Oesterreich-Ungarns, vol. 15, 1903, p. 89) and accepted by Abel (Odontocètes du Boldérien, 1905, p. 35). The basis of the genus is Lydekker's *Zeuglodon caucasicus* (Proc. Zool. Soc. London, 1892, pp. 559-561, pl. 36), based on a few remains, not certainly belonging together, found in Tertiary strata in the Caucasus: a small piece of a lower jaw with four cheekteeth, only two of which are tolerably complete, a humerus and a caudal vertebra. The teeth are serrate on both fore and hind margins of the crown. Abel referred

it at first to the Squalodonts, later he put it in a separate family. It plays an important part in Abel's studies of cetacean descent, whether rightly or not time will perhaps tell; meanwhile the genus is altogether too slightly known for anything positive to be built on it.

Eocetus described by Fraas (first called *Mesocetus* Fraas, not of Van Beneden, not of Moreno) is thought to be a connecting link between *Protocetus* and *Zeuglodon*, with long vertebræ. The remains are still too uncertain for judgment to be passed.

¹³ (P. 19.) Kükenthal (Vergl. -anat., etc., Unters. an Walthieren; Denkschr. medic. -naturw. Ges. Jena, vol. 3, pt. 2, 1893, p. 291) thinks that the bone in the hand of *Balæna mysticetus*, which is ordinarily regarded as a remnant of the first finger, a first metacarpal, is not that, but a finger before the first finger, a *præpollex*, in spite of the fact that the same bone in *Balæna australis* (as can also be seen in two skeletons in Copenhagen) may bear two well-developed phalanges, something that is not elsewhere seen in any "*præpollex*." As to the longest finger, which is usually reckoned as the third, he believes that it is not the third but the second, and that the third is absent. The reason for this remarkable interpretation is probably a desire to find agreement with *Balænoptera*, in which he thinks he has proved that the third finger is the one which is absent, and not the first as is generally supposed. If the first finger were present in *Balæna* in a more or less atrophied condition, it would be reasonable to suppose that it was this finger which is absent in the nearly related *Balænoptera*, which has only four digits; but that belief Kükenthal will not allow. Occasionally he has found in *Balænoptera musculus* something resembling a few atrophied phalanges lying loose in the palm between the fingers that are usually called the third and fourth. These structures Kükenthal regards as remnants of the third finger and thus to be proof that it is the third finger which is absent in the tetradactylous hand. Protest against Kükenthal's interpretation has already been made by Braun and Kunze (see Kunze, Zool. Jahrb., Abth. f. Anat., etc., vol. 32, 1912, pp. 639-641). There can be no doubt that there is here a case of malformation, a supernumerary digit, a kind of doubling of one of the fingers. Tendencies in this direction are indeed not rare in cetaceans, which on the whole show great indifference as to details in the structure of their abnormal hand.

¹⁴(P. 21.) On the Balenidæ see especially (Of the numerous works that deal with cetaceans there are many others that might have a claim to be mentioned. The choice that has been made here and in the corresponding lists for other families is somewhat arbitrary.

Most attention has been paid to indicating papers that describe the various forms of cetaceans, and especially to those which contain illustrations of the fossil members of the order.):

Cuvier: *Recherches sur les Ossemens fossiles*, ed. 4, vol. 8, pt. 2. 1836, pp. 250-321, pls. 226-228, with figures of skulls and other skeletal parts of *Balæna*, *Balænoptera*, *Megaptera*, *Plesiocetus*, mostly under other names.

Eschricht: *Undersøgelser over Hvaldyrene*, 2 den Afhandl., *Anatomisk Beskr. af de ydre Fosterformer hos to nordiske Finhval-Arter*; Kgl. Danske Vidensk. Selsk. naturv. mathem. Afhandl., pt. 11, 1845, pp. 203-279. 3 dje Afhandl., *Om Fosterformerne i Bardehvalernes Ernærings- og Forplantelsesredskaber*; *ibid.*, pp. 281-320, pls. 1-4. 5 te Afhandl., *Finhvalernes Osteologi og Artsadskillelse*; *ibid.*, pt. 12, 1846, pp. 225-396, pls. 4-16. *Balænoptera*, *Megaptera*. Figures of skulls and other skeletal parts, of embryos and adults, of external and other characters.

Eschricht and Reinhardt: *Om Nordhvalen (Balæna mysticetus L.)*; Kgl. Danske Vidensk. Selsk. Skrifter, ser. 5, naturv. mathem. Afd., vol. 5, 1861, pp. 433-592, pls. 1-6. Figures of the exterior, the entire skeleton, the skull of adult and young and other parts of *Balæna*, of the skull of *Balænoptera* and *Megaptera*.

Malm: *Monographie illustrée du Baleinoptère trouvé le 29 Octobre 1865 sur la côte occidentale de Suède*, 1867, pp. 1-110, pls. 1-20, with figures of the exterior, some skeletal parts and other features of *Balænoptera carolinæ* = *B. gigas*, *sibbaldii*.

Eschricht: *Ni Tavler til Oplysning af Hvaldyrenes Bygning, med Forklaring af Reinhardt*; Kgl. Danske Vidensk. Selsk. Skrifter, ser. 5, naturv. mathem. Afd., vol. 9, 1, 1869. On plates 1 and 2 are found figures of the skull of embryo *Balæna japonica* = *B. australis*.

Van Beneden and Gervais: *Ostéographie des Cétacés vivants et fossiles*, text and plates, 1868-80, pp. 1-634, pls. 1-67. As regards illustrations, with respect to both recent and extinct Cetacea, the most sumptuous work that exists. *Balænid*s especially pp. 29-291, pls. 1-17.

Dwight: *Description of the Whale (Balænoptera musculus Auct.) in the possession of the Society, with remarks on the classification of Fin Whales*; *Mem. Boston Soc. Nat. Hist.*, vol. 2, 1871-78, pp. 203-230, pls. 6-7. Exterior and skeleton.

Brandt: *Untersuchungen über die fossilen und subfossilen Cetaceen Europa's*; *Mém. Acad. Imp. Sci. St. Pétersbourg*, ser. 7, vol. 20,

- no. 1, 1873, pp. 1-372, pls. 1-34. Contains a section, pp. 18-202, on the then-known fossil Balænidæ, among them *Cetotherium* and *Plesiocetus*. On *Patriocetus*, see under *Squalodontidæ*.
- Brandt: Ergänzungen zu den fossilen Cetaceen Europa's; Mém. Acad. Imp. Sci. St. Pétersbourg, ser. 7, vol. 21, No. 6, 1874, pp. 1-54, pls. 1-5. Contains a section on the whalebone whales, pp. 2-12, pl. 1.
- Capellini: Della Balena di Taranto confrontata con quella della Nuova Zelanda e con talune fossili del Belgio e della Toscana; Memorie dell'Accademia delle Scienze dell'Istituto di Bologna, ser. 3, vol. 7, 1877, pp. 1-34, pls. 1-3, with illustrations of exterior, skull, ear bones, nasal, cervical vertebræ, other skeletal parts, etc. *Balæna tarentina*=*B. australis*.
- Gasco: Intorno alla Balena presa in Taranto nel febbrajo 1877; Atti della Reale Accademia delle Scienze Fische e Matematiche, Napoli, vol. 7, 1878, pp. 1-47, pls. 1-9, with figures of exterior, skull, other skeletal parts, etc. *Balæna biscayensis*=*B. australis*.
- Gasco: La Balæna Macleayius del Museo di Parigi; Annali del Museo Civico di Storia Naturale di Genova, vol. 14, 1879, pp. 509-551. *Balæna australis*. Description of skeleton.
- Gasco: Il Balenotto catturato nel 1854 a San Sebastiano (Spagna), *Balæna biscayensis*, Eschricht, per la prima volta descritto; Annali del Museo Civico di Storia Naturale di Genova, vol. 14, 1879, pp. 573-608. Description of skeleton.
- Van Beneden: Description des Ossements fossiles des environs d'Anvers, 2 partie, Genres Balænula, Balæna et Balænotus; Annales du Musée Royal d'Hist. Nat. de Belgique, série paleontol., vol. 4, Text, 1880, pp. 1-83, Atlas, 1878, pls. 1-39. 3 partie, Genres Megaptera, Balænoptera, Burtinopsis et Erpetocetus, *ibid.*, vol. 8, 1882, Text, pp. 1-90, Atlas, pls. 1-109. 4 partie, Genre Plesiocetus; *ibid.*, vol. 9, 1885, Text, pp. 1-40, Atlas, pls. 1-30. 5 partie, Genres Amphicetus, Heterocetus, Mesocetus, Idiocetus et Isocetus; *ibid.*, vol. 13, 1886, Text, pp. 1-139, Atlas, pls. 1-75.
- Burmeister: Atlas de la Description Physique de la République Argentine, sec. 2, mammif., pt. 1, Die Bartenwale der Argentinischen Küsten, 1881, pp. 3-40, pls. 1-7. Mostly on *Balænoptera*. Figures of exterior, skull, vertebral column and other skeletal parts.
- Struthers: On the bones, articulations and muscles of the rudimentary hind-limb of the Greenland Right-Whale, *Balæna mysti-*

- cetus; *Journal of Anatomy and Physiology*, vol. 15, 1881, pp. 141-176, pls. 14-17; *ibid.*, pp. 301-321.
- [Holder: *The Atlantic Right Whales: A Contribution*; *Bull. Amer. Mus. Nat. Hist.*, vol. 1, No. 4, pp. 99-137, pls. 10-13. May 1, 1883. External characters and skeleton.]
- Malm: *Skelettdelar af Hval insamlade under Expeditionen med Vega 1878-1880; Bihang till K. Svenska Vet. Akad. Handlingar*, vol. 8, No. 4, 1883, section pp. 17-98, with figures of parts of skulls, etc., of *Rhachionectes* and *Balæna*.
- Tullberg: *Bau und Entwicklung der Barten bei Balænoptera Sibbaldii*; *Nova Acta Reg. Soc. Sci. Upsal.*, ser. 3, 1883, pp. 1-36, pls. 1-7.
- Delage: *Histoire du Balænoptera musculus échoué sur la plage de Langrune*; *Archives de Zoologie expérimentale et générale*, ser. 2, vol. 3 *bis*, 1885, pp. 1-152, pls. 1-21. Exterior and anatomy.
- H. P. Gervais: *Sur une nouvelle espèce de Mégaptère (Megaptera indica) provenant du Golfe Persique*; *Nouvelles Archives du Muséum d'Hist. Nat. de Paris*, ser. 2, vol. 2, 1887-88, pp. 199-218, pls. 18-20. Figures of skeleton and skull.
- Struthers: *Memoir on the anatomy of the Humpback-Whale, Megaptera longimana*; Reprint from the *Journal of Anatomy and Physiology*, 1887-89, pp. 1-189, pls. 1-6.
- Graells: *Las Ballenas en las costas oceánicas de España*; *Mem. Real Acad. Cien.*, Madrid, vol. 13, pt. 3, 1889, pp. 1-115, pls. 1-9. Deals mostly with *Balæna biscayensis* (= *B. australis*) from San Sebastian. Figures of exterior, skull, skeleton.
- Rios Rial: *La Ballena Euskara*, 1890, pp. 1-105. *Balæna australis*, mostly on skeletons from San Sebastian.
- Lydekker: *Cetacean skulls from Patagonia*; *Anales del Museo de La Plata, Paleontologia Argentina*, vol. 2, 1893, pp. 2-4, pl. I. *Cetotherium*.
- Struthers: *On the rudimentary hind-limb of a Great Fin-Whale, Balænoptera musculus, in comparison with those of the Humpback-whale and the Greenland Right-Whale*; *Journal of Anatomy and Physiology*, vol. 27, 1893, pp. 291-335, pls. 17-20.
- Struthers: *On the carpus of the Greenland Right-Whale, Balæna mysticetus, and of Fin-Whales*; *Journal of Anatomy and Physiology*, vol. 29, 1895, pp. 145-187, pls. 2-4.
- Beddard: *Contrib. towards a knowledge of the osteology of the Pigmy Whale (Neobalæna marginata)*; *Transact. Zool. Soc. London*, vol. 16, pt. 2, No. 1, 1901, pp. 87-114, pls. 7-9.

Racovitz: Cétacés; Expédition Antarctique Belge; Résultats du Voyage du S. Y. Belgica en 1897-99, Rapports Scientifiques, Zoologie, 1903, pp. 1-142, pls. 1-4. Contains much information on the external characters and the habits of cetaceans, especially whalebone whales, and gives numerous references to earlier papers on the subject.

True: The whalebone whales of the Western North Atlantic compared with those occurring in European Waters with some observations on the species of the North Pacific; Smithsonian Contributions to Knowledge, vol. 33, 1904, pp. 1-332, pls. 1-50. Deals with species of the genera *Balæna*, *Rhachionectes*, *Balænoptera*, *Megaptera*. Numerous illustrations, especially of skulls and exterior. Copious references to earlier works on the subject.

Turner: The Right-Whale of the North Atlantic, *Balæna biscayensis*: its skeleton described and compared with that of the Greenland Right-Whale; Transact. Roy. Soc. Edinburgh, vol. 48, 1913, pp. 889-922, pls. 1-3, with text figures.

Abel: Die Vorfahren der Bartenwale; Denkschriften der k. Akad. der Wissensch. Wien, Mathem. naturw. Kl., vol. 90, 1914, pp. 155-224, pls. 1-12. *Patriocetus*, *Agriocetus*. Review of the origin of the whalebone whales.

Roy C. Andrews: Monographs of the Pacific Cetacea, I, The California Gray Whale (*Rhachianectes glaucus*); Mem. Amer. Mus. Nat. Hist., n. s., vol. 1, pt. 5, 1914, pp. 227-287, pls. 19-28, with figures of the exterior and of all parts of the skeleton.

Roy C. Andrews: The Sei Whale (*Balænoptera borealis*); Mem. Amer. Mus. Nat. Hist., n. s., vol. 1, pt. 6, 1916, pp. 289-388, pls. 29-42, with figures of the exterior and of all parts of the skeleton.

G. M. Allen: The Whalebone Whales of New England; Mem. Boston Soc. Nat. Hist., vol. 8, No. 2, 1916, pp. 105-322, pls. 8-16, with figures mostly of the exterior. *Balæna*, *Balænoptera*, *Megaptera*.

Besides *Plesiocetus* and *Cetotherium* many other genera of fossil Balænidæ have been described, especially in papers by Van Beneden, Brandt and Cope, but the bases for most of them are scanty. H. Winge (Om *Plesiocetus* og *Squalodon* fra Danmark, Vidensk. Medd. Naturhist. Foren. 1909) has attempted to estimate the value of a number of the genera in question: *Aulocetus*, *Mesoteras*, *Cetotheriopsis*, *Megapteropsis*, "*Burtinopsis*," *Herpetocetus*, *Eucetotherium*, *Plesiocetopsis*, *Cetotheriophanes*, *Cetotheriomorphus*, *Idiocetus*, *Heterocetus*, *Amphicetus*, *Mesocetus*, *Isocetus*, *Pachycetus*, *Siphonocetus*, *Ulias*, *Tre-*

tulias, *Metopocetus*, *Cephalotropis*, *Rhognopsis*. It is apparent that as regards most of them there is scarcely any reason for separation from *Plesiocetus* or *Cetotherium* or from recent genera, and that the few which appear to be more peculiar are so slightly known that they can scarcely be classified. True (The Genera of Fossil Whalebone Whales allied to *Balanoptera*, Smithsonian Misc. Coll., vol. 59, No. 6, 1912, pp. 1-8) who later went over the subject came in all essentials to the same conclusion.

Agriocetus is most likely a whalebone whale, but it is too slightly known to be classified. It was described by Abel (1914, *l. c.*, pp. 188-194, pls. 4, 5, 7) from a very imperfect and indistinct skull from Tertiary strata at Linz, referred to *Squalodon* by earlier authors. Abel regards it as a near relative of *Patriocetus*, a step nearer to the true whalebone whales. Only better discoveries will show whether he is right or not.

Perhaps *Patriocetus* belongs to the family *Balanidae* as it is understood in the present work, but it is not sufficiently known to be definitely placed. It was described by Abel (1914, *l. c.*) who has given a full account of the history of the remnants in question. The basis of the genus was partly some rather imperfect fragments which previously had most often been referred to under the name *Squalodon ehrlichii*, partly a quite well-preserved skull found later, all from Tertiary strata at Linz. If Abel's interpretations and conjectures are right he is no doubt correct in regarding *Patriocetus* as a precursor of the true whalebone whales. Abel refers it to the Archæoceti, or at least leaves the question undecided whether it actually belongs to this group or to the Mystacoceti (Die vorzeitl. Säuget., 1914, p. 88); most probably it should be regarded as a whalebone whale, a Balenid with the dentition still functional. But there is reason for doubt about certain details in Abel's account.

Patriocetus has in the skull a remarkably strong resemblance to *Agorophius*, a resemblance that was seen by Brandt (1873, *l. c.*, p. 324) although the remains then at hand were rather insignificant; and *Agorophius* belongs incontestably to the series of toothed whales as a near relative of *Squalodon*. The peculiarity which places *Agorophius* among the *Odontoceti* in opposition to the *Mystacoceti* is that the maxillary bone pushes itself posteriorly as a thin lamina over the supraorbital process of the frontal, but does not stop in front of it, or push itself in under it, or content itself with also covering it with a narrow margin anteriorly. According to the great resemblances which are found otherwise between the skulls of *Agorophius* and

Patriocetus one would expect that the two genera would resemble each other in this particular also; but according to Abel's representation *Patriocetus* is here like the whalebone whales. According to the photographic illustrations which accompany Abel's paper it is scarcely possible to see whether his exposition of the conditions is right or not; the skull is too weathered and obscure. There is, however, a detail in his description of the boundary between the maxillary and frontal, which probably must be wrong or at least must awaken doubt. He says of the maxillary that it, at its postero-internal extremity, does not extend nearly so far backward as the nasal process of the intermaxillary, which, on the contrary, like that of other whales, extends up, far backward, alongside the outer margin of the nasal and beyond. But there is elsewhere no cetacean, either among the *Archococeti*, *Mystacoceti*, or *Odontoceti*, in which the maxillary does not reach postero-internally as far back as the intermaxillary or even further, pushing itself up over the frontal. This is an inheritance from ancestors among the carnivores or from yet more distant forerunners. Abel says, it is true (*l. c.*, p. 162) that *Patriocetus* in this regard resembles *Rhachionectes*, one of the recent whalebone whales; but this is an error. In one of the figures of the skull of *Rhachionectes* published by Andrews (1914, *l. c.*, pl. 25) it can be clearly seen that a long process from the maxillary extends along the outer side of the intermaxillary to its hindmost end; and it is so described by Andrews (p. 261). In the second of Andrews' figures the process is not visible; it is obviously broken off, as it is in the figures published by Van Beneden (*Bull. Acad. Roy. Sci. etc., de Belgique*, ser. 2, vol. 43, No. 2, February, 1877, pl.) and True (1904, *l. c.*, pl. 47, fig. 1), both of which represent the same skull (it is True's figure to which Abel refers). A similar injury no doubt must have been suffered by the skull of *Patriocetus*; and if this process can be broken away without leaving visible traces behind it the same might be possible in the case of a thin plate-like process that originally covered the supraorbital process of the frontal. How readily something of the kind can take place is shown by the type of *Agorophius* (figured by Leidy, under the name *Squalodon pygmaeus*, *Journ. Acad. Nat. Sci. Philadelphia*, ser. 2, vol. 7, 1869, pl. 29, and by True, *Smithsonian Inst. Special Publ.*, No. 1694, 1907, pl.): on the right side of the skull large parts of the plate-like outgrowths from the maxillary over the supraorbital process of the frontal are broken away without having left behind any conspicuous traces on the frontal.

In Abel's treatment of the dentition in *Patriocetus* there are also various doubtful points. He asserts that the complement of teeth is the one which is typical of the placentalia, 11 teeth in each jaw; but it is impossible to see how he has arrived at this conclusion. The best skull in question lacks the anterior part of both upper jaw and mandible, and it is impossible to say how much is lacking, or how many teeth were implanted in the missing parts. Of teeth fixed in the jaws there are known for the most part mere stubs—sometimes nothing but roots. Besides these there are some dissociated teeth whose position in the jaws is not certain. All that can be said is that some of the teeth were simply conical with single root, and that most of the cheekteeth had serrate crown and double roots. Altogether there is not enough known to elucidate all the details of the dentition. It is not probable that Abel should be right in his belief that the teeth were present in the typical number. Such a cetacean as *Patriocetus*, the skull of which was already highly developed in the direction of the most advanced whales, scarcely could have had about the same dentition as the Zeuglodonts. It is much more likely that the number of teeth was increased above the typical as it is or has been in all the *Mystacoceti* and *Odontoceti* which are known in this respect. In order to believe in Abel's representation of the facts we must see more incontestable finds. (See also note 7, pp. 52-54.)

¹⁵ (P. 23.) The asymmetry in the skull of the toothed cetaceans has often been written about. Special treatises on the subject are due to Pouchet (*De l'asymétrie de la face chez les Cétodontes*; *Nouv. Arch. du Mus. d'Hist. Nat. Paris*, 1886, pp. 1-16 of separate), Abel (*Die Ursache der Asymmetrie des Zahnwalschädels*; *Sitzungsber. k. Akad. Wissensch. Wien, Math.-naturw. Cl.*, vol. III, pt. 1, 1902, pp. 510-526, pl.), Kükenthal (*Ueber die Ursache der Asymmetrie des Walschädels*; *Anat. Anzeiger*, vol. 33, 1908, pp. 609-618, with illustrations) and Steinmann (*Ueber die Ursache der Asymmetrie der Wale*; *Anat. Anzeiger*, vol. 41, 1912, pp. 45-54, with illustrations); Pouchet and Abel refer to various earlier papers by other writers.

As to the reason for the crookedness Pouchet says: "Nous en ignorons l'origine."

In 1893 Kükenthal said very nearly the same: "Die physiologische Ursache kennt man nicht, vielleicht ist sie in der eigenthümlichen Art der Locomotion vermittelt der Schwanzflosse zu suchen" (*Vergleich.-Anat. u. entwicklungsgesch. Untersuch. an Walthieren*, pt. 2; *Denkschr. med.-naturwiss. Ges. zu Jena*, vol. 3, pt. 2, p. 342), a

thought that was not at the time carried further. But in 1908 Kükenthal tried to give a more exact explanation. To begin with he thought he could prove that the asymmetry in the bones of the face is found not only in toothed cetacea, but also in the whalebone whales, though only slightly defined. In two skulls of *Balaenoptera* (of *B. rostrata* and *B. musculus*) he had found certain of the facial bones just a trifle broader on the right side than on the left. Next he discovered that some embryos of toothed cetaceans, of *Platanista*, *Steno*, *Globiceps*, *Delphinus*, *Phocana*, *Hyperoodon*, had the caudal fin set awry, not level but in such a position that the left fluke "etwas schräg nach aufwärts, der rechte schräg nach abwärts gerichtet war" (p. 614). In 12 embryos of *Delphinapterus* the fin was, on the contrary, horizontal. All the embryos of whalebone whales examined (of *Balaenoptera musculus* and *B. gigas*) had the fin oblique in the same manner as the toothed whales. How the fin is in adult cetaceans is said to be not clearly understood; a few observations by other investigators may, however, indicate that the obliquity is present in the adults also. When a whale propels itself forward by means of a sculling movement of the oblique caudal fin it is said to turn at the same time to the left: "Der Wal durchschneidet also bei derartiger schräger Bewegung der Schwanzflosse das Wasser nicht genau in der Richtung seiner Längsachse, sondern sein Weg verläuft von dieser Geraden etwas schräg nach links zu" (p. 616). And from this is said to result an oblique pressure of the water on the head, and consequently the obliquity of the skull, since the bones on the left side are pressed upon more than those of the right side, are made thicker, etc.: "Der Druck der beim Schwimmen durchschnittenen Wassermassen wird auf die linke Seite des Vorderkopfes stärker wirken als auf die rechte. Dieser Druck pflanzt sich durch die elastischen Weichteile des Vorderkopfes hindurch auf die darunter liegenden Schädelknochen fort. Die Wirkung dieses stärkeren Druckes muss sich zunächst in einer Verdickung der entsprechenden Schädelknochen äussern . . ." (pp. 616-617). That the bones in the left side of the face are not so wide as those of the right side is said to be connected with the fact that the bones of the left side are the thickest: "Es wird dadurch links eine kleinere Fläche als rechts geschaffen, welche den etwas stärkeren Druck auszuhalten hat und damit bis zu einem gewissen Grade einen Ausgleich gegenüber der rechten Seite herbeiführt" (p. 617).

Abel believes that the reason for the asymmetry of the skull in toothed whales is to be found in the atrophy of the nasal bones, etc.,

and in the shortening of the braincase, but cannot prove that asymmetry would be the necessary result of these causes.

Lillie (section The asymmetry of the Odontocete skull, in Observations on the anatomy and general biology of some members of the larger Cetacea, Proc. Zool. Soc. London, 1910, vol. 2, pp. 781-783, with figure) shows that the pharynx in *Physeter* is asymmetrical, divided by the projecting larynx, which is strongly displaced to the left, into a more spacious right and a narrower left section to accommodate the passage of food. In this circumstance should be found the source of the asymmetry of the face; why, is not further explained.

Steinmann starts from Kükenthal's assertion about the asymmetry in the caudal fin. Kükenthal had said nothing as to the cause of this crookedness, but Steinmann believes he has found it in the supposed fact that whales originated from Ichthyosaurs and other marine reptiles with a vertical fin, and that on its way to the horizontal position the fin has come to rest obliquely.

Kükenthal is doubtless the one who has come nearest to the truth. However, there are numerous objections to be raised against his explanation. It cannot be said with any degree of correctness that the skull in the whalebone whales has an asymmetrical face. A series of skulls is before me, representing *Balæna*, *Balænoptera* and *Megaptera*. Such asymmetry as can perhaps be shown here and there is similar to that which is found in most mammals. I myself have seen many cetacean embryos (in alcohol), representing both whalebone whales and odontocetes (of the former I have examined in this connection embryos of 3 *Balænoptera rostrata*, 2 *B. musculus*, 5 *Megaptera boops*, of the latter numerous embryos representing the genera *Delphinapterus*, *Monodon*, *Prodelphinus*, *Delphinus*, *Lagenorhynchus*, *Globiceps*, *Phocæna*, *Neomeris*; I have been content with examining the tails externally, I have not cross-sectioned them), but I have not been able to convince myself of the presence of obliqueness in the tail which did not appear to find its explanation in artificial pressure. I have also seen various adult newly dead cetaceans, both whalebone whales and toothed cetacea of different kinds. It is true I did not expressly examine them to observe obliqueness of the tail, but I cannot recall the slightest evidence of its existence. Neither can anything be detected in the numerous photographs of whales that are before me. That obliqueness of the tail can actually be present appears to be proved by Kükenthal's figure of a cut off tail of *Balænoptera*, which shows the flukes placed obliquely in relation to the caudal vertebræ; but it must probably be an exception. Even if it

were true that the caudal fin in cetaceans was usually obliquely set this would probably not hinder whales from swimming forward in a straight line if they so wished. That the obliquity of the tail, if it occurs as represented by Kükenthal, does not in any event necessarily carry with it the asymmetry of the skull is proved by the whalebone whales, whose tail is said to be oblique, but whose skull is without asymmetry in spite of Kükenthal's word to the contrary. And that the asymmetry of the face is not dependent on obliquity of the tail is proved by *Delphinapterus*, whose tail, also according to Kükenthal's interpretation, is not oblique, but whose skull is distinguished by a high degree of asymmetry. Should the water's pressure work most powerfully on the *left* side of the head it would be difficult, in spite of Kükenthal's attempt at an explanation, to understand why the bones on the left side of the skull are narrow while those on the right side are broad, or why the nasal passage is pushed over toward the left side, a point that Kükenthal does not try to argue. Of Kükenthal's explanations scarcely anything is left except the knowledge that it is the pressure of the water which is responsible for the asymmetry of the skull in the Odontoceti. Why the water presses obliquely is still unknown, but the reason is not likely to be anything else than a habit in the carriage of the head: the head presumably must be held a little obliquely even when the animal is swimming straight forward; and the pressure must be strongest on the right side.

¹⁶ (P. 24.) On the *Squalodontida* see especially:

Grateloup: Description d'un fragment de mâchoire fossile, d'un genre nouveau de reptile (Saurien), de taille gigantesque, voisin d'Iguanodon, trouvé dans le grés marin, à Léognan, près Bordeaux, 1840, pp. 1-8, pl. Separate from Actes de l'Acad. des sciences, belles lettres et arts de Bordeaux, vol. 2. *Squalodon*.

H. v. Meyer: Arionius servatus, ein Meersäugethier der Molasse; Palæontographica, vol. 6, 1856, pp. 31-43, pl. 6. *Squalodon*.

Jourdan: Descr. de restes fossiles de deux grands Mammifères constituant le genre Rhizoprion et le genre Dinocyon; Annales des Sciences Naturelles, sér. 4, Zoologie, vol. 16, 1861, pp. 369-372, pl. 10. *Rhizoprion* = *Squalodon*.

Van Beneden: Recherches sur les Squalodons; Mém. Acad. Roy. Belgique, vol. 35, 1865, pp. 1-85, pls. 1-4, with figures of the upper jaw of *S. antuerpiensis* (and of the skull of *S. ehrlichii* = *Patriocetus*).

Van Beneden: Recherches sur les Squalodons, Supplément; Mém. Acad. Roy. Belgique, vol. 37, 1868, pp. 1-13, pl., with figure of the under jaw of *S. antuerpiensis*.

- Gervais: Du Squalodon et de sa comparaison avec le Zeuglodon; Zoologie et Paléontologie Générales, ser. 1, 1867-69, pp. 170-182.
- Fischer: Descr. d'une mâchoire inférieure de Squalodon Grateloupi; Actes de la Soc. Linnéenne de Bordeaux, vol. 27, 1869, pp. 12-22, pl. 2.
- Delfortrie: Descr. d'une nouvelle mâchoire inférieure de Squalodon Grateloupi dans le grés marin de Léognan, Gironde; Actes de la Soc. Linnéenne de Bordeaux, vol. 27, 1869, pp. 133-136, pl. 5.
- Leidy: Extinct Mammalian Fauna of Dakota and Nebraska; Journ. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 7, 1869, pp. 416-424, pls. 28-30. *Squalodon* and *Agorophius* (under the name *Squalodon pygmaeus*).
- Delfortrie: Un Squalodon d'espèce nouvelle dans le Miocène supérieur du Midi de la France; Actes de la Soc. Linnéenne de Bordeaux, vol. 29, 1873, pp. 257-260, pl. 7.
- Brandt: Untersuchungen über die fossilen und subfossilen Cetaceen Europa's; Mém. Acad. Sci. St. Pétersbourg, ser. 7, vol. 20, No. 1, 1873. Contains a section on the Squalodonts, pp. 315-332, pl. 31-32. *Squalodon*, *Neosqualodon* (*S. gastaldii*) (and *Patriocetus*, *S. Ehrlichii*).
- Brandt: Ergänzungen zu den fossilen Cetaceen Europa's; Mém. Acad. Imp. Sci. St. Pétersbourg, ser. 7, vol. 21, No. 6, 1874. Contains a section on *Squalodon* (and *Patriocetus*), pp. 28-47, pls. 4, 5.
- Van Beneden et Gervais: Ostéographie des Cétacés vivants et fossiles, Text and Atlas, 1868-80, pp. 426-454, 519, pl. 28. *Squalodon*.
- Zittel: Ueber *Squalodon Bariensis* aus Niederbayern; Palæontographica, vol. 24, 1877, pp. 233-246, pl. 35.
- Lortet: Note sur le *Rhizoprion bariensis*; Arch. Mus. d'hist. Nat. de Lyon, vol. 4, 1887, pp. 315-319, pl. 25 bis and ter. *Squalodon*.
- Lydekker: Cetacean skulls from Patagonia; Anales del Museo de La Plata, Paleontología Argentina, II, 1893, pp. 8-10, pl. 4. *Prosqualodon*.
- Paquier: Étude sur quelques Cétacés du Miocène; Mém. de la Soc. Géol. de France, Paléontologie, vol. 4, pt. 4, Mém. No. 12, 1894, pp. 12-17, pl. 18. *Squalodon*.
- Lydekker: On the skull of a shark-toothed Dolphin from Patagonia; Proceed. Zool. Soc. London, 1899, pp. 919-922, with illustrations. *Prosqualodon*.

- Dal Piaz: Sopra alcuni resti di *Squalodon* dell' arenaria miocenica di Belluno; *Palaeontographia Italica*, vol. 6, 1900, pp. 303-314, pls. 26-29.
- Abel: Les Dauphins Longirostres du Boldérien des Environs d'Anvers; *Mém. Mus. Roy. d'Hist. Nat. de Belgique*, vol. 1, 1901, pp. 9-10. On the dentition in *Squalodon*.
- Dal Piaz: *Neosqualodon*, nuovo genere della famiglia degli *Squalodontidi*; *Abhandl. der Schweizerischen paläontologischen Gesellschaft*, vol. 31, 1904, pp. 1-21, pl.
- Abel: Les Odontocètes du Boldérien d'Anvers; *Mém. Mus. Roy. d'Hist. Nat. de Belgique*, vol. 3, 1905, pp. 25-38. On the dentition.
- True: Remarks on the type of the fossil Cetacean *Agorophius pygmaeus* (Müller); *Smithsonian Inst. Special Publ.*, No. 1694, 1907, pp. 1-8, pl.
- True: Descr. of a mandible and vertebrae of *Prosqualodon*, etc.; *Smithsonian Misc. Coll.*, vol. 52, pt. 4, 1910, pp. 447-456, pl. 43.
- Hall: On the systematic position of the species of *Squalodon* and *Zeuglodon* described from Australia and New Zealand; *Proc. Roy. Soc. Victoria*, n. s., vol. 23, pt. 2, 1911, pp. 257-265, pl. 36. *Parasqualodon*, *Metasqualodon*.
- Abel: Cetaceenstudien, III. Mitteilung, Rekonstruktion des Schädels von *Prosqualodon australe* (*sic*) Lyd. aus dem Miozän Patagoniens; *Sitzungsber. k. Akad. Wissensch. Wien, mathem.-naturw. Kl.*, vol. 121, pt. 1, 1912, pp. 57-75, pls. 1-3. The account contains various guesses; Lydekker's figures of the type cannot be dispensed with in forming an opinion about the genus. References to several other papers will be found in H. Winge, *Vidensk. Medd. Naturhist Foren.*, 1909, pp. 31-35.
- Microsqualodon* Abel is said to be identical with *Neosqualodon* Dal Piaz. Abel (*Odontocètes du Boldérien*, 1905, pp. 35-36) established the genus on the basis of Tertiary remains from Acqui which Brandt had called *Squalodon gastaldii*. In a letter to Abel, however, which Abel printed, Dal Piaz explains that these specimens, which he had had the opportunity to see, must be referred to the earlier described *Neosqualodon*.
- Parasqualodon* and *Metasqualodon* are proposed by Hall (1911, *l. c.*) to include Tertiary Australian species that previously were referred to *Squalodon*: *S. wilkinsoni* M'Coy and *S. harwoodii* Sanger. The genera are supposed to be nearly related to *Prosqualodon*, but they are known from loose teeth only and their status is still uncertain.

- ²¹ (P. 28.) On the *Platanistida* see especially:
- Cuvier: Recherches sur les Ossemens fossiles, ed. 4, vol. 8, pt. 2, 1836, pp. 88-90, 128-132, Atlas, pl. 223, with figures of skull of *Platanista*.
- Eschricht: Om Gangesdelphinen; Kgl. Danske Vidensk. Selsk. Skrifter, 5te R., naturv. og mathem. Afd., vol. 2, 1851, pp. 345-387, pls. 1-3. *Platanista*. Figures of exterior, skeleton, skull.
- Burmeister: Descripcion de cuatro especies de Delfinides de la costa Argentina en el océano Atlántico; Anales del Museo Público de Buenos Aires, vol. 1, 1864-69, pp. 389-445, pl. 23, 25-28. *Pontoporia*. Figures of exterior, skeleton, skull and other parts.
- Flower: Descr. of the skeleton of *Inia geoffrensis* and of the skull of *Pontoporia blainvillii*, with remarks on the systematic position of these animals in the order Cetacea; Trans. Zool. Soc. London, vol. 6, pt. 3, 1869, pp. 87-116, pls. 25-28.
- Van Beneden et Gervais: Ostéographie des Cétacés vivants et fossiles. Text and Atlas, 1868-80, pp. 454-482, pls. 29-33. On almost all the recent genera.
- Anderson: Anat. and Zool. Researches, compr. an Account of the two Exp. to Western Yunnan in 1868 and 1875; 1878; pp. 417-550, pls. 25, 26, 28-32, 34-41. *Platanista*. Figures of exterior, skeleton and soft parts.
- Burmeister: Exámen critico de los Mamíferos y Reptiles fósiles denominados por D. Augusto Bravard; Anales del Museo Nacional de Buenos Aires, vol. 3, 1883-91, pp. 138-144, pl. 2, figs. 12A-C. *Pontistes*. Figures of an imperfect skull.
- Burmeister: Adiciones al exámen critico, etc.; Anales del Museo Nacional del Buenos Aires, vol. 3, 1883-91, pp. 451-460, pl. 8. *Saurodelphis*. Figures of skull.
- Abel: Les Dauphins Longirostres du Boldérien des Environs d'Anvers; Mém. Mus. Roy. d'Hist. Nat. de Belgique, vol. 1, 1901, pp. 1-95, pls. 1-10. Contains a section dealing with the *Platanistida* both living and extinct, and on several plates gives figures of their skulls, mostly copied from other papers.
- Abel: Cetaceenstudien, II, Der Schädel von *Saurodelphis argentinus* aus dem Pliozän Argentinien; Sitzungsber. k. Akad. Wissensch. Wien, mathem.-naturw. Kl., vol. 118, pt. I, 1909, pp. 255-272, pl. I, and text figures. Tries to prove that Burmeister's figures of the skull of *Saurodelphis argentinus* are to a notable degree incorrect. Burmeister is said to have put together parts of two different genera that should bear the names *Saurodelphis* and

Pontoplanodes. At present the problem cannot be said to be solved; but there appears to be no good reason to doubt the correctness of Burmeister's determination. In the present paper his presentation of the subject is followed. A piece of the beak of *Saurodelphis* with the 8-shaped alveoli is in the Copenhagen museum.

Gerrit S. Miller: A new River-Dolphin from China; Smithsonian Misc. Coll., vol. 68, No. 9, 1918, pp. 1-12, pls. 1-13. *Lipotes*.

Ischyrorhynchus was based by Ameghino (Caracteres diagnósticos de cincuenta especies nuevas de Mamíferos fósiles argentinos; Revista Argentina de Historia Natural, vol. 1, 1891, pp. 163-165, with illustrations) on the anterior part of a lower jaw from the "oligoceno inferior del Paraná." The branches of the jaw, which are rather heavy, are grown together in a long symphysis menti; the rows of teeth are further apart than in *Saurodelphis* (*Saurocetes*), with which Ameghino associates the genus, and the roots in cross-section are almost what might be called ovate, not 8-shaped; the crowns are known only imperfectly. It is not possible to decide where the genus belongs.

Pontivaga was also based by Ameghino (*l. c.*, pp. 165-166, with illustration) on the anterior part of a lower jaw, from the "oligoceno superior" at Paraná. The branches of the jaw are slender and are grown together in a long symphysis. Each of them contains a long row of small teeth, to judge by the alveoli. Ameghino places the genus in the *Platanistidae*, in contrast with the *Saurocetidae*, whether rightly or not cannot be said.

A genus *Proinia* is established by True (A new genus of fossil Cetaceans from Santa Cruz Territory, Patagonia, etc.; Smithsonian Misc. Coll., vol. 52, pp. 441-447, pl. 43, 1910), who regards it as a near relative of *Inia*. Perhaps True is right; but the material on which the genus is based, a few fragments of a braincase and a cervical vertebra all distorted by pressure, is so scanty that an error is very possible.

Hesperocetus is established by True (A fossil toothed Cetacean from California, etc.; Smithsonian Misc. Coll., vol. 60, No. 11, 1912, pp. 1-7, pls. 1-2) on the strength of the anterior part of a long, narrow, lower jaw with long symphysis, with rows of rather strong, conical, slightly hooked teeth with wrinkled enamel. The teeth are placed rather wide apart and are separated by shallow depressions in the margin of the jaw into which the tips of the upper teeth pre-

sumably fitted. True refers it provisionally to the family *Iniidæ* (= *Platanistidæ*), perhaps rightly; there are other possibilities.

²⁸ (Pp. 26 and 31.) True (A Review of the Family Delphinidæ; Bull. U. S. Nat. Mus., No. 36, 1889, p. 10) believes he has observed a peculiarity in the relationships of the pterygoid that should distinguish *Delphinapterus* and *Monodon* from all other Delphinids and recall the Platanistids: "that in the narwhal and white whale the pterygoid bones, instead of merely forming the walls of the posterior nares, extend backward in the form of broad plates across the optic canal and articulate with the squamosals." But the case is different. We have to do with the bones which lie in the outer wall of the air-sac behind the palate. As may be seen in young or youngish skulls of *Delphinapterus* and *Monodon*, the pterygoid shares in the formation of the outer wall of the air-sac at the front only, in contrast with the condition in *Pontistes*, *Pontoporia* and *Platanista* in which it, recalling the Balænidæ and Physteridæ, forms most of the outer wall (in *Inia* the outer wall appears to be mostly membranaceous). As in other Delphinids the palatine, frontal, ala magna, and squamosal all share in bounding the outer side of the air-sac, each contributing its section (special ossifications may also be present). In the Delphinids under discussion the outer side of the air-sac is merely ossified more extensively than elsewhere, a difference, however, which is one of degree only.

²⁹ (P. 35.) As reasons for believing that *Neomeris* and *Phocæna* among recent Odontoceti are the ones which stand nearest to *Zeu-glodon* and *Squalodon* Abel (Dauphins Longirostres, 1901, p. 36) mentions the following: (1) that they still have traces of "l'ancienne dentition hétérodonte," (2) that teeth are still found (or more correctly may be found) in the intermaxillary, and that the intermaxillary extends further forward than the maxillary, (3) that they still have traces of "l'armure dermique," (4) that the nostrils are not pushed very far backward, and that therefore the parietal still extends up back of the frontal. Against this view there are the following objections: (1) The form of the teeth in the two recent genera is not primitive; fan-like broadened crown and single root is not the form of tooth that is found in the more primitive cetaceans of any kind. Conical crown and a trace of double root, in most of the teeth, is the transitional form between the tooth structure of the more primitive and the less primitive cetaceans. Even the anterior teeth in the jaws of *Phocæna* may have fan-shaped crowns, where in the most primitive whales they are unicuspid and conical. (2) Teeth in the inter-

maxillary, and a slightly projecting intermaxillary, may also be found in *Steno*, *Delphinus*, and several other of the recent *Delphinidæ*.

(3) There is no evidence that cetaceans are descended from mammals with bony armor; the so-called dermal bones that were found on rare occasions with remains of *Zeuglodon* and *Delphinopsis* are too doubtful to prove anything; in the great majority of instances no dermal armor has been found with bones of *Zeuglodon* and other *Archæoceti*. The "dermal armor," that is, the small spots of more or less tuberculate, mosaic-like skin, in *Neomeris* and *Phocæna* is assuredly a new development. (See pp. 56-58.) (4) It cannot be correctly said that the nostrils in *Phocæna* and *Neomeris* lie relatively far forward. It appears so merely because the anterior part of the face is somewhat shortened and the braincase is unusually large. In reality the nostrils lie, with respect to the orbits and other surrounding parts, in the same position as in most Delphinids. Neither can it be said that the parietals are excluded from the upper side of the braincase to a less degree than usual. As may be seen in the young skulls the parietals in *Phocæna* are widely separated by the large interposed interparietal quite as usual in other Delphinids.

²⁰ (P. 35.) On the Delphinidæ see especially:

Cuvier: *Recherches sur les Ossements fossiles*, ed. 4, vol. 8, pt. 2, 1836, pp. 75-170, Atlas, pls. 222-224, with figures of skull and some other skeletal parts, of most of the recent genera.

Schlegel: *Beiträge zur Charakteristik der Cetaceen; Abhandlungen aus dem Gebiete der Zoologie und vergl. Anatomie*, Heft. 1, 1841, pp. 1-44, pls. 1-6. Contains among other things a synopsis of the Delphinids, with figures of skulls of *Steno*, *Prodelphinus*, *Delphinus*, *Lagenorhynchus*, all under the name *Delphinus*.

J. E. Gray: *The Zoology of the Voyage of H. M. S. Erebus and Terror*, pts. 3-5, Mammalia, On the Cetaceous Animals, 1846, pp. 13-53, pls. 1-30. Most of the plates give figures of skulls of Delphinids: *Delphinapterus* ("Beluga"), "*Feresa*" (*Orca intermedia*), *Orca*, *Lagenorhynchus*, *Tursiops* (under the name *Delphinus*), *Prodelphinus* (under the name *Delphinus*), *Delphinus*, *Steno*.

Burmeister: *Descripcion de cuatro especies de Delfinides de la costa Argentina en el océano Atlántico; Anales del Museo Público de Buenos Aires*, vol. 1, 1864-69, pp. 367-388, pls. 21-24. *Pseudorca* (under the name *Globicephalus*), *Orca*, *Phocæna*. Figures of exterior, skulls and other parts.

- Owen: On some Indian Cetacea; *Transact. Zool. Soc. London*, vol. 6, pt. 1, 1866, pp. 17-47, pls. 3-14. Deals partly with the Delphinids. Skulls are figured of "*Sotalia*," *Lagenorhynchus*, *Delphinus*, *Prodelphinus* (all called *Delphinus*), *Orcella* (called *Phocæna*).
- J. E. Gray: Synopsis of the species of Whales and Dolphins in the Collection of the British Museum, 1868, pp. 1-10, pls. 1-30. The plates are the same as in the previously mentioned work by Gray.
- Van Beneden et Gervais: *Ostéographie des Cétacés vivants et fossiles*, Text and Atlas, 1868-80, pp. 482-512, 521-605, pls. 34-60, 63, 64. All recent genera and many fossil, among them *Champsodelphis*, *Schizodelphis*, *Eurhinodelphis*.
- Eschricht: Ni Tavler til Oplysning af Hvaldyrenes Bygning, med Forklaring af Reinhardt; *Kgl. Danske Vidensk. Selsk. Skrifter*, 5te R., naturv. mathem. Afd., vol. 9, I, 1869. On plate 8 are found figures of skull and teeth of *Delphinapterus*.
- Flower: Descr. of the skeleton of the Chinese White Dolphin, *Delphinus sinensis*; *Transact. Zool. Soc. London*, vol. 7, pt. 2, 1870 (72), pp. 151-160, pls. 17, 18. *Prodelphinus* ("*Sotalia*").
- Flower: On Risso's Dolphin, *Grampus griseus*; *Transact. Zool. Soc. London*, vol. 8, pt. 1, 1872, pp. 1-21, pls. 1-2. Figures of exterior and skeleton.
- Brandt: Untersuchungen über die fossilen und subfossilen Cetaceen Europa's; *Mém. Acad. Imp. Sci. St. Pétersbourg*, ser. 7, vol. 20, No. 1, 1873. Contains a section on the Delphinids, pp. 226-290, pls. 24-30, among them *Schizodelphis* and *Champsodelphis*.
- Brandt: Ergänzungen zu den fossilen Cetaceen Europa's; *Mém. Acad. Imp. Sci. St. Pétersbourg*, ser. 7, vol. 21, 1874, pp. 13-28, pls. 2-4. *Champsodelphis* among others.
- Murie: On the organization of the Caaing Whale, *Globiocephalus melas*; *Trans. Zool. Soc. London*, vol. 8, pt. 4, 1873, pp. 235-301, pls. 30-38. Exterior and anatomy.
- Van Beneden: Mémoire sur un Dauphin nouveau de la Baie de Rio de Janeiro désigné sous le nom de *Sotalia brasiliensis*; *Mém. Acad. Roy. Belgique*, vol. 41, 1874, pp. 1-44, pls. 1, 2, with figures of exterior, skeleton, skull. *Prodelphinus*.
- J. E. Gray: *Feresa attenuata*; *Journal des Museum Godeffroy*, vol. 8, 1875, p. 1, pl. 6, with figures of skull.
- Anderson: *Anat. and Zool. Researches*, compr. an Account of the two Exp. to Western Yunnan in 1868 and 1875; 1878; pp. 358-416, pls. 25, 25-A, 27-30, 33-38, 42, 43. *Orcella*. Figures of exterior, skeleton and soft parts.

- Van Beneden: Mémoire sur les Orques observés dans les mers d'Europe; Mém. Acad. Roy. Belgique, vol. 43, 1879, pp. 1-33, pls. 1-4, with figures of exterior, skeleton, skulls. *Orca*.
- Flower: On the characters and divisions of the family Delphinidæ; Proceed. Zool. Soc. London, 1883, pp. 466-513, with figures in the text representing the posterior part of the bony palate in several of the genera. One of the most important papers in elucidating the relationship among the recent Delphinids.
- Lütken: Kritiske Studier over nogle Tandhvaler af Slægterne Tur-siops, *Orca* og *Lagenorhynchus*; Kgl. Dansk Vidensk. Selsk. Skrifter, 6te R., naturv. mathem. Afd., vols. 4, 6, 1887, pp. 337-397, pls. 1, 2, also text figures: exterior, skull, other skeletal parts.
- Lütken: Spolia Atlantica, Bidrag til Kundskab om de tre pelagiske Tandhval-Slægter *Steno*, *Delphinus* og *Prodelphinus*; Kgl. Danske Vidensk. Selsk. Skrifter, 6te R., naturv. mathem. Afd., vol. 5, 1, 1889, pp. 1-61, plate with a figure of the exterior and skeleton of *Steno*; also figures in the text: exterior, skulls, other skeletal parts.
- True: A Review of the Family Delphinidæ; Bull. U. S. Nat. Mus., No. 36, 1889, pp. 1-191, pls. 1-47, with figures of exterior and skulls. In the conception of genera and their mutual relationships agrees closely with Flower's conclusions.
- Lydekker: Cetacean skulls from Patagonia; Anales del Museo de La Plata, Paleontología Argentina, vol. 2, 1893, pp. 10-12, pl. 5. *Argyroctetus*.
- Guldberg: On the development and structure of the Whale, pt. 1, on the development of the Dolphin; Bergens Museums Skrifter, vol. 5, 1894, pp. 1-70, pls. 1-7. *Lagenorhynchus*, *Phocæna*, *Orca*.
- Longhi: Sopra i resti di un cranio di *Champsodelphis* fossile scoperto nella molassa miocenica del Bellunese; Atti della Società Veneto-Trentina di Scienze Naturali, ser. 2, vol. 3, fasc. 2, 1898, pp. 1-60 in the separate, pls. 1-3.
- Abel: Untersuchungen über die fossilen Platanistiden des Wiener Beckens; Denkschr. d. k. Akad. Wissensch. Wien, math.-naturw. Cl., vol. 68, 1899, pp. 839-874, pls. 1-4, with figures of skulls. *Cyrtodelphis* and *Acrodelphis*=*Schizodelphis* and *Champsodelphis*.
- Abel: Les Dauphins Longirostres du Boldérien (Miocène supérieur) des Environs d'Anvers; Mém. Mus. Roy. d'Hist. Nat. de

- Belgique, vol. 1, 1901, pp. 1-95, pls. 1-10, with figures of skulls. *Cyrtodelphis* (= *Schizodelphis*), *Eurhinodelphis*.
- Dal Piaz: Sugli avanzi di *Cyrtodelphis sulcatus* dell' arenaria di Belluno; *Palaeontographia Italica*, vol. 9, 1903, pp. 187-220, pls. 28-31, with figures of skulls and teeth. *Schizodelphis*.
- Abel: Eine Stammtypen der Delphiniden aus dem Miocän der Halbinsel Taman; *Jahrbuch der k. k. geol. Reichsanstalt*, vol. 55, pt. 2, 1905, pp. 375-392, with text figures. *Palaeophocæna*.
- Abel: Les Odontocètes du Boldérien d'Anvers; *Mém. Mus. Roy. d'Hist. Nat. de Belgique*, vol. 3, 1905, pp. 1-155, with text figures. Includes a section on the Delphinids: *Eurhinodelphis*, *Cyrtodelphis* (= *Schizodelphis*), *Acrodelphis* (= *Champsodelphis*), *Protophocæna*, *Pithanodelphis*.
- C. v. Papp: *Heterodelphis leiodontus*, nova forma aus den miocenen Schichten des Conitates Sopron in Ungarn; *Mitteilungen aus dem Jahrbuche der k. ungarischen geol. Anstalt*, vol. 14, pt. 2, 1905, pp. 25-61, pls. 5, 6, also text figures. Skeleton.
- Abel: *Cetaceenstudien*, I, Das Skelett von *Eurhinodelphis cocheuxi* aus dem Obermiozän von Antwerpen; *Sitzungsber. k. Akad. Wissensch. Wien, mathem.-naturw. Kl.*, vol. 118, pt. 1, 1909, pp. 241-253, pl. 1, with a figure of the skeleton, partly conjectural.
- True: Observations on living White Whales, *Delphinapterus leucas*, with a note on the dentition of *Delphinapterus* and *Stenodelphis*; *Smithsonian Misc. Coll.*, vol. 52, pt. 3, No. 1864, 1909, pp. 325-330, pl. 23, with a figure of the exterior. Discusses among other things the projections on the tooth crowns of *Delphinapterus*.
- Lönnerberg: Remarks on the dentition of *Delphinapterus leucas*; *Arkiv för Zoologi*, vol. 7, No. 2, 1910, pp. 1-18, with illustrations. Taken up in part also in the paper Om Hvalarnes Härstamning; *K. Svenska Vetenskapsakademiens Årsbok för År 1910*, pp. 219-259, with illustrations.
- Roy C. Andrews: A new Porpoise from Japan; *Bull. Amer. Mus. Nat. Hist.*, vol. 30, 1911, pp. 31-51, pls. 1, 2, also numerous figures in the text. *Phocænoides*. Exterior and skeleton.
- Bassani e Misuri: Sopra un Delfinorinco del calcare miocenico di Lecce (*Ziphiodelphis Abeli* Dal Piaz); *Atti della R. Accademia dei Lincei*, Anno 309, 1912, ser. 5, Memorie della Classe di Scienze Fisiche, etc., vol. 9, fasc. 2, pp. 25-38, pl. 1, with figures of skull.
- True: Descr. of a new fossil Porpoise of the genus *Delphinodon* from the miocene formation of Maryland; *Journ. Acad. Nat.*

Sci. Philadelphia, ser. 2, vol. 15, 1912, pp. 165-194, pls. 17-26, with figures of skull, parts of the rest of the skeleton, teeth.

Lull: Fossil Dolphin from California; American Journal of Science, ser. 4, vol. 37, 1914, pp. 209-220, pl. 8, also figures in the text.

"*Delphinavus*."

Delphinopsis (see note 8) is placed by Abel (Jahrb. k. k. geol. Reichanst., vol. 55, pt. 2, 1905, pp. 384, 387, in the "Subfamily *Phocanina*" because it has "dermal armature." The remains are so imperfect and so uncertain that it is impossible to say where it belongs; not even the family can be determined from the specimen; the reference to *Phocanina* is pure guesswork.

Rhabdosteus was described in 1867 by Cope, who in 1890 (Amer. Nat., vol. 24, p. 607) gave figures of the specimens on which the genus was based, some remnants of a "beak," from a Tertiary North American deposit. These remains Cope reconstructed in a somewhat arbitrary manner. True (Remarks on the fossil Cetacean *Rhabdosteus latiradix* Cope; Proc. Acad. Nat. Sci., Philadelphia, vol. 60, 1908, pp. 24-29, pl. 6, and text figures), who has had the specimens in question under revision, together with some others more or less similar, says that Cope has scarcely put them together right. The specimens may recall *Eurhinodelphis* and its relatives; but the remains are altogether too incomplete and uncertain for anything to be decided.

Lophocetus, established by Cope in 1867, best known from Eastman's description (Types of fossil Cetaceans in the Museum of Comparative Zoology; Bull. Mus. Comp. Zool., vol. 51, 1907, pp. 79-94, pls. 1-4), Tertiary, North American, is most often placed in the *Platanistidae*. Brandt, however, counts it as a Delphinid (1873, *l. c.*, p. 288), most probably belonging to the "Abtheilung der Phocænen," perhaps to the genus *Delphinapterus*. In this determination he has been followed by a few other authors. The most important basis of the genus is a very imperfect skull, without teeth, with alveoli only, so obscure that nothing positive can be said about it. According to what can be seen of the form of the temporal fossa the genus appears to agree best with the Delphinids. On the other hand it does not seem possible to demonstrate anything that would especially recall the *Platanistids*.

Iniopsis was established by Lydekker (Proc. Zool. Soc. London, 1892, pp. 562-564, pls. 37-38) principally on an imperfect and obscure braincase from a Tertiary deposit in the Caucasus. Lydekker places it in the *Platanistidae* and finds similarities with *Pontistes*, *Stenodelphis* (= *Pontoporia*), *Inia*, etc. It appears, however, to be of another

type, very near the most usual Delphinid-type, differing from the *Platanistide* especially in the roofed over temporal fossa. Its more exact position among the Delphinids cannot yet be determined.

Cyrtodelphis is only a new name for *Schizodelphis* given by Abel in 1899 (*l. c.*) to include a series of species which previously were most often referred to *Schizodelphis*, among them the type of the genus, *S. sulcatus* Gervais. Eastman (Bull. Mus. Comp. Zool., vol. 51, 1907, pp. 83-84) has already protested against this superfluous new name as well as against the following.

Acrodelphis is likewise essentially a mere new name, a synonym of *Champsodelphis*. It was given by Abel in 1899 (*l. c.*). At first *Acrodelphis* was to include the type of *Champsodelphis*, *Ch. macrogenius* (Laurillard) Gervais or *macrognathus* Brandt. Later, in 1905, Abel excluded the type of *Champsodelphis* from the genus, with doubtful right; but most of the species which he now includes in *Acrodelphis* were earlier called *Champsodelphis*.

Palæophocæna was based by Abel (1905, Jahrb. k. k. geol. Reichsanst., vol. 55, *l. c.*) on an imperfect piece of a braincase and a few fragments of the rest of the skeleton from a Tertiary deposit on the coast of Crimea. Abel considers it proved that this is a near relative of *Phocæna*. Possibly it will sometime turn out that he is right; but for the present there is no means of deciding the question about nearest relationship. The known piece of skull shows only such general features that nothing exact can be said except that it comes from a Delphinid. Only in the form of the teeth have *Phocæna* and its relative *Neomeris* a peculiarity which distinguishes them from other quite ordinarily formed Delphinids; but the teeth in *Palæophocæna* are not known.

Protophocæna is also established by Abel (Odontocètes du Boldérien, 1905, pp. 139-141, with illustrations), on the anterior, very imperfect part of a skull, without teeth, from the Tertiary deposits at Antwerp. Abel refers it to the "*Phocæninæ*." There is actually nothing whatever, apart from the small size, that could lead one to think of *Phocæna*; on the contrary, the strong cushion-shaped swelling and the widening out which the intermaxillary shows in front of the nasal aperture suggests rather *Lagenorhynchus* or "*Grampus*." For the present the question about nearest relationship cannot be settled.

Pithanodelphis is established by Abel (Odontocètes du Boldérien, 1905, pp. 142-145, with illustrations) on the basis of *Phocænopis cornutus* du Bus from Tertiary strata at Antwerp. Abel refers it to

the "*Delphininae*." That which is known of it is an imperfect piece of a braincase and a few other parts. The characters, so far as they go, agree well with the ordinary dolphin type; the feature which especially distinguishes it is that the maxillary posteriorly is bowed inward unusually strongly behind the nasal. In this respect, however, dolphins show great variation. The more exact position of the genus cannot be determined.

Phocanoides is established by Roy Andrews (1911, *l. c.*) to include two recent species, one a new species, *Ph. truei* from Japan, the other a species which True had called *Phocæna dalli*, likewise from the northern part of the Pacific Ocean. The deviations from typical *Phocæna* are very small; perhaps the most noticeable is that the teeth are smaller, with the fan-like widening of the crown less pronounced. There can scarcely be sufficient ground for generic separation.

Xiphiodelphis ("*Ziphiodelphis*") (see especially Bassani e Misuri and Dal Piaz, 1912, *l. c.*) is established on fragments of skulls from Tertiary Italian deposits. There can be no doubt that it is a near relative of *Schizodelphis*, etc., but its more exact position is not yet clear.

Delphinavus is established by Lull (1914, *l. c.*) on an imperfect and compressed, indistinct skeleton from a no doubt Miocene deposit in California. The genus is supposed to stand very near to *Delphinus* in the narrow sense. The form of the palate, however, the only character that distinguishes *Delphinus* from nearly related Delphinids, does not seem to have been ascertained. One of the most important peculiarities is that the atlas and axis are mutually free. According to what is known it is not possible to clear up the relationship of the genus to other Delphinids; but it ought to be especially compared with *Heterodelphis*.

²¹ (P. 38.) It is Flower who has especially emphasized the difference between Delphinids and Physeterids with regard to the relationship of the hindmost ribs to the vertebræ. It is likewise he, in his paper on *Inia* (Trans. Zool. Soc. London, vol. 6, 1869, pp. 98-100) and elsewhere, who has pointed out the intermediate position of the Platanistids. The question about the interpretation of the transverse processes, etc., had previously been discussed, among others by Eschricht in his paper on *Platanista* (1851, pp. 369-370). Later it has been extensively dealt with by Gerstaecker (Das Skelet des Döglings, *Hyperoodon rostratus*, etc., 1887) and it is also taken up by Abel (Sitzungsber. k. Akad. Wissensch. Wien, math.-naturwiss. Kl., vol. 118, pt. 1, 1909, pp. 247-249).

- ²² (P. 43.) On the *Physeteridae* see especially:
- Cuvier: Recherches sur les Ossemens fossiles, ed. 4, vol. 8, pt. 2, 1836, pp. 117-247, Atlas, pls. 225, 228, with figures of skulls of *Physeter* and *Hyperoodon* and parts of fossil skulls of *Mesoplodon*, *Chonoxiphius* and *Xiphius* (all under the name "*Ziphius*").
- Eschricht: Under:øgelser over Hvaldyrene, 4de Afhandl., Om Næblvalen; Kgl. Danske Vidensk. Selsk. naturv. mathem. Afhandl. 11te Del, 1845, pp. 321-378, pls. 5-8, with figures, mostly of soft parts. *Hyperoodon*. On the dentition in the embryo and other things.
- Owen: On some Indian Cetacea; Transact. Zool. Soc. London, vol. 6, pt. 1, 1866, pp. 17-47, pls. 3-14. Contains a section on "*Cogia*" under the name *Physeter* (*Euphysetes*). Exterior, skeleton and skull are figured.
- Fischer: Mémoire sur les Cétacés du genre *Ziphius*; Nouvelles Archives du Muséum d'Hist. Nat. de Paris, vol. 3, 1867, pp. 41-79, pl. 4, with figures of skulls of *Xiphius cavirostris*.
- Van Beneden et Gervais: Ostéographie des Cétacés vivants et fossiles, Text and Atlas, 1868-80, pp. 303-324, 514-518, pls. 18-27 bis, 61-63. All the recent genera and most of the fossils, among them *Xiphistrostrum*, *Chonoxiphius*, *Hoplocetus*.
- Burmeister: Descripción detallada del *Epiodon australe* (*sic*); Anales del Museo Público de Buenos Aires, entrega quinta, 1868, pp. 312-366, pls. 15-20. *Xiphius*. Figures of exterior, skeleton, skull, and other parts.
- Eschricht: Ni Tavler til Oplysning af Hvaldyrenes Bygning. med Forklaring af Reinhardt; Kgl. Danske Vidensk. Selsk. Skrifter, 5te R., naturv. mathem. Afd., vol. 9, 1, 1869. On plates 6 and 7 are found figures of the skull of adult *Hyperoodon* and of the exterior and skeleton of the fetus.
- Flower: On the osteology of the Cachalot or Sperm-whale (*Physeter macrocephalus*); Trans. Zool. Soc. London, vol. 6, 1869, pp. 309-372, pls. 55-61.
- Owen: Monogr. of the British fossil Cetacea of the Red Crag; Palæontogr. Society, vol. for 1869, 1870, pp. 1-40, pls. 1-5, and with figures in the text. Mostly on the skull and "beak" of "*Ziphius*" (= *Xiphius*, *Chonoxiphius*, *Mesoplodon*, "*Berardius*").
- Flower: On the recent Ziphioid Whales, with a descr. of the Skeleton of *Berardius arnouxi*; Trans. Zool. Soc. London, vol. 8, pt. 3, 1872, pp. 203-234, pls. 27-29.

- Turner: On the occurrence of *Ziphius cavirostris* in the Shetland Seas and a comparison of its skull with that of Sowerby's Whale, *Mesoplodon sowerbyi*; Trans. Roy. Soc. Edinburgh, vol. 26, 1872, pp. 759-780, pls. 29, 30, with figures of skulls.
- Brandt: Untersuchungen über die fossilen und subfossilen Cetaceen Europa's; Mém. Acad. Imp. Sci. St. Pétersbourg, ser. 7, vol. 20, No. 1, 1873. A section, pp. 204-226, gives a synopsis of the then-known fossil Physeterids.
- Flower: A further contrib. to the knowledge of the existing Ziphioid Whales, genus *Mesoplodon*; Trans. Zool. Soc. London, vol. 10, pt. 9, No. 2, 1878, pp. 415-437, pls. 71-73, with figures of skulls and skeleton.
- Turner: Report on the bones of Cetacea collected during the voyage of H. M. S. Challenger in the years 1873-1876; Report on the Scientific Results of the voyage of H. M. S. Challenger, Zoology, vol. 1, pt. 4, 1880, pp. 1-45, pls. 1, 2. Mostly on *Mesoplodon*. Figures of skulls and other parts.
- De Sanctis: Monografia zootomica-zoologica sul Capidoglio arenato a Porto S. Giorgio; Atti della R. Accademia dei Lincei, Mem. Cl. sc. fisiche, ser. 3, vol. 9, 1881, pp. 160-242, pls. 1-7. *Physeter*. Exterior and viscera.
- Capellini: Resti fossili di *Dioplodon* e *Mesoplodon*; Memorie della R. Accademia delle Scienze dell' Istituto di Bologna, ser. 4, vol. 6, 1885, pp. 291-306, pl. 1, with figures of "beak" and other parts. *Mesoplodon*.
- Capellini: Del Ziphiode fossile (*Choneziphius planirostris*) scoperto nelle sabbie plioceniche di Fangonero presso Siena; Atti della R. Accademia dei Lincei, Mem. Cl. sc. fisiche, ser. 4, vol. 1, 1885, pp. 18-29, pl. 1, with figures of the skull. *Chonoxiphius*.
- Malm: Om Sowerby's hval; Öfversigt af kgl. Svenska Vetensk.-Akad. Förhandlingar, 1885, No. 5, pp. 121-153, pl. 9, with figures of the skull and other parts. *Mesoplodon*.
- Gerstaecker: Das Skelet des Döglings, *Hyperoodon rostratus*, ein Beitrag zur Osteologie der Cetaceen und zur vergleichenden Morphologie der Wirbelsäule, 1887, pp. 1-175, pl. 1, with figures of the vertebræ.
- Pouchet et Beauregard: Recherches sur le Cachalot; Nouvelles Archives du Muséum d'Hist. Nat. de Paris, ser. 3, Mémoires, vol. 1, 1889, pp. 1-96, pls. 1-8, with figures of the exterior, skeletal parts, teeth and their development. *Physeter*. Suite, Mém., vol. 4, 1892, pp. 1-90, pls. 1-12, with figures of the exterior, viscera, etc.

- Moreno: Lijeros apuntes sobre dos géneros de Cetáceos fósiles de la República Argentina; Revista del Museo de La Plata, vol. 3, 1892, pp. 13-20, in the separate, pls. 10, 11. *Mesocetus*=*Hypocetus*, *Notocetus*=*Argyrodelphis*.
- Forbes: Observ. on the development of the rostrum in the Cetacean genus *Mesoplodon*, with remarks on some of the species; Proceed. Zool. Soc. London, 1893, pp. 216-236, pls. 12-15.
- Lydekker: Cetacean skulls from Patagonia; Anales del Museo de La Plata; Paleontología Argentina, vol. 2, 1893, pp. 4-8, 12-13, pls. 2, 3, 6. *Physodon* (= *Hoplocetus*), *Hypocetus*, *Argyrodelphis*.
- Moreno: Nota Sobre los restos de Hyperoodontes conservados en el Museo de La Plata; Anales del Museo de La Plata, Seccion Zoologica, vol. 3, 1895, pp. 1-8, pls. 1, 2. *Hyperoodon*. Figures of entire skeletons and of skulls.
- Benham: On the anatomy of *Cogia breviceps*; Proc. Zool. Soc. London, 1901, vol. 2, pp. 107-134, pls. 8-11. See also, on the larynx, Proc. Zool. Soc. London, 1901, vol. 1, pp. 278-300, pls. 25-28.
- Benham: Notes on the osteology of the Short-nosed Sperm-Whale; Proc. Zool. Soc. London, 1902, vol. 1, pp. 54-62, pls. 2-4. "*Cogia*."
- Grieg: Bidrag til kjendskab om *Mesoplodon bidens*; Bergens Museums Aarbog, 1904, No. 3, with figures in the text. Exterior, skull and various skeletal parts.
- Abel: Die phylogenetische Entwicklung des Cetaceengebisses und die systematische Stellung der Physteriden; Verhandl. d. Deutsch. Zool. Gesellschaft, 1905, pp. 84-96.
- Abel: Les Odontocètes du Boldérien (Miocène supérieur) d'Anvers; Mém. Mus. Roy. d'Hist. Nat. de Belgique, vol. 3, 1905, pp. 1-155, with figures in the text. Deals largely with the Physterids, especially with *Scaldicetus* (= *Hoplocetus*), *Thalassocetus*, *Physterula*, *Prophyseter*, "*Placoziphius*," "*Palaeoziphius*," *Cetorhynchus*, "*Mioziphius*" (= *Xiphirostrum*), "*Choneziphius*," *Mesoplodon*.
- Danois: Recherches sur l'anatomie de la tête de *Kogia breviceps* Blainv.; Archives de Zoologie expérimentale et générale, ser. 5, vol. 6, 1910, pp. 149-174, pls. 5-8, and with text figures.
- True: Descr. of a skull and some vertebræ of the fossil Cetacean *Diochoticus Vanbenedeni* from Santa Cruz, Patagonia; Bull. Amer. Mus. Nat. Hist., vol. 28, 1910, pp. 19-32, pls. 1-5. *Argyrodelphis*.

True: An account of the Beaked Whales of the family Ziphiidæ in the Collection of the United States National Museum, with remarks on some specimens in other American Museums; Bull. U. S. Nat. Mus., No. 73, 1910, pp. 1-89, pls. 1-42. *Mesoplodon*, "*Ziphius*," "*Berardius*," *Hyperoodon*. Figures of skulls and skeletal parts.

Danois: Recherches sur les viscères et le squelette de *Kogia breviceps* Blainv. avec un résumé de l'histoire de ce Cétacé; Arch. Zool. expér. et génér., ser. 5, vol. 6, 1911, pp. 465-489, pls. 23, 24.

[Schulte: The skull of *Kogia breviceps* Blainv.; Bull. Amer. Mus. Nat. Hist., vol. 37, pp. 361-404, pls. 35-43. June 28, 1917.]

[Schulte and Smith: The external characters, skeletal muscles, and peripheral nerves of *Kogia breviceps* (Blainville); Bull. Amer. Mus. Nat. Hist., vol. 38, pp. 7-72, figs. 1-21. February 23, 1918.]

[Kernan and Schulte: Memoranda upon the anatomy of the respiratory tract, foregut, and thoracic viscera of a foetal *Kogia breviceps*; Bull. Amer. Mus. Nat. Hist., vol. 38, pp. 231-267, figs. 1-16. April 18, 1918.]

[Kernan: The skull of *Ziphius cavirostris*; Bull. Amer. Mus. Nat. Hist., vol. 38, pp. 349-394, pls. 20-32. August 1, 1918.]

Cetorhynchus was established by Gervais on remains from Tertiary strata in southern France. The most important fragment was the anterior portion of an under jaw (figured in *Ostéographie des Cétacés*, pl. 57, fig. 12). The genus is discussed by Abel (*Odontocètes du Boldérien*, 1905, pp. 94-98), who refers to it a piece of a lower jaw from the Tertiary deposits at Antwerp. The mandible has a long symphysis menti and a long row of close-placed alveoli for rather large teeth. It is a peculiar fact that the alveoli are not completely separated from each other. Only low transverse ridges separate the teeth at their bases; otherwise the teeth lay in a common groove. Abel thinks that he sees in these conditions a beginning to the peculiarities of the "*Ziphius*" group. Perhaps he is right, but there are still other possibilities.

Anoplonaassa probably belongs to the group *Xiphi*, quite likely as a near relative of *Xiphrostrum*. It was described by Cope (*Proc. Amer. Philos. Soc.*, vol. 11, 1871, pp. 188-190, pl. 5, fig. 5) on the basis of the anterior part of the mandible from Tertiary deposits at Savannah, Georgia; but it is best known from a paper by True (*Observations on the Type specimen of the fossil Cetacean Anoplonaassa forcipata* Cope; Bull. Mus. Comp. Zool., vol. 51, 1907, pp. 97-106, pls. 1-3). The fragment in question shows the mandibular rami

grown together in a very long symphysis menti. They are staff-shaped, each with a cup-like pit left by a large tooth at the very front, a somewhat indistinct alveolus further back, and also with more or less indistinct traces of other teeth in a degenerate dental groove. Abel (*Odontocètes du Boldérien*, 1905, p. 92) compares *Anoplonassa* with *Palæoziphius*; but True is no doubt right in finding a greater likeness to "*Mioziphius*" (= *Xiphistrostrum*). However, *Anoplonassa* is still too slightly known to be exactly placed.

"*Palæoziphius*" is established by Abel (*Odontocètes du Boldérien*, 1905, pp. 90-94, with figure) on the basis of a piece of the anterior end of a lower jaw from the Tertiary at Antwerp. The specimen had previously been referred by others to *Champsodelphis* and by Abel himself doubtfully to *Acrodelphis* (= *Champsodelphis*). The jaw has a long symphysis menti and a long series of alveoli left by good-sized teeth. Abel says of it with great positiveness that it belonged to a member of the family "*Ziphiidae*" (a group that about corresponds to the *Xiphiini* of the present paper; it was, he thinks, one of the first links in the series that leads from the oldest, many-toothed Ziphiids to the living two-toothed forms. His reason for believing this is that he finds the first and seventh alveoli larger than the others, a condition that he considers a first beginning of the condition found in the recent genera of the group. But in the photograph of the jaw it is impossible to see this difference in the alveoli. There is the greatest possibility of a mistake; and it cannot be asserted with any positiveness where the genus belongs.

"*Placoziphius*" is established by Van Beneden on the basis of pieces of a skull from the Tertiary deposits at Antwerp (figured in the *Ostéographie des Cétacés*, pl. 27, fig. 11). It is discussed by Abel (*Odontocètes du Boldérien*, 1905, pp. 85-88), who considers it a near relative of *Physcter*. In this he is no doubt right, but any final decision is still impossible.

Hypocetus was described as a special genus by Moreno (1892, *l. c.*) under the name *Mesocctus* Moreno (nec Van Beneden). It was called *Hypocctus* by Lydekker (1893, *l. c.*, in title and in explanation of plates, *Paracetus* in text). From Ameghino (*Énumération synoptique des espèces de Mammifères fossiles de Patagonie*, 1894, p. 181) it received the name *Diaphorocetus*. It is based on a much-broken skull from the Tertiary of Patagonia. Of the genus it can be said that it no doubt belongs to the section *Physcterini* as a rather near relative of *Hoplocctus*, but a more exact opinion is scarcely possible.

Thalassocetus is based by Abel (Odontocètes du Boldérien, 1905, pp. 70-74, with figures) on a few pieces of forehead of skulls from the Tertiary deposits at Antwerp. Abel is no doubt right in considering it a near relative of *Hoplocetus* ("*Scaldicetus*"); but the genus is too slightly known to be definitely placed.

Prophyseter is based by Abel (Odontocètes du Boldérien, 1905, pp. 82-85, with figures) on very imperfect remains from the Tertiary deposits at Antwerp. If the interpretation of the bones is right (whereof, according to the photographs, there seems to be some reason for doubt) the remains represent two pieces (perhaps belonging together) of the left side of a snout-tip, a piece of intermaxillary and a piece of maxillary, both with alveoli but no teeth. Abel believes that *Prophyseter* was a relative of *Hoplocetus* ("*Scaldicetus*"), but that it had gone a step further in the direction of *Physeter*, since the upper teeth had begun to degenerate. This refers to the fact that the alveoli in the intermaxillary appear to be in course of obliteration after the disappearance of the teeth. With regard to this there might be other explanations also. The specimens are too doubtful for anything final to be said about the animal's relationship.

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