THE TELESCOPING OF THE CETACEAN SKULL

(WITH EIGHT PLATES)

BY
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SIGNIFICANCE OF THE WORD "TELESCOPING"

The skeleton of the cetaceans shows more conspicuously than that of any other group of mammals the simultaneous action of two opposite trends of modification : the first toward reduction and elimination of those parts which have been rendered useless by a change from an original mode of life to another of a very different kind, the second toward the extreme remodeling of the parts which remain actively functional under such new conditions. The changes of the second type are those which present the greatest interest. Among them the most important are shown by the skull.

In mammals whose skulls have departed widely from the generalized original form the modifications have usually been made through great changes in the shape or size of individual bones with comparatively little alteration in the mutual contact-relationships of the parts concerned in the process. In the rare instances when such changes of contact-relationship occur, as the extension of the premaxillary backward over the frontal above the orbit in the elephants, or the covering of the parietals by the forward advancing occipital shield in the burrowing rodents of the genus *Spalax,* the changes are recognizable as exceptions to the general course of modification which the skull is undergoing. By the more usual process have

been produced such specialized types of skull as are seen in elephant, seacow, brontothere, anteater and man. In striking contrast to this kind of remodeling, the process which the skulls of all known cetaceans except the zeuglodonts have undergone is a highly developed system of " telescoping " ; that is, the portion of the skull lying behind the rostrum has been shortened, not so much by a reduction of the anteroposterior diameter of individual bones (except the parietal), as by a slipping of one bone over another or by the interdigitating of some of the elements. Alteration of contact-relationship is here not the exception but the rule. In this manner unusual conditions have arisen; such as contact of the premaxillary and supraoccipital (pl. 7, fig. 3; pl. 8, fig. 7), the presence at one transverse plane of parts of the nasal, premaxillary, maxillary, parietal, and frontal (pl. 8, figs. 6, 7), the partial covering of the supraorbital process by the lacrimal (pl. 5, fig. 6), the entire covering of the palatine and alisphenoid by the pterygoid (p. 31) or the presence at one perpendicular plane of parts of the occipital, frontal and nasal (pl. 8, fig. 9). These rearrangements of the elements of the skull are not in any general sense mere degenerative changes. They affect the skull's fundamental structure, and they are peculiar to cetaceans. With little doubt, therefore, they represent responses to stimuli which are in some way directly connected with the conditions under which these animals live—perhaps most particularly with the habit of rapid, fish-like, pelagic swimming ; in other words they are active adaptations in one of the parts of the skeleton most essential to cetacean existence. Hence the varying degree of their perfection may properly be regarded as indicating the varying extent to which different cetaceans have departed from the original land mammal type. While the fact of telescoping in cetacean skulls has long been known, the details of the process throughout the group have never to my knowledge been studied, nor does any one appear to have attempted to show what phylogenetic importance these details may present.

Considered purely from this point of view the cetacea are divisible into two groups: those in which telescoping is entirely absent and those in which it is conspicuously developed. There are no known intermediate stages between these two conditions. All of the zeuglodonts belong in the first group. All of the other cetaceans whose skulls have been described belong in the second. As the zeuglodonts are not known to have existed since early Tertiary times, the members of the second group, abundantly represented in the seas of to-day, may be alluded to collectively, whether living or fossil, as modern cetacea.

GENERAL CONDITIONS IN ZEUGLODONTS

Concerning the zeuglodonts there is little to say. All of the published figures as well as the rather scanty material which I have been able to examine agree in indicating that the bones of the skull retain their original relationships (pl. 5, fig. 1). Highly specialized on this primitive ground plan, and in a direction toward elongation and narrowing of the post-rostral portion, the zeuglodont skull, in its general structure, appears to be removed from rather than antecedent to the line of development which led to the telescoped, broadened condition of the post-rostral region seen in the skulls of all modern cetacea. It seems not improbable that the zeuglodonts were for the most part animals with relatively long bodies and small heads as compared with the living whales and porpoises [1] and that the culminating point in their characteristic line of development is indicated by *Basilosaurus,* the genus in which these tendencies appear to have been carried to the greatest extreme. The superficial resemblance which the zeuglodonts bear to reptiles as a result of these peculiarities has often been noticed; and it should be observed in the present connection, that, like the zeuglodonts, the extinct marine reptiles seem to have been without any tendency toward cranial telescoping. It may not be impossible that in both instances the relatively small head was not subjected to the mechanical forces needed to call forth the peculiar reaction which has been the dominant factor in the development of the skull in modern cetaceans (see pp. 38-39). A further reason for regarding the known zeuglodonts as probably not directly ancestral to any of the recent whales is the circumstance that in spite of the extreme degree and peculiar character of the general specialization attained by some members of the zeuglodont group the dentition of these animals appears to have been, even in such an aberrant type as *Basilosaurus,* uniformly undergoing a simple and not very unusual process of reduction in the normal mammalian manner, a tendency which would not lead by any known process to the remarkable and unique condition of polyodonty through which the modern cetacea have either once passed or are now in. [2] While it appears to me

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[1] The proportion of head length to total length in *Basilosaurus* is about as 1 to 12. It is not sufficiently known in other members of the group. In living whales it is usually somewhere near 1 to 6 (less in *Kogia* and more—even as high as 1 to 2½—in the balænids).

[2] The two principal explanations of the origin of this polyodonty—intercalation of milk teeth among the teeth of the permanent dentition, and the splitting up of serrate permanent teeth into numerous simple elements—are purely hypothetical, resting on no processes actually observed. See Winge, Smithsonian Misc. Coll., Vol. 72, No. 8, pp. 50-56, July 30, 1921.

doubtful that the known zeuglodonts were ancestral to any of the recent whales it seems probable that they came from a terrestrial stock which was nearly related to the latter's forerunners; and there can be little question that in certain details of structure they possess features which are morphologically intermediate between those of early land mammals and those of some living cetaceans. These features will be dealt with in discussing the probable course of development of the modern whales (pp. 11-12).

GENERAL CONDITIONS IN MODERN CETACEA; SUGGESTIONS AS TO THE POSSIBLE MECHANICAL ORIGIN OF THESE CONDITIONS

Concerning the modern cetacea the most conspicuous facts are these: (a) That the telescoping of the skull was far advanced in the earliest known extinct genera, and (b) that this process has developed according to two different plans. No transitional stages between these two plans of development are known; and no fossil cetacean has yet been described in which the skull has been definitely shown to be so constructed as to furnish the elements needed for the development of both. While there are important variations in details, the fundamental schemes of the two plans or types are as follows. In one type (pl. 1, figs. 1a, 1b) the entire proximal portion of the maxillary (a. pr.) passes up over the frontal and backward to approach or meet the supraoccipital at a level behind the orbit (orb.); laterally it spreads out over the expanded supraorbital wing of the frontal. Backward motion of anterior elements is the most obvious feature of this first process. In the other type (pl. 1, figs. 2a, 2b) the broad outer part of the hinder maxillary border (o. pl.) projects obliquely downward and backward under the anterior margin of the great supraorbital wing of the frontal, while the narrow inner part (a. pr.) fits closely into the body of the frontal on the upper surface of the forehead; the upper surface of the expanded supraorbital wing of the frontal is thus left bare. As though further backward progress of the maxillary were rendered difficult by this double interlocking of maxillary and frontal, telescoping is chiefly accomplished by forward extension of the occipital and parietal to and beyond the median orbital level (orb.). Forward motion of posterior elements is the most obvious feature of this second process. The first plan is peculiar to the dolphins and toothed whales, the second is confined to the baleen whales.

The opposite trends of motion in the elements chiefly concerned with the telescoping process according to the two plans are especially

well shown by figures 2 (*Platanista*) and 3 (*Balænoptera*) of plate 6. Here it will at once be seen that in the toothed cetacean the long axes of the frontal, parietal and squamous portion of the squamosal slope upward and backward as though forced into this position by some backward-crushing power acting through the elongated ascend- ing process of the maxillary. In the baleen whale, on the contrary, these axes all slope upward and forward as though they had been dominated by a foreward-crushing power acting through the elongated occipital shield. The horizontal position of the same axes in a normal skull, where no elongation of the maxillary or the occipital has taken place, is shown in figure 1 of plate 7.

The skull of a finback whale is thus seen to be telescoped in a manner so unlike that of a dolphin that it is at first difficult to under- stand how two such opposite types could have originated. The fossils thus far described give no clue to the probable history of the two processes of telescoping. Such extinct genera as *Cetotherium, Archæodelphis,* and *Agorophius* show conditions less advanced than those found in living forms; but no extinct cetacean has yet been made known in which there is certainly a confusing or blending of the two types, or in which there has been demonstrated the presence of a structure from which both plans could be elaborated.

A clear understanding of some of the more important mechanical features of the two types can be gained by examining the different ways in which contact between the bones concerned in the telescoping process is established in other mammals. Without attempting to work the subject out in detail I have found that in mammals which have a broad area of contact between the maxillary and frontal above the anterior part of the orbital rim two kinds of relationship can be seen: (a) The maxillary may slide over the frontal in the form of a thin plate or tongue of bone (fox, pl. 2, fig. 1, *a. pr.*), or (b) the edges of the bones may be solidly locked by interdigitating processes (bear) or by slipping the edge of the maxillary obliquely downward into the substance of the frontal (furseal, sea-lion, pl. 2, fig. 2, *a. pr.*). Sometimes the two methods are combined so that the maxillary extends freely up over the frontal alongside of the nasal but sends a well developed flange downward into the frontal at the edge of the orbit (cat, some mustelines). Turning to the line of contact between the occipital and parietal it is again seen that various kinds of juncture occur: the bones may come solidly together (bear, raccoon), or either may slightly override the other (parietal over occipital in fox, pl. 2, fig. 1, and domestic cat, occipital over parietal in furseal and sea-

lion, pl. 2, fig. 2). It is not now essential to try to explain the significance of these various forms of interlocking in mammals whose skulls are not telescoped. The important point is to recognize that among such mammals are found some primary structural elements from which it would appear to be mechanically possible to initiate both of the processes that have been elaborated in the skulls of the modern whales. In the fox (pl. 2, fig. 1) may be observed the combination of peculiarities which, so far as they go, are the ones seemingly needed to lead to the toothed whale type. Anteriorly the broad ascending process of the maxillary (*a. pr.*) overrides the margin of the frontal in a direction which, if continued, would carry it freely back over the base of the postorbital process and beyond to the highest point of the braincase. At the back of the skull the occipital fits so solidly against the bones in front of it that any forward progression of the upper part of the occiput would apparently need to be accomplished by eating into the substance of the hinder portion of the parietals, a process which can easily be imagined to present greater mechanical difficulty than the unobstructed backward sliding of the maxillaries over the upper surface of the frontals. The final approximation or contact of occipital and maxillary might therefore be expected to take place at a level decidedly behind the orbit, exactly as happens in the great majority of toothed cetacea (see especially pl. 1, fig. 1*a;* pl. 5, fig. 5; pl. 7, figs. 2, 4). In the furseal and northern sea-lion (pl. 2, fig. 2), on the other hand, a combination occurs which would seem to furnish a structural beginning that might lead equally well toward telescoping according to the other plan. Here the maxillary (*a. pr.*) is so firmly locked with the frontal as to have the appearance of opposing a serious check to backward movement, while the occipital overlaps the parietal as freely as the maxillary overlaps the frontal in the fox. Thus the mechanical elements are provided which might finally lead to the forward extension of the occipital shield to the level in front of the orbit which it reaches in the baleen whales. No series of ancestral or of less specialized living forms is known in which the skulls show stages intermediate between the conditions seen in the brain case of the sea-lion and the baleen whales, but a nearly parallel morphological series can be observed leading from the large occipital shield which conspicuously overrides the parietals in *Spalax* (pl. 8, fig. 8) back through such cricetine rodents as *Myospalax* and the more fossorial species of *Arvicola* to a completely unmodified occipital region like that of *Neotoma*. Longitudinal sections of the skulls of these rodents show

that the overlapping of the posterior elements is strictly of the sea-lion type, and that the specialized structure of *Spalax* is based on the working out of a condition latent in allied rodents whose skulls have remained normal.

While the obvious superficial characters of the two methods of telescoping as just described are easily observed in adult cetacean skulls, the more essential underlying features of the processes can only be studied in specimens young enough to permit of disarticulation.[1]   When such material is examined it becomes evident that the key to an understanding of the differences is probably to be found in the structure of the posterior portion of the maxillary, the region whose morphology appears to be more fundamentally essential in this connection than that of any other part of the skull.   In the baleen whales the orbital portion of the body of the maxillary[2] is present and well developed as a large " horizontal ventral " plate projecting conspicuously behind and beneath the infraorbital foramen.   The jugal comes in contact with the postero-external portion of this plate, at a level below, behind and considerably lateral to the foramen (pl. 1, fig. 2*b*; pl. 3, fig. 3 ; pl. 4, fig. 3).   In the toothed cetacea (pl. 1, fig. 1*b*; pl. 3, figs. 5 and 6 ; pl. 4, fig. 2) the horizontal orbital portion of the maxillary is absent, and the jugal is interlocked with the maxillary at a point close to the infraorbital foramen and usually in front of it ; always at a level very different from that at which contact is established in the baleen whales.   It is therefore evident that the difference between the two kinds of relationship of the maxillary to the frontal in the modern cetacea is much greater and more significant than is implied by the usual idea that in the toothed whales the maxillary passes backward over the frontal while in the baleen whales it passes backward mostly under the frontal.   For the large and conspicuous part of the maxillary which passes under the frontal in the latter group is a structure which the toothed cetacea do not possess (compare especially pl. 1, figs. 1*b* and 2*b*; pl. 3, figs. 3 and 6 ; pl. 4, figs. 2 and 3).   On the other hand the part of the maxillary which is common to the two groups, the ascending process, has in reality a homologous relationship to other structures in both types ; the essential part of the great apparent difference is merely that in

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[1] I have at my disposal young representatives of the genera *Balænoptera, Berardius, Delphinapterus, Delphinus, Globicephala, Grampus, Kogia, Lagenorhynchus, Physeter.*

[2] In normal mammals this part of the maxillary forms the floor of the anterior region of the orbit (see Jayne, Mammalian Anatomy, pt. 1, fig. 266).

the toothed whales the process (pl. 1, fig. 1*a, a. pr.*) is widely spread over almost the entire surface of the frontal including the outwardly expanded orbital wing, while in the baleen whales it is narrowly interlocked with the body of the frontal close to the nasal, leaving the orbital wing uncovered (pl. 1, fig. 2*a, a. pr.*).

At the same time that it has been telescoped the modern cetacean skull has been subjected to a process of widening, flattening, and basining in the frontal and basirostral regions. There appears to be little if any indication of this flattening or basining among the zeuglodonts. In most of the modern cetacea it is a noticeable feature of the skull (see particularly pl. 5, fig. 5; pl. 6, fig. 1; pl. 7, fig. 3). As the basining centers about the region of the base of the maxillary its details and results may have been modified by the two types of structure that have just been described. In the baleen whales the horizontally expanded supraorbital process or wing of the frontal seems to have been forced down from the normal mammalian position of the process seen in a sea-lion (pl. 2, fig. 2) or a zeuglodont (pl. 5, fig. 1) until its anterior half has come to lie against the similarly expanded orbital portion or " horizontal ventral " plate of the maxillary (pl. 1, fig. 2; pl. 6, fig. 3). The anterior part of the original orbital cavity is thus obliterated (compare pl. 1, fig. 2*b* with pl. 1, fig. 1*b*). The two bones are essentially in contact over a wide surface, but there is no semblance of fusion or interlocking between them, nor does their very unusual relationship appear to add anything to the strength or efficiency of the skull. On the contrary this broad approximating of the two expanded plates is to me more suggestive of a fortuitous and structurally unharmonious adjustment of these particular parts to that general necessity for widening and flattening of the basirostral region which the skulls of all the modern cetacea seem to be subject to. This appearance of mechanical weakness arises primarily from the excessive contrast between the very large orbital plate and the relatively minute ascending process by which alone the huge maxillary bone is directly fastened to the frontal (see pl. 1, fig. 2*a;* pl. 3, fig. 3; pl. 4, fig. 3); it is heightened by the thinness of the plate, the irregularity of its free margin (pl. 1, fig. 2*b*), and by the frequent presence of vacuities in its substance, features which strongly suggest an advanced stage of degeneration. In the toothed cetacea, however, the entire structure of this part of the maxillary has an aspect of mechanical efficiency and of perfect adjustment to free depressing and basining. The enlarged ascending process, widely expanded both backward and laterally (pl. 1, fig. 1*a;*

pl. 3, figs. 5, 6), provides adequate support for the rostral portion of the maxillary. Its superficial area in a skull of *Delphinus* (pl. 5, fig. 4) is about equal to that of the rest of the bone, in one of *Grampus* it is about twice as great; while in a pike whale it is less than one-twelfth.[1] There is, furthermore, no orbital portion of the bone to interfere with lowering the expanded postorbital process of the frontal to any required level. Basining, therefore, as might be expected, is, in this group, carried to the extreme, culminating in the conditions seen in the sperm whale (pl. 6, fig. 1) and *Kogia* (pl. 7, fig. 3).

In order to explain the origin of the two kinds of telescoping it appears to be necessary to look for some other factor than the work of different forces applied to the remodeling of one original type of structure (see pp. 35-39). Special elements of a kind which seemingly might have an important bearing on the initiation of two such processes in the superficial portion of the skull have already been shown (pp. 5-6) to exist among mammals that have not undergone cetacean modification. The skull of the fox and sea-lion respectively, furnish combinations resembling those which might be supposed to be required (pl. 2). Turning to the base of the disarticulated maxillary in the same two animals it immediately becomes obvious that here once more are apparently the looked-for conditions. The maxillary of a sea-lion (pl. 3, fig. 1), like that of a furseal (pl. 3, fig. 2), when viewed from behind, is seen to have essentially the same structure as that which has been found (pp. 7-8) to exist in the disarticulated maxillary of a baleen whale (pl. 3, fig. 3), while that of a fox (pl. 3, fig. 4) might pass, by a series of relatively unimportant changes, into that which is found (pp. 7-8) in the similarly treated maxillary of a toothed cetacean (pl. 3, figs. 5 and 6). The essential feature of difference between the proximal portion of the maxillary of a northern sea-lion or a furseal and that of a fox is that in the seal type the orbital part of the bone is developed outward beyond the alveolar level as a broad horizontal plate (*o. pl.*) independent of the tooth row, while in the fox type it is confined to the region directly above the alveoli; its entire base, in the fox, serves as a support to the teeth, and its outer portion is tilted upward and outward at a conspicuous angle. In the maxillaries of both animals the "malar process" extends along the margin of the orbital plate from the

[1] A further indication of the mechanical weakness of this part of the mysticete skull is the relatively great frequency with which weathered or fossil specimens are found lacking the rostrum.

postero-external angle of the plate to a point distinctly above the antorbital foramen. To develop the baleen whale type from a starting point at which the structure resembled that which is now present in the furseal or sea-lion it is merely necessary to suppose that the pressing together of the orbital plate of the maxillary and the expanding postorbital process of the frontal may have forced the jugal bone to abandon its connection with all of the " malar process " of the maxillary except the lowest, most posterior portion. The development of the toothed cetacean type from a starting point resembling the fox structure might equally well be conceived as primarily the result of degeneration of the orbital plate accompanying complete elimination of the large teeth to which, in the fox, this plate is intimately adjusted.[1] In the fox the heaviest, widest teeth lie behind the level of the antorbital foramen; but in no modern cetacean are any functional teeth whatever known to occur in this region. With the elimination of the posterior teeth and the subsequent degeneration of the orbital plate in a maxillary resembling that of a fox the posterior portion of the malar process might be expected gradually to disappear, thus cutting away or shriveling up the area of connection for the jugal bone with the maxillary until this area became restricted to the highest, most anterior part of its original extent. The differences just described as distinguishing the maxillary of the fox from that of the furseal or sea-lion may be at least partly connected with the relatively very different size of the eye in the two animals. The wide, horizontal orbital plate of the seal and sea-lion acts as a support to the enlarged eye while the narrow oblique plate of the fox meets all the requirements of a normal eye. The orbital plate's persistence in one suborder of modern cetaceans and its absence in the other may therefore point, perhaps, to a difference in the history of the eye in the two groups.[2]

The foregoing comparison between cetacean structures and the conditions found in living pinnipeds and carnivores must not be misinterpreted as implying an idea of immediate affinity among any of the animals in question; each group appears to have had its own independent history. I do not know of any reason to suppose that a

[1] In the actual ancestors the plate was almost certainly not developed to the extent that it is in the fox; this does not lessen the value of the fox as a convenient illustration of the general mechanical course of the process.

[2] Pütter has recorded various peculiarities of the eye and its accessory structures which appear to have this meaning (Zool. Jahrb., Anat., Vol. 17, pp. 99-402, Nov. 10, 1902).

baleen whale on the one hand, is directly related to a sea-lion, while a dolphin, on the other, is near kin to a fox. No more would it seem reasonable to suppose that the first pair might represent two widely divergent offshoots from one phylogenetic stock while the second pair might represent similar developments from another. My object is merely to show that several fundamental features of difference between the skulls of members of the two suborders of living cetaceans are, in the present absence of evidence derived from fossils, most readily explained by assuming that the ancestral forms of one group, at the time when telescoping was about to begin, had certain critical regions of the skull built on essentially the same lines as the corresponding regions in the skull of the northern furseal or the northern sea-lion, while the forerunners of the other, at the corresponding period of the group's history, had them arranged essentially as they are now seen in the fox. Terms of comparison better both structurally and phylogenetically could without doubt be obtained from the skulls of creodonts; but these fossils cannot be disarticulated for use in preparing illustrations such as those on plates 2, 3 and 4, and I have therefore preferred to limit my detailed morphological studies to recent material. Rather hasty examination of the creodonts in the U. S. National Museum and the American Museum of Natural History (in company with Dr. William K. Gregory) has not resulted in the discovery of any genus in which the furseal-mysticete conditions are clearly marked out. The most that can be said is that these conditions are suggested by the structure of the maxillary in *Sinopa* and others. On the contrary the fox-odontocete type of condition is definitely present in the maxillary of *Hyænodon* and *Pterodon*, in a form which, so far as its actual structure is concerned, appears to be leading toward the anatomical features present in the toothed cetacean type; or, perhaps more properly, the structure in the fossils is one which could give rise to both fox and odontocete types of maxillary through two slightly different courses of modification. The posterior teeth of these creodonts are narrow and are situated close under the anterior base of the zygoma so that there is practically no orbital plate. These features are nearly the same as in *Prozeuglodon* (pl. 4, fig. 1 and pl. 5, fig. 1). Comparison of the skulls of *Prozeuglodon* and *Delphinus* (pl. 5, figs. 1 and 4) and the maxillary bone of *Prozeuglodon* and *Grampus* (pl. 4, figs. 1 and 2) shows that the transition from the earlier to the later type, so far as the particular structures under discussion are concerned, would probably be mainly a matter of simple degenera-

tion of the zygoma accompanying the loss of the posterior teeth and the consequent disuse of the masseter muscle. The outward pushing of the lacrimal beyond the base of the jugal, characteristic of the extreme type of toothed cetacean skull, is already well indicated in the zeuglodont (see especially Andrews's pl. 21, fig. 1, Tert. Vert. Fayûm, 1906). On the other hand, it will at once appear from comparison of the maxillary of a zeuglodont with that of a baleen whale (pl. 4, figs. 1 and 3) that here a transition from the earlier to the later type would involve the inexplicable complication of introducing a large new structure, the freely projecting orbital plate (pl. 4, fig. 3, *o. pl.*), in a position where it meets no recognizable mechanical need, and in a condition which suggests a well advanced stage of degeneration.

THE THREE CETACEAN PHYLA OR SERIES

The facts which have just been reviewed appear to be most simply and fully explained by assuming that the known cetacea represent three distinct lines of descent and that the directions in which these lines were to develop were determined by peculiarities of structure established at or before the beginning of pelagic life. The idea that the phylogeny of the cetacea has been multiserial [1] is not new. In different forms and for various reasons it has been put forward by several authors who have dealt with the question of the group's history. The whole subject has recently been reviewed by Kükenthal (Sitzungsber. Preuss. Akad. Wissensch., Phys.-math. Kl., 1922, pp. 72-87. Meeting of March 16, 1922). As I understand it this assumption does not imply that the separate lines represent convergence from widely different ancestral stocks. Such heterogeneous origin is made to appear improbable by the resemblances between zeuglodonts, baleen whales, and toothed whales in features which are not readily explained as the mere retention of primitive characters or as the separate remolding into similar structure of originally unlike parts applied to a single new and peculiar mechanical use. The auditory

[1] The term *polyphyletic,* often used in this sense, is open to the objection that it has two meanings: *multiserial* and *polygenetic.* Apart from the context, therefore, we can never know whether a "polyphyletic group" is a group consisting of several genetic lines coming up out of the past in a direction parallel with each other and never uniting, or whether it is a group formed by the uniting of several lines coming up from different directions. Ambiguity would be avoided by the consistent use of *multiserial* to express the first idea and *polygenetic* to express the second. For *monophyletic* it might be well to substitute *uniserial.*

bones and the scapula have been alluded to by Winge in this con-
nection (Smithsonian Misc. Coll., Vol. 72, No. 8, p. 48, July 30,
1921). To account for the observed morphological conditions it now
appears to me unnecessary to assume that the three points of origin
were farther apart than adjacent families in some carnivore-like,
perhaps early creodont, stock; one which might have also given rise
to the modern carnivores and pinnipeds. When independently be-
ginning to undergo cetacean modifications one of these ancestral
forms may be supposed to have had some resemblance to *Pterodon,*
with a tendency toward narrowing the cranial portion of the skull
similar in character to the tendency which may now be seen in the
aquatic *Cynogale* (pl. 7, fig. 1) among the *Viverridæ* but carried to a
much greater extreme. It might have led to the zeuglodont type
(pl. 5, fig. 1). The two others may have been more like *Palæonictis*
in general form of the skull, but with a tendency toward broadening
of the cranial region such as that which is now displayed by the
aquatic otters among the *Mustelidæ,* thus leading to the modern
cetacean type. In these broader-headed animals two sets of peculiari-
ties, somewhat analogous on the one hand to those which I have de-
scribed as now existing in the fox and on the other to those now found
in the furseal and northern sea-lion, might be supposed to have sup-
plied the bases for developing, respectively, the skull of the toothed
cetaceans and that of the baleen whales. On account of their ap-
parently essential community of origin and fundamental structure
the three series should for the present be regarded as forming a
single order. All the known members of each series, including the
oldest fossils sufficiently well preserved to merit serious discussion,
have developed in strict accordance with the definite, and, as it would
seem, mutually exclusive tendencies of their respective groups. These
three groups show such entire independence throughout the geologi-
cal periods during which they are known to occur that, as is generally
recognized, they are best treated as distinct suborders. Their char-
acters may be summarized as follows:

KEY TO THE SUBORDERS OF CETACEA

Bones of both rostral and cranial portions of the skull retaining their
  normal mammalian relationships; braincase narrow and elongate; teeth
  present in about the maximum normal eutherian number, the hinder
  ones tending to disappear.....................................ARCHÆOCETI.
   [Cheekteeth retaining distinct traces of the inner portion of the crown.
                                                            Protocetidæ.
   Cheekteeth without traces of inner portion of the crown
    Centra of vertebræ normal............................*Dorudontidæ.*
    Centra of vertebræ greatly elongated..................*Basilosauridæ.*]

Bones of both rostral and cranial portions of the skull departing con-
spicuously from their normal mammalian relationships; braincase broad
and short; teeth increased above the normal eutherian number or
secondarily reduced or absent.

Maxillary with orbital plate present; ascending process of maxillary
small and narrow, interlocked with body of frontal, not spreading
over the expanded supraorbital process; braincase telescoped chiefly
from behind; bones forming wall of narial passage always retaining
essentially normal relationships; region of base of mesethmoid roofed
over by nasals and by median portion of frontals; teeth present in
large numbers in embryos but not known to occur in adults; baleen
always present in adults [For key to families and genera see
page 20] ....Mysticeti.

Maxillary with orbital plate absent; ascending process of maxillary
large and broad, not interlocked with body of frontal, spreading out-
ward over the expanded supraorbital process; braincase not tele-
scoped chiefly from behind; bones forming wall of narial passage
usually departing conspicuously from normal relationships; region
of base of mesethmoid usually not roofed over by nasals or by
median portion of frontals; teeth normally present in adults; baleen
always absent [For key to families see page 33]............Odontoceti.

THE DETAILS OF TELESCOPING AND THEIR RELATION TO CLASSIFICATION

While telescoping in each of the suborders of modern cetacea has
followed a course which is very consistent as to its main features
the various genera are found to arrange themselves according to
stages and minor variations of the process. Each of these special
peculiarities of detail is well marked and constant for the genera in
which it occurs, a circumstance that would of itself indicate definite
importance in classification. This importance is, however, greatly in-
creased by the fact that with every stage or detail of telescoping
there is associated, in other parts of the skull and skeleton, a special
set of characters which are often so well marked that they would by
themselves be sufficient to define the same groups, but which do not
necessarily present in their degrees of development any parallelism
with the progress of telescoping. Conditions of this kind appear to
be most clearly expressed by according family rank to the various
groups and by arranging the groups primarily in accordance with
the progress of that essential process by which the excessively modi-
fied modern cetacean skull seems to have been developed from the
ordinary mammalian structure. The course of this advance appears
to have been influenced in each individual case by varying combina-
tions of the same two general tendencies which have been seen (p. 4)
to underlie the differentiation of the two main types of telescoping.

According to one of these tendencies the forward movement of the posterior elements of the skull seems to have held precedence over the backward movement of the anterior elements; according to the other the opposite seems to have been true. While, within each main type, the predominance of one movement is usually evident, there are phases of each type in which the two movements are so combined as to give rise to a somewhat balanced or less one-sided form of telescoping, and others in which the skull appears as if it may have been first subjected to one movement and later to the other. In a general way these varying conditions are distributed somewhat as follows: occipital thrust conspicuously dominant in the balænoids and less so in the balænopteroids; maxillary thrust conspicuously dominant in most of the odontocetes; the two thrusts more intimately combined in the odontocetes of the physeterine type and *Platanista;* a final occipital thrust subsequent to a strongly developed maxillary thrust in the ziphiids. In the following discussion of the details of telescoping among the cetaceans whose skulls are sufficiently known to show these essential characters the use of expressions conveying the ideas of early and late or before and after, is (unless something else is clearly shown by the context) to be understood as applying to the process and not to time; a very late stage of a process might be quickly reached in one animal at a very early geological time, while an early stage might persist in another animal, or in a different part of the same one, to the present day.

DETAILS IN THE BALEEN WHALES

In the general structure of their skull the baleen whales have departed less widely than the toothed cetacea from the ordinary mammalian type. The choanæ still lie distinctly behind the anterior nares as in other mammals. The bones forming the nasal passage retain a general arrangement which is essentially normal, agreeing with the conditions present in the furseal and sea-lion in their fundamental relationships, including the complete roofing over of the proximal ethmoid region by the nasals and the median portion of the frontals, and the exclusion of the palatine from the anterior wall of the narial passage; primitive features which have for the most part disappeared in all known adontocetes except the agorophiids and physeteroids, where some or all of them may persist. The maxillary retains the orbital portion of the body of the bone, while the rostrum is never developed into the attenuated beak which is characteristic of many though not all toothed cetaceans.

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Telescoping with excessively dominant occipital thrust is seen in the genera *Balæna, Eubalæna* and *Neobalæna.* A diagram showing the general relationships of the bones at the vertex is given in figure 1 of plate 8. It is taken from the photograph of a skull of *Eubalæna,* but it will answer sufficiently well for the plan of all three.[1] The occipital shield will be seen to have extended forward to a level distinctly anterior to the orbits and to the articular level of the squamosals, completely excluding the parietal from the dorsal surface of the skull, and reducing the median dorsal exposure of the frontal to a narrow transverse strip of bone; the nasal and nasal branch of the premaxillary lie entirely in front of the orbit and of all of the frontal except its unimportant median angle or projection. The nasals and nasal branches of the premaxillary are thus situated obviously in the rostrum with their posterior margins well in advance of the orbital level; and the base of the rostrum has no appearance of having been pushed back against or into the structures which lie behind it. A transverse line drawn across the dorsal aspect of the skull through the base of the nasal will traverse also the premaxillary and maxillary but no part of the frontal other than the unimportant median projection (this projection is most strongly developed in *Balæna*). Such a relationship of the parts in the base of the rostrum presents no very unusual features as compared with the conditions existing in ordinary land mammals. A slight lengthening of the nasal branch of the premaxillary would bring it about in dogs or cats or various ungulates; it is almost realized in some of the bears and pinnipeds, and it may be seen exactly reproduced so far as essential features are concerned, in squirrels, pocket gophers and other rodents (pl. 8, fig. 8). The side view of such a cetacean skull (pl. 6, fig. 4) shows even more clearly how the post-rostral portion has been overridden by the occipital shield while the rostrum has not interlocked with the structures behind it. The intermaxillary has extended backward to the same level as the base of the maxillary; but neither of these bones shows any tendency to encroach upon the frontal. On the contrary the forward push of the occipital region seems to have crushed the frontal broadly against the maxillary,

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[1] In the case of *Neobalæna,* the skull of which I have not seen, I have based my comparison of the conditions existing in the region of the vertex on the figures published by Hector (Trans. and Proc. New Zealand Inst., Vol. 2, pl. 2B, 1869) and Oliver (Proc. Zool. Soc London, 1922, Oliver, pl. 1, September, 1922). They appear to have been made from a better point of view than the one published by Beddard (Trans. Zool. Soc. London, Vol. 16, pl. 8, 1901).

flattening the posterior border of the latter bone until in the region of the ascending process there is nothing more than a broad postero-superior angle. These peculiarities may be due in part to the arching which the skull has undergone in connection with the development of the greatly elongated plates of baleen within the mouth cavity; but, whatever their origin, they appear to have resulted in modification almost exclusively through forward overthrust and movement from behind. Of the genera in which this kind of telescoping has taken place *Balæna* and *Eubalæna* present the extreme of specialization in the development of the food-straining apparatus, a specialization which involves increase in the size of the head as compared with that of the body, and a great upward-arching of the whole skull accompanied by lengthening of the baleen plates and enlarging of the suspension area for the lower jaw. In *Neobalæna* on the other hand the skull is moderately arched, and the form of the rostrum is peculiar among the living baleen whales; broad at the base and narrowing rapidly to an attenuate tip; mandible excessively robust, strongly bowed outward. The rib-bearing portion of the vertebral column in *Neobalæna* shows the maximum condition of development known in the group, but the cervicals are completely fused with each other, and the hinder part of the column is so remarkably reduced by suppression of some of the caudals and all but two of the lumbars that the number of vertebræ behind the dorsals does not exceed that of the dorsals themselves, while in all other baleen whales it is at least twice that of the dorsals. The ribs are large and broad, but all except three or four at the anterior end of the series are unattached to the vertebræ, a condition not known in other whalebone whales. These characters of *Neobalæna* indicate such a fundamental divergence on the part of this genus from *Balæna* and *Eubalæna* that it should be placed in a separate family.

In all of the other mysticete genera except the extinct near relatives of the balænids the backward movement of the anterior elements of the skull appears to have been an important part of the process of telescoping. The nasal bones and the nasal branches of the premaxillaries are no longer situated obviously and conspicuously out in the rostrum. Their bases are forced back to or beyond the level of the anterior border of the supraorbital portion of the frontal, thus finally reaching a position which they do not occupy in any known land mammals and which gives them the appearance of belonging to the facial part of the skull.

The extinct genus *Cetotherium* and its allies represent the least modified known stage (pl. 8, fig. 2). The anterior point of the occipital shield lies decidedly behind the level of the orbit as well as of the anterior margin of the articular portion of the squamosal, while in front of the shield the parietals come into contact with each other on the vertex, usually forming a distinct transverse band in front of the occipital shield. Beyond the parietals the frontals also cross the vertex as a wide band. They pass directly and broadly into the supraorbital processes. A peculiarity which distinguishes the skull of *Cetotherium* and its allies from that of all the other known baleen whales is the gradual slope of the supraorbital process from the dorsal level of the interorbital region downward and outward toward the margin of the orbit. In all other members of the suborder the basal part of the process is abruptly and conspicuously depressed below the median dorsal level, so that the main outwardly-extending dorsal surface of the process is more nearly horizontal in position.

In the genus *Rhachianectes* a more advanced stage (pl. 8, fig. 3) is represented. On comparing the diagrams it will be seen that this stage is readily derived from the last. The principal peculiarities as compared with *Cetotherium* are that the supraorbital process of the frontal is broader at base (where it is abruptly depressed below the dorsal level), the nasal is greatly enlarged, the nasal processes of the maxillary and intermaxillary are lengthened, and the overthrust of the occipital shield, while not enough to carry the front of the shield beyond the level of the anterior margin of the articular portion of the squamosals, has progressed forward sufficiently to push apart the parietals on the vertex, where, however, these bones are transversely united by a narrow band of interparietal. Interdigitation of frontal, maxillary, intermaxillary and nasal is well marked, but it is not sufficiently seconded by forward thrusting of the elements of the braincase to involve the parietal. This bone is broadly exposed on the surface of the braincase along the inner side of the temporal fossa, its extremity just appearing on the vertex. It lies entirely behind the nasals and the nasal branches of the intermaxillaries and maxillaries. It is behind the frontal everywhere except in the region where the supraorbital portion of the frontal joins the part which is exposed on the vertex. Here the parietal sends forward a very short, wide, triangular process which interlocks with the frontal. In many important details of structure *Rhachianectes* stands apart from all the known whalebone whales both recent and fossil. The nasals are larger than in any other known cetacean. Notwithstanding the large

area which the nasals occupy, the frontals, owing to the slight for-
ward extension of the occipital shield and the exclusion of the
parietals from the middle of the vertex, share with *Cetotherium* and
its allies the maximum known degree of exposure on the vertex.
The surface of the relatively small occipital shield is noticeably tuber-
culate-roughened for muscle attachment. The rostrum and jaws have
been developed according to tendencies different from those seen in
other whalebone whales: rostrum moderately arched, rather narrow
at base, gradually tapering, straight-sided, and with a general inclina-
tion to deepening rather than to widening; intermaxillaries con-
spicuously produced upward above maxillaries to form a raised rim
to the nasal cavity; mandible very heavy, and so remarkably little
bowed outward that a straight line can be drawn from its base to its
tip without passing conspicuously outside of the general contour;
no definite coronoid process. The portions of the skull serving as
suspensorium to this unusually heavy mandible are smaller and less
specialized than in any of the other living baleen whales.

The most extreme stage of the mysticete type of telescoping (pl. 8,
figs. 5, 6, 7) is found in the finbacks and humpback. In all of these
whales, as in *Balæna, Eubalæna* and *Neobalæna,* the occipital shield
is carried forward beyond the level attained by the anterior part
of the articular processes of the squamosal, a peculiarity which im-
mediately distinguishes them from the living *Rhachianectes* and the
extinct cetotheres. The general interlocking of the rostrum with
the cranium is in some respects like that which has been seen in
Rhachianectes. But it has gone a definite step farther; accompanying
the forward extension of the occipital shield the pointed antero-
external termination of the parietal, which projects slightly into the
frontal of *Rhachianectes,* has now been developed as a thin plate
extending far forward along the inner wall of the cavity above the
orbital wing of the frontal (pl. 6, fig. 3) in a direction parallel with
the nasal and nasal branches of the intermaxillary and maxillary, the
level of whose bases it overlaps. In the less pronounced examples
of this type (pl. 8, figs. 5 and 6) seen in *Balænoptera* and *Megaptera*
a distinct strip of the frontal, lying between the forward-projecting
plate of the parietal and the backward-projecting nasal process of
the maxillary, connects the supraorbital wing with the narrow
exposure of the frontal on the vertex; but in the more pronounced
condition (pl. 8, fig. 7) present in *Sibbaldus* the frontal practically
disappears from the surface of this part of the skull, the parietal
almost applies itself to the outer margin of the nasal branch of the

maxillary,[1] and the occipital shield comes in contact with the maxillary, premaxillary and nasal. A definite set of other characters is associated with these final stages of telescoping. The straining-bag formed by the mouth is increased in capacity not by an arching of the rostrum as in the balænoids, but by a bowing outward of the lower jaws, a broadening and flattening of the rostrum, and a longitudinal folding of the skin of the entire throat and underside of the mouth to allow for great distention. While the jaw is not conspicuously increased in size relatively to the size of the skull the parts of the cranium serving as its suspensorium are enlarged and specialized to a greater degree than in *Rachianectes*. The characters just enumerated distinguish this group of genera as a family separate from the four other families of baleen whales. Within the limits of the group the humpbacks, *Megaptera,* are sharply contrasted with the finbacks, *Balænoptera* and *Sibbaldus,* by the unusual structure of the scapula and by the great elongation of the manus. In the finbacks the scapula retains the form characteristic of the baleen whales in general: the coracoid and acromion are large, functional processes. In the humpbacks the processes are reduced to mere tubercles. Humpbacks and finbacks differ from each other sufficiently to be regarded as the representatives of two subfamilies.

The more important characters of the genera and higher groups of baleen whales are tabulated in the following key:

KEY TO THE FAMILIES AND GENERA OF BALEEN WHALES

Telescoping of skull accomplished chiefly by forward movement of posterior elements; interdigitation of rostral and cranial elements of skull absent or slight, the nasals and nasal branches of the intermaxillaries situated entirely anterior to the level of the orbital wings of the frontals; no definite " nasal process " of maxillary ever present (Balænoids).

    Supraorbital wing of frontal narrow, its antero-posterior diameter at middle less than one-third its transverse diameter; rostrum so highly arched that a straight line cannot be drawn from its extremity to any part of its base without passing outside of the general contour; general outline of rostrum when viewed from above attenuate; most of the ribs attached to the vertebræ; lumbar vertebræ 10 or more.

                                                                            BALÆNIDÆ.

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[1] In a 20-foot skull of *Sibbaldus musculus* (No. 49757, U. S. Nat. Mus.) the upper edge of the parietal rises to the same level as the dorsal surface of the maxillary; it is separated from the maxillary by a groove about 10 mm. wide and 20 mm. deep, at the bottom of which can be seen the superior margin of the frontal.

· Entire skull when viewed from the side arched more abruptly at base than in rostral portion, the general curve therefore not approximately following the arc of a circle; length of skull contained about three times in length of vertebral column; depth of skull from highest part of arch to lower border of mandible less than greatest depth of thorax..........................*Eubalæna.*

Entire skull when viewed from the side arched rather uniformly in a curve which approximately follows the arc of a circle; length of skull contained about one and one-half times in length of vertebral column; depth of skull from highest part of arch to lower border of mandible conspicuously greater than greatest depth of thorax..*Balæna.*

Supraorbital wing of frontal broad, its antero-posterior diameter at middle more than one-half its transverse diameter; rostrum so slightly arched that a straight line can be drawn from its extremity to its base without passing outside of the general contour; general outline of rostrum when viewed from above tapering rapidly from a broad base to slender tip; most of the ribs free from the vertebræ; lumbar vertebræ 2 (*Neobalæna* only)...................NEOBALÆNIDÆ.

Telescoping of skull accomplished by a combined forward movement of posterior elements and backward movement of anterior elements which produces at least some obvious indication of interdigitation between rostral and cranial elements; nasals and nasal branches of premaxillaries not situated entirely anterior to the level of the orbital wings of the frontals; a definite " nasal process " of the maxillary always present (Balænopteroids).

Parietal entirely behind posterior level attained by nasals and nasal branches of maxillaries and intermaxillaries; occipital shield not extending forward over level of orbit or beyond anterior level attained by articular portion of squamosal; frontal broadly exposed on vertex; expanded lateral (articular) portion of squamosal relatively small, its under surface not deeply concave.

Supraorbital process of frontal sloping gradually downward and outward from level of dorsal surface of interorbital region; parietals coming in contact or nearly so on vertex between occipital shield and frontal; nasals small (normal), their combined dorsal area equal to much less than half that of supraorbital portion of frontal; rostrum tending toward breadth rather than depth; mandible slender, conspicuously bowed outward (*Cetotherium* and related genera).................CETOTHERIIDÆ.

Supraorbital process of frontal abruptly depressed at base to a level noticeably below that of dorsal surface of interorbital region; parietals not coming in contact or nearly so on vertex between occipital shield and frontal; nasals greatly enlarged, their combined dorsal area equal to more than half that of supraorbital portion of frontal; rostrum tending toward depth rather than breadth; mandible heavy, slightly bowed outward (*Rhachianectes* only) .........................RHACHIANECTIDÆ.

Parietal extending forward laterally beyond posterior level attained by
nasals and nasal branches of maxillaries and intermaxillaries;
occipital shield extending forward over level of orbit and beyond
anterior level attained by articular portion of squamosal; frontal
scarcely or not exposed on vertex; expanded lateral (articular) por-
tion of squamosal relatively large, its under surface deeply concave
[supraorbital process of frontal abruptly depressed at base to a level
noticeably below that of dorsal surface of interorbital region;
rostrum tending toward breadth rather than depth; mandible con-
spicuously bowed outward]...........................BALÆNOPTERIDÆ.

Scapula with acromion and coracoid processes rudimentary
[Rostrum and frontal with general relationships as in *Balœnop-
tera*] (*Megaptera* only)...........................MEGAPTERINÆ.
Scapula with acromion and coracoid processes well developed.
BALÆNOPTERINÆ

Rostrum approaching maximum development, triangular in
outline when viewed from above, its sides straight or slightly
and evenly curved; telescoping of braincase nearly at maxi-
mum, the portion of frontal exposed on vertex of skull
narrow but evident.............................*Balœnoptera*.
Rostrum at maximum known development, its sides parallel
with each other through most of basal half, then rather
strongly curved to tip; telescoping of braincase at maxi-
mum, the portion of frontal exposed on vertex of skull so
narrowed that parietal is essentially in contact with maxil-
lary, and occipital touches base of nasal.............*Sibbaldus*.

DETAILS IN THE TOOTHED CETACEA

In general structure of the skull the toothed cetacea have departed
more widely than the baleen whales from the ordinary mammalian
type. Except in members of the extinct family *Agorophiidœ* the
anterior nares have been forced back over the choanæ so that the
arrangement of the bones forming the nasal passage is no longer
essentially normal; the proximal ethmoid region is completely ex-
posed from above (pl. 1, fig. 1*a*), without over-roofing by the nasals
or by the median portion of the frontals; the palatine takes part in
forming the anterior wall of the narial passage. The maxillary
(pl. 1, fig. 1*b*) has no trace of a horizontal orbital plate, even, ap-
parently, in the peculiar genera just alluded to. The rostrum is
often developed into a slender beak widely different in character
from the corresponding part of the skull in any other mammals.
While the process of telescoping in this group has without exception
followed the general course whose main features have already been
described (p. 4, etc.), the two chief variations in this course appear to
be almost as clearly indicated as in the case of the baleen whales.
In one (pl. 5, figs. 4, 5; pl. 7, figs. 2, 4) the backward thrust of the

maxillaries seems to have been either more pronounced than the forward thrust of the occipital or to have reached advanced stages of development earlier in the process of telescoping than the period when the forward advance of the occipital became conspicuous; in the other (pl. 6, figs. 1, 2; pl. 7, fig. 3) the discrepancy between the two movements is less obvious, and their share in the remodeling of the skull appears to have been less unequal. One of the most noticeable results of the first tendency has been to carry the maxillary back in such a manner that the frontal, except in the orbital rim, is practically excluded from view in the region lying above and behind the eye; at most it may be visible as a band of varying width extending upward and backward along the margin of the temporal fossa behind but not over the orbit (pl. 5, figs. 4, 5; pl. 7, fig. 4). The second tendency, on the contrary, brings about conditions in which a relatively wide area of the frontal is visible in the region directly above the orbit (pl. 6, figs. 1, 2; pl. 7, fig. 3). Each of these tendencies has been worked out in great detail; the dominant maxillary thrust is particularly well shown in *Stenodelphis* (pl. 7, fig. 2), the more balanced condition in *Kogia* (pl. 7, fig. 3). Contrary to what might be expected it is the second tendency which has led to the development of the cetacean skulls (pl. 6, fig. 2, and pl. 7, fig. 3) whose structure is most fundamentally removed from a characteristic terrestrial mammalian type (pl. 7, fig. 1) .

The least modified structure positively known to exist occurs in the genera *Agorophius* (pl. 5, fig. 2), *Archæodelphis* (pl. 5, fig. 3), and *Xenorophus* (pl. 5, fig. 6), the first and third from the Eocene or Oligocene of South Carolina, the second perhaps from the same region and horizon.[1] The skull is broad and short (for dorsal view of *Agorophius* see True, Remarks on the type of the fossil cetacean *Agorophius pygmæus* (Müller), Smithsonian Inst., Publ. No. 1694, 1907. For other figures of *Archæodelphis* see G. M. Allen, Bull. Mus. Comp. Zool., Vol. 65, No. 1, August, 1921). The process of telescoping is well advanced and strictly of the modern odontocete type. The occipital, however, contrary to the conditions existing in all other known toothed cetaceans except the zeuglodonts, has not yet extended far enough forward to meet the frontal. The parietals are therefore still present on the vertex of the braincase, where they form the roof of a short but obvious postorbital constriction the width

[1] An essentially similar structure may be present in *Patriocetus* from the Oligocene of Austria; but the published facts concerning this genus are not sufficiently conclusive to warrant any generalizations (see pp. 42-44).

of which, in *Agorophius* at least (the skulls of the two other animals are imperfect in this region), is equal to about one-third or one-fourth the greatest width of the skull.   (The entire braincase of *Xenorophus* is lost, but the essential agreement with the two other genera is shown by the structure of the orbits and the interorbital region.)   In this character there is a close analogy with the condition present among the *Cetotheriidæ*. The maxillary in two of the known specimens is imperfect. It is sufficiently well preserved, however, to show that in *Agorophius* and *Xenorophus* it had already overridden the frontal in very much the same manner as that which is normally seen in porpoises, and to such an extent that it overlaps the anterior edge of the temporal fossa, while in *Archæodelphis* it has apparently not pushed backward quite to the level of the posterior border of the orbit.   In *Archæodelphis* the maxillary is described and figured as forming part of the anterior orbital rim, a generalized mammalian feature not known in any other odontocete. In *Xenorophus* the maxillary is excluded from the orbital rim by the jugal. Which of these two conditions existed in *Agorophius* the type specimen was too much damaged to show. Other primitive features known to occur in *Archæodelphis* and *Xenorophus* but not demonstrable in the figures of *Agorophius* are connected with the narial passage. This passage slopes backward essentially as in the baleen whales; the proximal ethmoid region is roofed by the nasals and the median portion of the frontals; the palatines form no part of the anterior wall of the narial passage, thus agreeing with the structure present in normal mammals, baleen whales, and physeterine toothed whales. While it appears unlikely that a family existing so recently as the upper Eocene or lower Oligocene could have been genetically ancestral to any considerable number of cetacean types, two of these early odontocetes seem clearly to represent morphological stages of development through which the ancestors of some of the modern toothed cetacea might have passed. I think it can be appreciated after comparing the skull of *Agorophius* (pl. 5, fig. 2) with that of recent *Delphinus* (pl. 5, fig. 4) that a structure like that which is seen in the living delphinoids might not improbably have been developed from the one present in the fossil by a process which consisted primarily in a forward movement of the occipital region until the supraoccipital came in contact with the upper margin of the frontal, and the anterior extremity of the articular portion of the squamosal arrived at a point beneath the tip of the postorbital process. Similarly the relationship of the maxillary to the orbit and frontal in *Archæo-*

delphis might be regarded as giving some hint of an early stage in the development of conditions like those now seen in *Platanista* (pl. 6, fig. 2) and the physeterines (pl. 6, fig. 1 ; pl. 7, fig. 3). In the genus *Xenorophus*, however, specialization appears to have advanced in directions which have not been followed by later members of the group. This is shown by the wide spreading of the lacrimal over the supraorbital process of the frontal to the level of the hinder margin of the eye ; by the abrupt widening of the intermaxillary in the region behind the narial aperture, this widened portion forming a thin plate spreading outward underneath the maxillary over apparently the basal half of the supraorbital process ; and finally by the very abrupt and conspicuous depression of the maxillary in the region immediately in front of the orbit, the sudden slope thus formed giving the horizontal portions of the bone lying respectively above the orbit and above the roots of the teeth (in the regions marked *mx* and *a. pr*, pl. 5, fig. 6) somewhat the profile of upper and lower river terraces separated by an escarpment. The under-thrust premaxillary appears to have no analogue in other known odontocetes. In some living genera (*Pseudorca, Globicephala*) the lacrimal sends up a thin, inconspicuous ridge-like process closely applied to the curved anterior border of the supraorbital process and occasionally extending over the rim of the process to the extreme anterior edge of the dorsal surface. Such a structure might be interpreted as the last trace of a backwardly spread portion of the lacrimal like that of *Xenorophus* which had been almost obliterated by a subsequent out-ward-extending of the maxillary. In *Stenodelphis* the maxillary shows a slight trace of terraced structure, but I do not find it present in other living genera. The most natural explanation of this struc-ture seems to be a depression of the rostrum subsequent to a backward extension of the maxillary in a horizontal direction over the orbit.

Another stage is found in all of the remaining known members of the suborder, living and extinct, except *Platanista, Physeter* (with its extinct relatives), and *Kogia;* this statement naturally not apply-ing to fossils so imperfectly preserved that the characteristic struc-ures cannot be determined. The braincase has now enlarged and the upper margin of the occipital has come into contact with the frontal ; thus the postorbital constriction has been obliterated and the parietal has been excluded from the vertex (pl. 1, fig. 1*a*). The maxillary extends backward over the frontal nearly or quite to the anterior margin of the occipital. Laterally it may (pl. 1, fig. 1*a*) or may not spread out so as to cover practically the entire dorsal surface of the

supraorbital process of the frontal; but its position in the region directly over the middle of the orbit is always (see particularly the constancy of this feature in two such diverse types as *Stenodelphis* and *Hyperoodon,* pl. 7, figs. 2, 4), like that of the dorsal surface of the expanded process, essentially horizontal in striking contrast to its oblique position in *Physeter, Platanista* (pl. 6, figs. 1, 2) and *Kogia* (pl. 7, fig. 3). The orbital cavity, in other words, is roofed over, at least in its median portion, by two flattened plates of bone which lie in or nearly parallel to a plane representing the backward prolongation of the median horizontal plane of the rostrum. With the crushing together of the anterior and posterior elements of the skull the narial passages have been forced back so that they occupy an almost vertical position closely following the contour of the convex outer side of the anterior wall of the braincase, down which they extend like a pair of gutter pipes. The nasals and the median portion of the frontals (pl. 1, fig. 1*a*) have been pushed backward until they no longer roof the proximal ethmoid region. The palatine has a much reduced exposure on the roof of the mouth (pl. 1, fig. 1*b*) ; but it has developed a large new narial plate which forms an important part of the anterior wall of the narial passage.

This stage of telescoping is found in the great majority of members of the suborder. It was fully established in the Miocene of both Europe and America; and its fundamental importance seems clearly indicated by the fact that it has remained constant in animals whose skulls and dentitions have diverged in other characters as strikingly as those of *Squalodon* and *Monodon, Eurhinodelphis* and *Orcella,* or *Hyperoodon* and *Orcinus.* That it should present numerous secondary degrees and variations of development would, however, be expected. The conditions which in some respects are the least far removed from the ordinary mammalian type and from the *Agorophiidæ* are most clearly shown by the extinct *Squalodon* and the existing genera *Inia* and *Lipotes.* Here the braincase, though relatively larger than in *Agorophius* and *Archæodelphis,* has not reached its maximum development, and the region of juncture between the occipital and frontal bones has not pushed forward into any noticeable proximity to the level of the orbit ; a considerable part of the frontal remains visible on the side of the braincase ; the temporal fossa has not suffered marked reduction (its size, when the skull is viewed from behind, obviously exceeds the combined area of the occipital condyles and the foramen magnum). A slight variation of this condition occurs in *Stenodelphis* (pl. 7, fig. 2) : frontal conspicuously exposed

on side of braincase, but area of temporal fossa considerably reduced
through the drawing inward of the large articular processes of the
squamosal. In *Monodon* and *Delphinapterus* the region of contact
between the occipital and frontal is about as far behind the level of
the orbit as in *Squalodon* or *Stenodelphis,* but the braincase has
become so much enlarged that it causes a marked reduction of the
temporal fossa (the fossa, when skull is viewed from behind, is
obviously smaller than the combined area of the occipital condyles
and the foramen magnum) and very considerably reduces the area
of the frontal exposed on its side. A condition whose main features
apparently resemble those found in *Monodon* and *Delphinapterus*
seems to occur in most of the Miocene dolphins. Such material
as I have examined (representing several genera) from the Calvert
formation of Maryland agrees with these two living genera and
with the published figures of skulls from the Antwerp Crag in the
great backward extension of the maxillary behind the orbit and the
posterior position of the region of contact between the occipital and
frontal. In these extinct dolphins the size of the temporal fossa
appears to be reduced as compared with the condition seen in
Squalodon, Inia and *Lipotes;* but the state of preservation of the
specimens makes it unsafe to generalize on the subject. The area
of the frontal exposed on the side of the braincase also seems to have
undergone the corresponding restriction. It must always be remem-
bered, however, that characters of this kind are easily obscured by
the crushing and other injuries which fossils usually have suffered.
Returning to the recent genera we find that in all of those not pre-
viously mentioned among the types showing dominance of the maxil-
lary thrust (that is in all except *Inia, Lipotes, Stenodelphis, Monodon,*
and *Delphinapterus*) the posterior border of the maxillary has not
been carried very far behind the level of the orbit, and at the same
time the region of contact between the occipital and frontal has been
advanced to a position not conspicuously behind the posterior orbital
level (compare *Delphinus,* pl. 5, fig. 4 with *Stenodelphis,* pl. 7, fig. 2).
This condition might be interpreted as a regression of the hinder
maxillary edge under the influence of forward pressure of the oc-
cipital; but I am inclined to believe that in most instances it really
indicates a course of development independent from that which was
followed by those members of the group in which the maxillary
reached its extreme backward extension. Had the hinder margin
of the maxillary been secondarily pushed toward its original posi-
tion by a forward-advancing occipital some overlapping, or at least

a strong tendency to unusually close contact of the two bones, would be expected to occur; but no such conditions are found, except, perhaps, among the ziphiids (pl. 5, fig. 5; pl. 7, fig. 4), where the forward curling of the posterior extremity of the maxillary suggests the possibility of development through secondary occipital encroachment on a structure previously resembling that of *Stenodelphis* (pl. 7, fig. 2). With this possible exception the developmental tendency of all these recent genera appears to have been less strongly dominated by the backward thrust of the maxillary than in *Inia, Lipotes, Stenodelphis, Monodon,* and *Delphinapterus;* the braincase has enlarged more freely, and the area for attachment of the neck muscles has been increased by some forward extension of the occipital beyond the level of the condyle (compare the occipital of *Delphinus,* pl. 5, fig. 4, with that of *Stenodelphis,* pl. 7, fig. 2). This combination has given rise to the most efficient and successful of all cetaceans, the recent dolphins, a type which shows great plasticity and at the same time little tendency toward extravagance and gigantism. Some of the more conspicuous results to which this plasticity has led are as follows. In the ziphiids (the fundamental similarity of whose skull to that of the delphinids may be seen on comparison of pl. 5, figs. 4 and 5) the beak tends to be deepened and solidified into a peculiar and characteristic form; the upper teeth have disappeared as functional organs; most of the lower teeth have similarly disappeared while the few that remain have been enlarged and specialized; the region of contact between the occipital and frontal is unusually elevated and is situated not far behind the orbital level (see the point marked + in fig. 5, pl. 5, and fig. 4, pl. 7); the entire posterior part of the skull seems to have advanced forward; the maxillary appears to turn secondarily forward in its hindermost and uppermost part (see especially pl. 5, fig. 5); the lacrimal is free from the jugal; the pterygoid is greatly enlarged, but its reduplications are represented by mere ridges; the hindermost ribs are supported by transverse processes which have peculiarities making them seem to be perhaps not serially homologous with those which support the others, the change taking place abruptly between two contiguous vertebræ ranging in position from the 6th and 7th (*Hyperoodon;* two processes visible on the 7th dorsal vertebra) to the 10th and 11th (*Berardius*). In the delphinoids the beak may be lengthened or broadened, but it is never deepened and solidified as in the ziphiids; the lacrimal is fused with the jugal; the pterygoid is not specially enlarged and its internal reduplication is well developed (pl. 5, fig. 4); the hindermost ribs are sup-

ported by transverse processes which ordinarily, in living forms at least, have no obvious peculiarities making them appear to be not serially homologous with those which support the others. Normally the intermaxillary does not extend forward much beyond the maxillary, but in the extinct eurhinodelphines it is said to be so greatly produced as to form about one-third of the excessively attenuate beak (I do not regard the published evidence as conclusive; see pp. 49-50). The teeth are of two types. In the more usual form, found in most of the *Delphinidæ* except *Delphinapterus* and *Monodon,* their structure and method of growth is like that of simple conical teeth in other mammals; that is, the crown consists of a dentine shaft capped with enamel and with or without a deposit of cement on the lower portion; the pulp cavity closes when the tooth has reached its full size, and the crown gradually wears down to the level of the gum. In the other form their structure and method of growth are tusk-like; that is, the enamel cap is so reduced as to be visible in very young teeth only, and to be of no functional importance at any time,[1] while the cement is so increased that it becomes a conspicuous mechanical portion of the shaft of the tooth; the pulp cavity remains open throughout much or all of the animal's life, and the wearing away of the crown is continually compensated for by new growth from below. This tusk-like type of growth occurs in its typical condition in *Delphinapterus* (described and illustrated by Lönnberg, Arkiv för Zoologi, Vol. 7, No. 2, July 5, 1910), where each moderate sized functional tooth in the adult is the constantly worn down base of a tusk, which, if entire, would be not less than 120 mm. in length when fully grown. The enormously enlarged tusk of the male *Monodon* appears to be a development from a tooth of this kind. Modifications of an essentially similar tusk-like condition are found in the beaked whales as well as in the more distantly related *Physeteridæ* and *Kogiidæ,* and in several fossils of doubtful affinity.

Though the toothed cetacean type which seems to be the most efficient has been developed by those members of the group in which the maxillary bone passes horizontally backward over the entire

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[1] Flower says of some young sperm whale teeth about 40 mm. in length: ". . . . they show no trace of an enamel covering to the apex, a point which has hitherto been one of uncertainty" (Trans. Zool. Soc. London, Vol. 6, p. 325). Teeth 10 mm. and 15 mm. long in the U. S. National Museum (No. 49488) show irregular patches of a substance which appears to be enamel at the extreme tip and scattered over the rapidly tapering terminal half of the crown. These patches probably represent the last remnants of the degenerating enamel cap.

width of the orbit, the type which represents the most extreme struc-
tural departure from normal mammals is realized among those
toothed cetaceans in which the maxillary bone passes obliquely up-
ward and backward from the orbit's anterior margin (pl. 6, figs. 1
and 2; pl. 7, fig. 3; compare especially the skull of *Kogia*, pl. 7, fig. 3,
the genus in which these peculiarities are most obvious in the lateral
view, with that of a normal mammal, pl. 7, fig. 1). Whatever may
have been its origin this second type of telescoping appears to be not
mechanically derivable from a condition in which the orbit had first
been roofed by two plates in horizontal position (compare *Kogia,*
pl. 7, fig. 3, with *Stenodelphis,* pl. 7, fig. 2, and *Hyperoodon,* pl. 7,
fig. 4). Telescoping by this system carries the maxillaries upward
and backward from the anterior margin of the orbit at an angle of
from 50 to 70 degrees above the line representing the backward pro-
longation of the rostral axis and leaves the frontal broadly exposed in
the region lying above and behind the eye; the orbit is immediately
roofed by a thick mass of the frontal alone, and not, as in the more
usual type of telescoping, by two thin approximately horizontal plates,
one formed by the frontal and the other by the maxillary. An ex-
planation of these conditions appears to demand the presence of
some factor radically different from those which brought about the
development of the typical dolphin type. Seemingly at a stage when
the maxillary had not yet been forced back over the orbit, the occipital,
and with it the entire braincase, may have been pressed forward suf-
ficiently to have modified the primitive form of the supraorbital region
of the frontal seen in the orbital roof of *Prozeuglodon* (pl. 5, fig. 1)
and retained in ordinary dolphins (as in pl. 5, figs. 4 and 5), by elevat-
ing it posteriorly so that it no longer lay in its original approximately
horizontal position. Thus when the maxillary, in its backward move-
ment, reached the mid-orbital level it would have been made to slope
upward away from the anterior edge of the orbital rim by a pre-
viously established upward slope of the frontal. While this hypothesis
is not based on any observed intermediate stages of structure, and
may therefore prove to be entirely wrong, it appears to offer an
explanation that involves fewer difficulties than those which are met
in any attempt to show that the conditions found in the sloping type
could have been developed after the maxillary had first established
itself over the orbit in a horizontal position. Another possibility
which must be considered is suggested by the structure which appears
to exist in *Archæodelphis* (pl. 5, fig. 3). In the only known specimen
of this animal the rostrum is broken away at its base, but the remain-
ing portion indicates that the entire rostrum was so depressed that its

upper margin lay at a level slightly if at all superior to that of the
upper margin of the occipital condyle, much as in *Platanista* (pl. 6,
fig. 2). Such a depression of the rostrum at a period when the
backward advance of the maxillary was beginning might conceivably
place the telescoping elements in such a position as to initiate an
upward slope from the anterior orbital rim, the eye acting as a pivot.
Depression of the rostrum after an extensive backward movement of
the maxillary had taken place would be expected to result in the ter-
raced condition of the maxillary seen in *Xenorophus* (pl. 5, fig. 6) and
less conspicuously in *Stenodelphis*.

One form of this kind of telescoping occurs in *Platanista* (pl. 6,
fig. 2). The maxillary rises from the front of the orbit at an angle
of about 50 degrees ; the occipital extends far forward in the median
region, but at the side it is held back by the rather large parietal.
Associated with these peculiarities there occurs a remarkable com-
bination of special characters. The edge of the maxillary above the
orbital region is developed into a high thin plate apparently homo-
logous with the maxillary ridge present in *Physeter, Kogia, Hy-
peroodon* and elsewhere (compare especially pl. 6, fig. 2, with pl. 7,
fig. 4), but so unusually large and of such peculiar form that, with its
fellow of the opposite side, it completely arches over the front of the
face and incloses the space occupied by the oily facial cushion [1] ; the
squamosal portion of the zygoma is extremely large and the jugal is
correspondingly short ; the pterygoid is spread laterally so as to cover
the alisphenoid, and its outer plate is so developed as to be an almost
exact duplication of the inner plate, the two plates everywhere closely
approximated, the space between them occupied by a loose network
of bony filaments : palatines widely separated from each other by the
vomer, each entirely covered by the two plates of the pterygoid except
where it appears on the surface in the anterior wall of the essentially
vertical narial passage ; infraorbital foramen situated at a level con-
spicuously behind the much reduced orbit. The teeth, though unusual
in form, are normal in structure ; the relationship of the ribs to the
vertebræ is the same as in the *Delphinidæ*, that is, all the ribs are sup-
ported by serially homologous transverse processes.

Another form occurs in the sperm whale (pl. 6, fig. 1). Here the
frontal and maxillary are essentially like those of *Platanista,* but the
occipital and the squamous portion of the squamosal have advanced
laterally to a level not far behind the orbit, thus reducing the parietal

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[1] Hinton and Pycraft (Ann. and Mag. Nat. Hist., ser. 9, Vol. 10, p. 234,
August, 1922), have suggested that these plates originated as bony stoppers
to the blow hole.

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to a small element not visible in adults but appearing in very young skulls (like the one figured) as a thin cap overlying the upper portion of the squamosal. Associated characters are: an enormously developed facial depression; a heavy jugal unlike that of any other known toothed cetacean, and suggesting, in its robustness, the jugal of the baleen whales; a long rostrum much widened by building out the sides beyond the level of the tooth row, and strikingly contrasted with a narrow lower jaw with extremely long symphysis; an unusually large occipital condyle extending upward to involve the supraoccipital; palatine large, essentially normal in position, not forming any part of the anterior wall of the slightly backward-sloping narial passage; pterygoid spreading forward over much of the palatine, but not extending laterally over the alisphenoid and not developing any secondary plate; maxillary teeth present in young only, their position normal with regard to the lower toothrow (not carried outward by the widening of the rostrum as has been suggested); mandibular teeth large, tusk-like in structure and in manner of growth; hindermost ribs supported by transverse processes which are perhaps not serially homologous with those which support the others.

The most advanced stage, so far as the upper portion of the skull is concerned, is reached by *Kogia* (pl. 7, fig. 3). The parietal is now obliterated as a separate element, even in skulls so young that the bones of the cranium are readily disarticulated, and the summit of the occipital has been carried forward to a level nearly over the posterior border of the orbit. The median region of the frontal, underneath the maxillary, has largely disappeared, so that a considerable part of the anterior wall of the braincase is seen, on disarticulation of the skull, to be formed by the maxillary. In contrast with *Physeter* the entire skull is shortened and the facial depression is less extremely developed relatively to the occipital depth; the jugal is represented by its anterior extremity only, not distinguishable from the lacrimal except in very young individuals; the symphysis mandibuli is short, and the form of the lower jaw as a whole presents no contrast to the short, wide rostrum; occipital condyle not unusually large and not extending upward to involve the supraoccipital. The structure of the palatine and pterygoid resembles that present in *Physeter;* the narial passage slopes slightly backward; the teeth are tusk-like in structure and in manner of growth; the hindermost ribs are supported by transverse processes which may not be serially homologous with those which support the others.

The more important characters of the supergeneric groups of modern toothed cetaceans are tabulated in the following key:

KEY TO THE FAMILIES AND SUBFAMILIES OF TOOTHED CETACEA

Combined enlarging of brain and pushing together of braincase and anterior part of skull so little advanced that a distinct trace of the primitive postorbital constriction remains visible from above; parietals in contact on vertex behind frontals; maxillary sometimes (in *Archæodelphis*) forming part of anterior rim of orbit [palatine normal in position, not forming part of anterior wall of backward-sloping narial passage] (*Agorophius, Archæodelphis* and *Xenorophus*) .... Agorophiidæ.

Combined enlarging of brain and pushing together of braincase and anterior part of skull so much advanced that no evident trace of the primitive postorbital constriction remains visible; parietals not in contact on vertex behind frontals; maxillary never forming part of anterior rim of orbit.

    Palatine normal in position, not forming part of anterior wall of slightly backward-sloping narial passage [Relation of maxillary to frontal such that the line of contact between these bones extends upward at a conspicuous angle from the anterior border of the orbit, leaving a broad area of the frontal exposed over middle of orbit when skull is viewed from the side; parietal not visible as a separate element on side of braincase in adult; palatine partly covered by pterygoid, its only surface exposure situated in the normal position on the roof of the mouth; hindermost ribs supported by transverse processes which appear to be not serially homologous with those which support the others; teeth tusk-like in structure].

        Facial depression greatly developed, obliterating the longitudinal ridge behind narial orifice; brain relatively small, situated far behind orbit; zygoma complete; (*Physeter* only; exact position of related extinct genera not certain) .... Physeteridæ.

        Facial depression moderately developed, distorting but not obliterating the longitudinal ridge behind narial orifice; brain relatively large, extending forward to level of orbit; zygoma incomplete; (*Kogia* only; exact position of related extinct genera not certain) .... Kogiidæ.

    Palatine not normal in position, forming part of anterior wall of essentially vertical narial passage.

        Anterior teeth single-rooted; posterior teeth double-rooted, their crowns flattened laterally and with serrate margins.. Squalodontidæ.

        Anterior and posterior teeth alike single-rooted, their crowns rarely flattened laterally, and never with serrated margins.

            Pterygoids completely covering the palatines on ventral aspect of skull; palatines widely separated from each other and from median line of palate; external reduplication of pterygoid as large as original plate and closely simulating the original plate in form (*Platanista* only) .... Platanistidæ.

            Pterygoids not completely covering the palatines on ventral aspect of skull; palatines in contact or virtually so in median line of palate; external reduplication of pterygoid, when present, never as large as the original plate and never closely simulating the original plate in form ; [Relation of maxil-

lary to frontal such that the line of contact between these bones extends backward in a nearly horizontal direction over the entire orbit, leaving no broad area of the frontal exposed over middle of orbit when skull is viewed from the side].

Maxillary with a freely projecting plate-like process extending backward toward squamosal; pterygoid without reduplication either external or internal........INIIDÆ.

Maxillary with no backward-extending plate-like process; pterygoid with reduplication, either external or internal or both.

Pterygoid greatly enlarged [covering alisphenoid], the area of its outer side equal to that of base of braincase [its reduplications low and ridge-like]; teeth of adult reduced to one or two in lower jaw, absent in upper jaw; rostrum deepened and solidified; hindermost ribs supported by transverse processes which appear to be not serially homologous with those which support the others..............ZIPHIIDÆ.

Pterygoid not enlarged, the area of its outer side less than that of base of braincase; teeth of adult not reduced to one or two in lower jaw, normally present in upper jaw; rostrum not deepened and solidified; hindermost ribs (except possibly in some extinct genera) supported by transverse processes which appear to be serially homologous with those which support the others.................DELPHINIDÆ.

Alisphenoid not overspread by pterygoid; internal reduplication of pterygoid present, usually well developed; no external reduplication.

Teeth not tusk-like in manner of growth; dentition never reduced to a single forward-projecting tusk.

Intermaxillary never extending conspicuously forward beyond maxillary.
Delphininæ.

Intermaxillary said to extend conspicuously forward beyond maxillary.
Eurhinodelphininæ.

Teeth tusk-like in manner of growth; dentition reduced to a single forward projecting tusk, usually present in one maxilla of male only ....*Monodontinæ.*

Alisphenoid overspread by pterygoid; both internal and external reduplications of pterygoid normally present.

Pterygoid with reduplications large; teeth of normal delphinine type.......*Stenodelphininæ.*

Pterygoid with reduplications small; teeth tusk-like in manner of growth.*Delphinapterinæ.*

BEHAVIOR OF THE MODERN CETACEAN SKULL

Having now reviewed the details of the results accomplished by the process of telescoping it becomes possible to conjecture something as to the probable behavior of the skull while undergoing its modifications. Telescoping of the braincase and basining of the forehead appear to have been mechanical necessities in the development of the modern cetacean skull. These processes have followed two courses, which may be most readily understood by examining the structure of the proximal portion of the maxillary bone (pp. 9-10, pls. 3-4). In the baleen whales the maxillary is seen to have retained the orbital portion of its body, while the ascending process has interlocked with the body of the frontal. Basining appears thus to have been interfered with, and telescoping appears to have been made less feasible from before than from behind. In the toothed cetacea the maxillary has lost the orbital portion of its body, while the ascending process has slipped freely over almost the entire frontal. Basining seems thus to have been favored, and telescoping from the front seems to have been rendered more feasible than telescoping from the rear. The opposite interpretation should be considered, namely, that the orbital portion of the maxillary might have been destroyed in the toothed cetacea by an especially strong tendency to basining in the members of this group, arising, perhaps, in connection with the development of the facial fat mass, and that in the baleen whales the orbital portion might have been permitted to remain, partly because the facial fat mass did not develop, and partly because the tendency toward telescoping from behind was for some unknown reason more pronounced than that toward modification from in front. While it is probably true that the mechanical forces to which the skull has been subjected have not been exactly alike in the members of the two groups, such differences as can be discovered do not appear to be sufficient, either in degree or in kind, to have been solely responsible for marking out and maintaining two entirely distinct courses of modification. Furthermore we find that the orbital portion of the maxillary is as completely absent in those toothed cetaceans whose skulls are practically not basined at all (*Stenodelphis*, for instance, pl. 7, fig. 2) as it is in those which show the basining process highly developed (*Mesoplodon*, pl. 5, fig. 5 ; *Physeter*, pl. 6, fig. 1 ; *Kogia*, pl. 7, fig. 3; *Hyperoodon*, pl. 7, fig. 4).

Whatever the true history may prove to have been, when revealed by the discovery of fossils now unknown, it is safe to say that throughout the course of remodeling the skull seems to have behaved,

in the main, as if it had consisted of three loosely joined masses of plastic material arranged serially and acted upon by two opposing, compressing, forces. One of these forces would have pushed forward from behind, the other would have resisted or pushed backward from in front, with the result that forward motion was established in the posterior mass and backward motion was established in the anterior mass, these two masses acting at the expense of the one which lay between them, covering it, eating into it, and finally obliterating a great part of it (compare the large frontal and parietal in a normal skull, pl. 7, fig. 1, with the completely eliminated parietal and excessively modified frontal in *Kogia,* pl. 7, fig. 3). Of the three masses the anterior would be represented by the rostrum, the posterior by the occipitals and squamosal, the intermediate by the frontal, parietal and sphenoids. While motion of the cranial elements has occurred in every known modern cetacean the dominant direction of this motion has not always been the same; sometimes it has been chiefly a forward thrust of the posterior elements (pl 1, fig. 2; pl. 6, fig. 4), sometimes most conspicuously a backward thrust of the anterior elements (pl. 1, fig. 1; pl. 7, fig. 2), occasionally a less one-sided combination of the two thrusts (pl. 7, fig. 3; pl. 8, figs. 3, 4). The causes which actually determined these differences in the motions of the various bones are now unknown; but the special peculiarities in the behavior of the moving cranial elements in each of the two main types seem to have been predominantly such as might be imagined to have resulted from the encountering of definite mechanical obstacles, varying in their degree of efficiency, lying some of them in the region of juncture between the occipital and the parietal, others in that between the maxillary and the frontal.

The possible character of the obstructions to the telescoping process, and the reason why these obstructions, instead of being uniform in all cetaceans, were more effective checks to movement at one point in the mysticetes and at another in the odontocetes, can be surmised from the rather unexpectedly conspicuous differences which have been found to exist in the details of the devices by which the bones of the skull are interlocked in mammals whose heads have not been subjected to compression (pp. 5-6; pls. 2-3). As to the nature of the compressing forces: the one acting from behind would probably be represented mostly by the mere forward push of the rapidly swimming body; that acting from the front would be the resistance of the water. In the toothed cetaceans the modifications seem to have pro-

ceeded as though influenced by forces which were relatively simple
in both directions. In the baleen whales, on the contrary, the op-
posing forces may have been more complex. They perhaps might be
analyzed as follows: (1) From in front: (a) the resistance of the
water through which the animal moved, (b) the constant downward
pull exercised by the increased weight of the rostrum and jaws con-
sequent on their enlargement as the framework of the food-straining
apparatus, and (c) the very unusual downward pull which must
occur when the animal in feeding swims forward with the lower
jaw lowered and the under part of the mouth distended by the
enormous quantities of water taken in for straining through the
baleen plates: (2) From behind; (a) the forward push of swimming,
and (b) the upward pull needed to counteract 1b and 1c. The
presence of some special downward-pulling force seems to be re-
quired as part of the explanation of the great forward extension of
the upper margin of the occipital shield which has been one of the
noticeable features in the developmental history of the baleen whale
group. This oblique extension of the shield gives increased area for
the insertion of the muscles which hold the head in its horizontal
position, and at the same time it gives increased length to the power
arm of the lever by which any downward force applied to the anterior
part of the head is opposed. An analogous mechanical problem has
been solved by a parallel though much less extreme modification of
the skull in some of the burrowing rodents, particularly in those
which have not developed specially enlarged fore feet. Such animals
make free use of the teeth and snout in digging; consequently the
fore part of the skull must be pressed upward against the soil through
which a passage is being made. This active upward-forcing of the
rostrum against a resistant medium appears to have brought into
play the same muscles that would be required for maintaining the
horizontal position of the fore-weighted head of a baleen whale. It is
therefore not surprising to find that a distinct parallelism should be
present between the vertical portion of the skulls of such widely
unrelated mammals as *Rhachianectes* and *Spalax*. In the rodent
(pl. 8, fig. 8) the occipital shield has extended far enough forward
over the parietals to reduce their exposed portion to small elements,
while in the whale (pl. 8, fig. 3) it has obliterated the parietals on the
vertex and has continued forward beyond them far enough to reduce
the frontals in their turn to elements whose size relatively to the
neighboring structures is not greatly unlike the exposed area of the

parietals of the rodent.[1]   The fact that the modification has gone farther in whales than in rodents may perhaps be not entirely unrelated to the circumstances that the muscular activity in the one instance is needed during the act of burrowing only, while in the other it is needed at its maximum whenever the animal feeds; and the part of it which is required to oppose gravitation must be continuous from birth to death.   An additional reason to believe that the forward extension of the frontal shield in the baleen whales may be in part related to the great development and peculiar function of the rostrum and jaws is furnished by the fact that this extension is in general more pronounced throughout the mysticete group than it is in the toothed cetacea.   Among the latter there is no enlarging of the mouth to engulf great quantities of water; the combined weight of the rostrum and jaws is almost without exception much less, relatively to the weight of the cranium, than it is in the mysticetes; and in no dolphin or toothed whale, no matter what the degree or kind of telescoping, even in such excessively compressed types as *Hyperoodon* and *Kogia* (pl. 7), does the occipital shield increase its area by pushing obliquely forward noticeably beyond the level of the articular region, a level which it normally passes in all of the more specialized baleen whales.   (Compare *Stenodelphis,* pl. 7, fig. 2, a dolphin with greatly elongated rostrum, and *Eubalæna,* pl. 6, fig. 4, a member of the other group; in the former the anterior border of the occipital lies slightly behind the articular level while in the latter it lies far in front; the articular area in each is situated below the reference letters *sq,* and the position of the anterior edge of the occipital is marked by the sign +.)

The probability that water pressure has been one of the main factors in determining the behavior of the modern cetacean skull seems to be much strengthened by an examination of the characters of the two other groups of mammals whose members have assumed an exclusively aquatic mode of existence.   These groups are the zeuglodonts and the sea-cows.   In the former the skull has retained most of its generalized mammalian structure, in the latter it has

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[1] A definite overlapping of the hinder border of the parietal by the occipital occurs in the pigs and peccaries, both of which use the snout for " rooting " in an upward direction; but the process in these animals differs from that which is seen in the baleen whales and *Spalax* in that it takes place in a nearly vertical direction so that the occipital shield faces backward on the occipital aspect of the skull. It appears to be associated with a pushing forward of the base of the braincase which would indicate the action of some remodeling force which does not operate in the whales and rodents.

departed widely from this primitive type; but in neither is there any telescoping: the bones unite with each other in the normal way. Both zeuglodonts and sea-cows are contrasted with modern cetacea in three peculiarities which must be directly related to the mechanical pressures which are brought to bear on the skull. These are: (a) Smaller size of the head in proportion to that of the body, (b) greater length of the neck in relation to that of the head, and (c) distinctly less enlargement of the vertebral processes which serve as areas of attachment for the muscles that operate the caudal propellor. It seems obvious therefore that the head, in these aquatic mammals with non-telescoped skulls, has been subjected to a less violent conflict with the water than that of the modern cetaceans, because (a) its area opposed to the water in the act of swimming is less, (b) it is not held so stiffly and uniformly pressed into the resisting element, and (c) it is driven against the water at a lower speed. This last factor is probably the most important of the three. The resistance which water presents to a moving body increases as the square of the velocity. Hence if a porpoise swims twice or three times as fast as a sea-cow its head will be subjected to from four to nine times the backward pressure encountered by the head of the less rapidly moving animal.

Cetaceans, as is well known, are born in the water. The young must therefore acquire the ability to swim rapidly at an early age. Exactly how soon they gain the power of freely accompanying the adults cannot be stated with any degree of certainty; but there can be no doubt that the habit of rapid swimming is established long before the skull has reached its full growth. The peculiar behavior of the modern cetacean skull may therefore, as it seems, not impossibly be connected with this fact: that during much of that critical period in which the skull of an ordinary land mammal is rapidly and, so to speak, peacefully accomplishing its process of loose-jointed growth the skull of a young cetacean is fighting its way to adult stature against the two opposing forces of body push from behind and water resistance from in front.

It may be possible to form a better understanding of the subject of behavior when a considerable number of cetacean embryos representing the earliest stages of growth of the principal bones of the skull can be examined. Unfortunately I have not had access to such material, and I have found very scant published information which bears directly on the problem in question. As regards the odontocetes there appears to be little or nothing on record concerning the stages

intervening between the formation of the chondrocranium and the essentially final structure of the skull. Early conditions in two of the mysticetes were figured many years ago by Eschricht in his well-known accounts of *Balæna mysticetus* and *Balænoptera acutorostrata;* recent contributions to the subject have been made by Schulte (Mem. Am. Mus. Nat. Hist., n. s., Vol. I, pls. 54-56, 1916; *Balænoptera borealis*) and Ridewood (Phil. Trans. Roy. Soc. London, ser. B, Vol. 211, pp. 209-272, May 8, 1922; *Megaptera* and *Balænoptera*). In the absence of more complete information I shall not attempt any discussion of the evidence furnished by the structure found in embryos.

REMARKS ON THE CLASSIFICATION HERE ADOPTED

The classification of the cetacea to which the present study of telescoping has led is as follows:

Order Cetacea.
    Suborder Archæoceti (= Series I).
        Family *Protocetidæ* (*Protocetus*).
        Family *Dorudontidæ* ("Zeuglodon" with short vertebræ).
        Family *Basilosauridæ* (*Basilosaurus*).
    Suborder Mysticeti (= Series II).
        Family *Balænidæ* (*Balæna, Eubalæna*).
        Family *Neobalænidæ* (*Neobalæna*).
        Family *Cetotheriidæ* (*Cetotherium* and allied extinct genera).
        Family *Rhachianectidæ* (*Rhachianectes*).
        Family *Balænopteridæ*.
            Subfamily *Megapterinæ* (*Megaptera*).
            Subfamily *Balænopterinæ* (*Balænoptera, Sibbaldus*).
    Suborder Odontoceti (= Series III).
        Family *Agorophiidæ* (*Agorophius, Archæodelphis, Xenorophus;* perhaps *Patriocetus*).
        Family *Physeteridæ* (*Physeter;* position of extinct related genera uncertain).
        Family *Kogiidæ* (*Kogia;* position of extinct related genera uncertain).
        Family *Squalodontidæ* (*Squalodon; Prosqualodon ?*).
        Family *Iniidæ* (*Inia, Lipotes,* and several extinct South American genera).
        Family *Delphinidæ*.
            Subfamily *Delphininæ* (The typical dolphins).
            Subfamily *Eurhinodelphininæ* (*Eurhinodelphis* if correctly described).
            Subfamily *Stenodelphininæ* (*Stenodelphis, Palæopontoporia;* perhaps *Argyrocetus*).
            Subfamily *Delphinapterinæ* (*Delphinapterus* only).
            Subfamily *Monodontinæ* (*Monodon* only).
      Family *Ziphiidæ* (The beaked whales).
      Family *Platanistidæ* (*Platanista* only).

It will be seen that this arrangement of the order does not differ materially from those which have been most generally in use (for a summary of the principal attempts at classifying the cetaceans see Winge, Smithsonian Misc. Coll., Vol. 72, No. 8, pp. 58-62) except in the greater independence now attributed to all three of the suborders, and, among the members of the Odontoceti, in the wide separation of the ziphiids from the physeteroids, and especially in the separation of the rather primitive iniids from *Platanista,* the genus which I regard as presenting the greatest total of modifications known in any cetacean. Aside from these admittedly controversial details the departures from accepted usage, so far as such usage can be said to exist, chiefly pertain to questions of judgment with regard to the limits of the minor groups and the relative importance assigned to some of these groups. That a classification based on a mostly untried set of characters should coincide in the main with the classifications already in existence indicates the general soundness of the broader results of work on cetacean taxonomy. The differences in detail are mostly the result of two causes: first, that some of the characters hitherto regarded as indices to relationship now appear to be parallel and independent modifications, and, second, that comparatively few of the extinct members of the order are known from remains complete enough to show the features which are now seen to be needed for a natural classification. Examples of the first are furnished by the beak form supposed to bring together the otherwise excessively different *Platanista* and *Inia* or *Lipotes;* the tusk-like tooth structure supposed to indicate relationship to the sperm whales on the part of various fossil cetaceans known from teeth only (this structure now appears to be merely a mechanical strengthening of the teeth by means which have been independently adopted in the sperm whale, the white whale and the ziphiids; probably elsewhere under the influence of appropriate stimulus) ; the unusual relationship of the hindermost ribs to the vertebræ supposed to be evidence in favor of placing the ziphiids in the same group with the sperm whale notwithstanding the fundamental differences presented by the structure of the skulls. Examples of the second are so numerous that detailed listing is scarcely necessary in the present connection. A few characteristic instances are furnished by the remains which formed the bases of the following 30 generic names: *Agriocetus, Cetophis, Cetorhynchus, Delphinavus, Delphinopsis, Dinoziphius, Eucetus, Hesperocetus, Hoplocetus, Iniopsis, Ixacanthus, Kekenodon, Metasqualodon, Microcetus, Microzeuglodon, Ontocetus, Orycetero-*

cetus, Palæodelphis, Patriocetus, Phocænopsis, Phocagenius, Physodon, Priscodelphinus, Prophyseter, Prosqualodon, Protophocæna, Rhabdosteus, Scaldicetus, Stenodon, Tretosphys.

Most of the supergeneric groups here recognized have already been sufficiently discussed for the purposes of this paper. Concerning some of them further observations may not be out of place.

Archæoceti.—Cabrera (Manual de Mastozoología, p. 316, 1922) has recently placed the zeuglodonts in an order separate from the modern cetacea. This may be the first step toward the eventual elevation of all three of the currently recognized major groups to the rank of orders.

According to Pompeckj (Senckenbergiana, Vol. 4, pp. 43-100, October 20, 1922) the structure of the periotic bone in the zeuglodonts resembles that now found in the baleen whales. The presence of such conditions is not likely to mean anything more than a parallel development of the ear in the two groups, or more probably, the existence of similar ear structure in the two ancestral stocks from which these groups took their origin. The difficulties in the way of deriving a mysticete skull from one which had first assumed the form present in all known zeuglodonts appear to be little short of insuperable.

Agorophiidæ.—The three American genera now placed in this family are well differentiated from each other though they probably represent one stage of the telescoping process. Whether the genus *Patriocetus* belongs in the same family or whether it represents a distinct group are questions which the descriptions and figures do not furnish the data for answering. The photographs published by Abel (Denkschr. kais. Akad. Wissensch. Wien, math.-naturw. Kl., Vol. 90, pls. 1-4, 1914) indicate (a) that the general form of the skull in both dorsal and lateral view is essentially like that of *Agorophius* (Smithsonian Inst., Special Publ., No. 1694, pl. 6, 1907), and *Archæodelphis* (Bull. Mus. Comp. Zool., Vol. 65, No. 1, figs. 1, 2 and plate, 1921), (b) that the braincase is similarly small as compared with the rest of the skull, and (c) that a deep postorbital constriction is present. Apparently the maxillary may have formed part of the anterior orbital wall as in *Archæodelphis*. The most obvious difference from *Agorophius* clearly shown by Abel's photographs is the presence of a thin overhanging ledge sloping upward and backward from the hinder margin of the orbit, and partly obscuring the postorbital constriction. The surface of the fossil is thickly covered with grains of sand which obscure most of the finer details. (See remarks

by König, Jahres-Ber. Mus. Franc.-Carol., Linz, Vol. 69, p. 111, 1911.) Such details as can be seen are, however, in accord with the conditions present in both the kind and stage of telescoping represented by *Agorophius* and *Archæodelphis*. The reconstructions given by Abel in plates 6 and 11 show, on the contrary, a structure which differs fundamentally from that known to occur in any other cetacean. The maxillary is represented as broadly united with the frontal by a straight suture extending directly inward to the intermaxillary from a point situated on the side of the rostrum in front of the anterior margin of the orbit. No part of the maxillary extends behind this level either above or below the frontal; yet the intermaxillary runs far back behind both maxillary and orbit, its extremity touching the parietal. The fronto-maxillary suture, if correctly interpreted, is not very different from that usually seen in the zeuglodonts. The relative degree of backward extension of the maxillary and intermaxillary is, on the contrary, something unknown either in zeuglodonts or in cetaceans with telescoped skulls. It should further be noticed that essentially normal conditions, not very different from those which appear to have been present in *Agorophius* were described by König as occurring in the specimen afterward interpreted by Abel. In the zeuglodonts the relationships of these two bones have remained normal, and the posterior border of the maxillary lies behind the extremity of the intermaxillary (pl. 5, fig. 1). During the process of telescoping in all known cetaceans it appears to be the maxillary which leads in the backward move, so that in rare instances only does the intermaxillary attain the more posterior level, and then by such a mere trifle as to form no real exception to the general rule (see diagram of *Rhachianectes,* pl. 8, fig. 3). That the intermaxillary in any cetacean should have extended backward to the parietal while the maxillary remained stationary in front of the orbit is so contrary to probability that the evidence of an unusually well preserved specimen would be necessary before anything of the kind could be believed to have taken place. If such a condition should ever be demonstrated to occur it would indicate the existence of a third type of telescoping not directly related to or derivable from either of those now known. That the genus *Patriocetus* as interpreted by Abel would be unlikely to represent a stage ancestral to the modern baleen whales appears to be clearly enough indicated by the character just mentioned; it is made practically certain by the absence of the orbital plate of the maxillary, no trace of which appears either in Abel's photographs or restoration (based chiefly on the

second specimen), or in Van Beneden's drawing of the original type skull. The absence of the plate, which seems to be real and not due to mutilation of the fossils, is an indication that *Patriocetus* belongs definitely among the toothed cetaceans; as it is probable that in any form actually preceding the modern baleen whales the plate would necessarily be present, and its size would with little doubt be relatively greater than in existing members of the group.

Physeteridæ.—The family *Physeteridæ* is not definitely known to be represented by more than two genera, the living *Physeter* and the Miocene "*Paracetus*" of Cope. Its characters consist primarily of a combination of telescoping-type, development of the facial depression, structure of the zygomatic arch, palatine and pterygoid, and the relation of the posterior ribs to the vertebræ; features which are not commonly preserved in fossils, but without a knowledge of which no positive classification of a cetacean genus is possible. The palatine bone retains its horizontal position in the roof of the mouth. It is overridden from behind by the pterygoid; but the general relationships of the two bones to the neighboring cranial elements is otherwise so normal that the conditions present in *Physeter* can readily be explained as the result of simple telescoping of elements originally in about the same relative positions as those in ordinary carnivores. While the narial passage shows a distinct trace of the primitive backward slant it is situated mostly behind the level of the orbit. There is no longitudinal median ridge on the forehead behind the narial aperture. The posterior orifice of the infraorbital canal is formed by the maxillary and lacrimal, the relationship of these two bones, so far as the orifice of the canal is concerned, being not very different from that which exists in the fox (pl. 3, figs. 4 and 5). Atlas distinct, the other cervical vertebræ fused with each other and with the first dorsal, a combination of relationships unknown in the cervicals of any other cetacean. Among the insufficiently known extinct cetaceans the genus *Thalassocetus* appears to be the one which is most probably a member of the physeterine group. Its frontal and maxillary are figured as not widely unlike those of *Physeter,* but the remains are very fragmentary. The possibility that *Diaphorocetus* ("*Hypocetus*") may belong in the same group must also be considered. On the other hand *Physeterula* is more likely to be a delphinid with the orbital edge of the frontal thickened in a manner that is unusual though not unknown among the dolphins; and the *Physodon patagonicus* of Lydekker, as described and figured, can with equal probability be referred to the *Delphinidæ*. In this animal

the structure of the orbit and of the maxillary above and behind the orbit differs in no essential feature, so far as can be judged from the plate representing the lateral aspect of the skull, from the conditions present in *Globicephala;* on the other hand the positions of the foramina near the orbit as figured from in front suggest those in the type specimen of Cope's *"Paracetus" mediatlanticus.* The names *Eudelphis* and *Homœocetus* were based on vertebræ resembling the peculiar atlas of the sperm whale. It is therefore not impossible that they refer to members of the family *Physeteridæ.* Various names of supposed physeteroids, such as *Balænodon, Eucetus, Hoplocetus, Palæocetus, Physetodon,* have been applied to isolated teeth. Some of these teeth as described and figured are of the same tusk-like type as those of the sperm whale. Others resemble the enlarged teeth of such delphinids as *Orcinus* and *Pseudorca,* in which the growth is not tusk-like, the portion below the well-defined, enamel-covered crown being merely enlarged and thickened, but with a closed base. The systematic position of the animals which bore these teeth is conjectural. Though nothing of the kind is yet known it does not seem impossible that a physeteroid might have teeth of the *Orcinus* type ; while the inconclusiveness of the evidence furnished by isolated tusk-like teeth is shown by the fact that this kind of tooth growth occurs not only in the sperm whale and *Kogia,* but also in the beaked whales, the narwhal and the white whale. Although in appearance extremely specialized, chiefly on account of the unusual basining of the facial region, the skull of *Physeter* is, like that of *Kogia,* more primitive in its ground plan, as shown by the structure of the narial passage, the palatine and the pterygoid, than that of any other known toothed cetaceans except the agorophiids.

Kogiidæ.—While the living genus *Kogia* agrees with *Physeter* in general structure it differs so much in details that it probably represents a special family. The discovery of fossil forms may, however, eventually result in obscuring the apparent distinctness of the two groups. The more important of the details which, taken together, now seem of family value are : the fusion of all the cervical vertebræ into a single mass distinct from the first dorsal as in the ziphiids and the typical dolphins ; the situation of the orbit at a level mostly behind that of the narial passage ; the presence on the forehead of a distorted but evident longitudinal median ridge extending backward from the narial orifice ; the fusion of the jugal and lacrimal into a mass lying entirely anterior to the orbit and having a superficial exposure nearly equal to that of the frontal. No fossil representative of the family

Kogiidæ has yet been identified. Cope supposed that his " *Paracetus* " *mediatlanticus* from the Upper Miocene of Maryland was related to *Kogia;* but an examination of the original specimen shows that it really belongs near *Physeter.* The tooth on which Leidy based the name *Orycterocetus* may have come from a cetacean not unlike *Kogia,* and the same is true of some teeth of a supposed physeterid figured but not named by Abel (Mém. Mus. roy. Hist. Nat. Belgique, Vol. 3, p. 74, figs. 9 and 10, 1905) from the Antwerp Crag.

Squalodontidæ.—Chiefly on account of their peculiar teeth the squalodonts are usually regarded as constituting a special family. In this position they may be allowed to remain, though it must be observed that their distinctness from the living *Iniidæ* (*Inia* and *Lipotes*) does not rest at present on characters that are very satisfactory or very well understood. The telescoping of the braincase is of the same kind and degree as in the existing iniids, and the frontal appears to share to the same extent in the formation of the lateral wall of the braincase; the orbit, as in the living animals, is situated a little in front of the level of the narial passages. The ethmoid is less reduced than in existing iniids. I have not seen a specimen of *Squalodon,* nor can I find one described, in which the structure of either the palatine, the pterygoid, or the basal portion of the maxillary is sufficiently well preserved to show the characters needed for definite classification; but there is apparently nothing known about the fossils to prove that the conditions as regards these very important elements of the skull differed from that which is now found in the iniids. The peculiarities of the squalodont dentition, however, especially the tendency of the posterior teeth to assume a conspicuously trenchant character appears to indicate a line of development which was not leading directly toward any of the existing groups of porpoises.

The genus *Prosqualodon* as described and figured by Lydekker would appear to be a member of this family. As restored by Abel, however (Sitzungsber. k. Akad. Wissensch. Wien, Math-naturwiss. Kl., Vol. 121, pp. 57-75, pls. 1-3, 1912), the skull is, in important features, intermediate between that of *Squalodon* and that of *Agorophius.* Abel describes the parietals as forming a broad band across the vertex between the frontals and the occipital shield, a condition not mentioned by Lydekker and not shown in his figure of the type or of the specimen in London afterward studied by Abel. Such a character, if verified, would show the presence of a stage of telescoping decidedly anterior to that present in *Squalodon,* and would place the genus *Prosqualodon* in a family of its own.

Iniidæ.—There has been much difference of opinion as to the systematic position of *Inia* and its allies, though they have, perhaps, been most frequently united with *Platanista* and *Stenodelphis* to form a special family. The unnaturalness of this grouping has been recognized by Abel, True and Rovereto. The genus *Platanista* is widely separated from the others by the physeteroid character of its telescoping (compare pl. 6, fig. 2, with pl. 7, fig. 2) and by the excessively specialized structure of its palatine and pterygoid. The South American *Stenodelphis,* though less distinct from the iniids than from *Platanista,* is definitely separated from both *Inia* and *Lipotes* by the structure of its palate (it agrees with them in type of telescoping). This leaves these two existing genera and their extinct allies to stand alone. Considered as a group they resemble the *Delphinidæ* in the type of telescoping and in some other characters of the skull. The braincase, however, has not attained its extreme size, and has not encroached on the temporal fossa so much as in the typical modern dolphins, peculiarities which suggest the squalodonts. A character which might be interpreted as vaguely squalodont is also indicated by the tendency of the posterior teeth to differ in form from those at the anterior end of the series; but the broadened teeth of *Inia* obviously resemble the tuberculate teeth of *Delphinodon* rather than the narrow trenchant posterior teeth of *Squalodon.* The structure of the palate is less specialized than in any of the known toothed cetacea except the physeteroids and agorophiids. (The more important characters of the palate in the squalodonts, it must be remembered, are not known.) The narial passage has become perpendicular, and the palatine bone has lost its primitive position on the roof of the palate; the orbits are situated in front of the level of the nares; narial process of palatine well developed and forming an important part of the anterior wall of the narial passage. Pterygoid simple, not spreading laterally over alisphenoid, and not reduplicated along either margin. Posterior orifice of infraorbital canal apparently formed by maxillary alone. A peculiar specialization is seen in the presence of a narrow, freely projecting plate given off by the posterior extremity of the maxillary and extending back nearly to the squamosal in somewhat the same position as that which is occupied by the outer reduplication of the pterygoid in such delphinids as *Delphinapterus* and *Stenodelphis.* In addition to the living genera *Inia* and *Lipotes,* I would regard as probably members of this group the fossils which have formed the bases of the following names: *Anisodelphis, Argyrocetus* (perhaps better referred to the *Stenodelphininæ*), *Ischyorhyn-*

chus, Pontivaga, Pontoplanodes, Proinia. No extinct porpoise refer-
able with any high degree of probability to the family has yet been
found outside of South America. The living *Lipotes* of China is the
only cetacean, recent or fossil, definitely known to represent the group
in the Northern Hemisphere or in the Old World. Various extinct
European genera, such as *Champsodelphis, Cyrtodelphis,* and *Acro-
delphis* have been supposed to be related to *Inia,* chiefly because of the
presence of a deep longitudinal groove on each side of the under
surface of the mandible. While some of these porpoises may eventu-
ally prove to be iniids it must be remembered that the development
of grooves, in both mandible and beak, appears to be merely a general
though not universal tendency in dolphins with slender rostrum and
long symphysis. Among living forms this grooving tendency is best
developed in *Stenodelphis.* Its next degree is found in the distantly
related *Platanista.* In *Lipotes* and *Inia* it is very slightly indicated,
though these genera are more nearly related to *Stenodelphis* than any
of the three is to *Platanista.* By itself, therefore, this feature is not
an index to affinity. The presence of *Lipotes* in the Old World makes
the eventual discovery of extinct members of the subfamily appear
certain; but their positive identification will depend on the finding
of material sufficiently well preserved to show the true structure of
the pterygoid and maxillary as well as the size of the temporal fossa
and the extent to which the frontal participates in forming the lateral
wall of the braincase.

Delphininæ.—After removal of *Inia* and *Lipotes* as a family, and
of *Stenodelphis, Delphinapterus, Monodon,* and, provisionally, *Eurhi-
nodelphis,* as the representatives of four subfamilies, the dolphins
become a rather compact group chiefly characterized by the high
degree of telescoping of the braincase, the small temporal fossa, the
small pterygoid reduplicated on its inner side only, and not spreading
over the alisphenoid; teeth normally-growing (never tusk-like);
posterior orifice of antorbital canal usually formed by maxillary alone,
though sometimes (*Lissodelphis, Neophocæna*) its lower edge is nar-
rowly touched by the palatine. The orbits are situated so far pos-
teriorly as to lie in the same transverse plane as the narial passages.
Since the narial passages have been moved as far back as the brain
will allow, it seems at first sight as though the equally posterior posi-
tion of the orbits might be regarded as a feature of high specialization
in comparison with the more anterior position which they occupy in
Monodon, Delphinapterus, the iniids, and even more conspicuously
in *Platanista,* a position which appears to be less of a departure from

the condition found in ordinary mammals. That such may not be the case, however, is indicated by the fact that the posterior opening of the antorbital canal lies under the anterior border of the orbit in the *Delphininæ* in a position (pl. 1, fig. 1*a*, *a. o. for.*) essentially the same as that which may be seen in a sea-lion (pl. 2, fig. 2*a*, *a. o. for.*), while in the skulls with more anteriorly placed orbit the orifice of the canal usually though not always lies behind the position which it normally occupies with regard to the orbit. This would appear to show that a readjustment of parts had taken place (most con- spicuous in *Platanista*), a process representing a higher degree of specialization than that indicated by a greater pushing backward of the orbit without readjustment of relative positions. The form of the rostrum is variable and of little importance for distinguishing groups higher than genera. This typical subfamily includes the great majority of both living and fossil members of the family. The recent genera are so well understood that they do not require special mention here. Among the fossils which I would refer without too great hesitation to the *Delphininæ* as thus restricted are those which have formed the bases of the following generic names: *Acrodelphis, Champsodelphis, Delphinodon* (as understood by True, Proc. Biol. Soc. Washington, Vol. 24, pp. 37-38, February 24, 1911; crowns of posterior teeth with a broadened inner portion suggesting that which occurs in the living *Inia*.), *Heterodelphis, Lophocetus, Palæo- phocæna, Palæoziphius, Physeterula, Physodon* of Lydekker 1893 (probably not of Gervais 1872), *Pithanodelphis, Pomatodelphis* (may be referable to the *Iniidæ*). Others which may belong here are: *Cetorhynchus, Delphinavus, Delphinopsis, Dinoziphius* (teeth sug- gesting those of a very large *Orcinus*), *Hesperocetus, Iniopsis, Ixa- canthus, Phocænopsis, Priscodelphinus, Protophocæna*. The names in this second list are, however, based on such fragmentary material that no clear idea can at present be formed regarding the animals to which they are applied.

Eurhinodelphininæ.—The genus *Eurhinodelphis* has been placed in a special group, principally on account of the supposed forward extension of the intermaxillary in front of the maxillary to form the entire anterior third of the greatly elongated beak. In other respects there appear to be few highly exceptional peculiarities to separate the genus from ordinary delphinids. While such a development of the intermaxillary would undoubtedly be reason for regarding the animal as the representative of a distinct subfamily the evidence for its occurrence is inconclusive. Mr. Remington Kellogg has called my

attention to the fact that there is no reason to regard the structure of
the rostrum in *Eurhinodelphis* as different from that in any other long-
beaked porpoise, at least so far as regards the specimen collected by
True near Chesapeake Beach, Maryland, and briefly recorded in 1908
(Proc. Amer. Philos. Soc., Vol. 47, p. 388). This skull (No. 10,464,
U. S. National Museum), well preserved except for the base and
sides of the braincase, agrees in all essential respects with Abel's
figures (Mém. Mus. roy. Hist. Nat. Belgique, Vol. 1, pls. 6-8, 1901)
of the European animal. The structure of the rostrum is not very
different from that of the rostrum of *Stenodelphis*. As is commonly
the case in long-beaked dolphins the boundaries between the maxil-
lary and intermaxillary bones are obliterated. Obliquely crossing
the side of the rostrum, from the main lateral sulcus to the alveolar
level, in the position marked by the white suture line in Abel's plates
there occurs a faint groove about 3 mm. wide and so shallow as to
be almost invisible in unfavorable light. It appears to indicate the
course of some nerve or blood vessel that ran forward and down-
ward along the surface of the maxillary from the lateral sulcus to the
anterior part of the roof of the mouth. There is nothing in the
appearance of this shallow, wide groove that suggests the narrow,
smooth suture which joins the maxillary and intermaxillary in the
skulls of porpoises which retain traces of this juncture. If the char-
acters of the European specimens are no more unusual than those
of this Maryland skull there would appear to be no grounds for
regarding *Eurhinodelphis* as the representative of a distinct group.

Stenodelphininæ.—The genus *Stenodelphis* has been placed in the
Delphinidæ, the "*Platanistidæ*" and the *Iniidæ*. The position which
it seems to occupy most naturally is that of a subfamily in the
family *Delphinidæ*. With it should be associated the extinct *Palæo-
pontoporia* and perhaps *Argyrocetus*. The characters of the group
are to be found in the structure of the braincase, the temporal fossa,
and the pterygoid, not in the elongated beak. The pterygoid is widely
spread over the surface of the alisphenoid, completely covering this
bone and coming into broad contact with the frontal as in *Delphin-
apterus*. The external reduplication of the pterygoid is like that of
Delphinapterus, but even better developed ; the internal reduplication
is large and apparently of the same type as in the true dolphins, but
the only specimen which I have examined is not in entirely satis-
factory condition. Orbits relatively smaller than in the *Delphininæ,*
their position immediately in front of the transverse plane occupied
by the narial passages ; these peculiarities agreeing with the condi-

tions present in the iniids, and perhaps representing a structure more primitive than that now existing in the true dolphins. Posterior orifice to the infraorbital canal formed by the maxillary alone. Teeth of normal delphinine type, with no tendency toward a tusk-like manner of growth. Cervical vertebræ retaining their primitive condition of separateness. The living genus *Stenodelphis*, with its extinct relatives, appears to represent a well defined group best treated as a subfamily of the *Delphinidæ*. The structure of the pterygoid and the absence of a backwardly projecting maxillary plate at the side of the palate distinguish it sharply from the *Iniidæ* and connect it with the *Delphinidæ* through morphological features similar to those present in the otherwise very different *Delphinapterus*. Its even more fundamental unlikeness to *Platanista* is shown by the strictly delphinine type of telescoping and of pterygoid structure, as well as by the large size of the palatine and the absence of other modifications connected with extreme backward-forcing of the base of the beak.

Delphinapterinæ.—A similarly isolated position as regards the ordinary dolphins is occupied by the genus *Delphinapterus* which shares some of the peculiarities of *Monodon* and some of those of *Stenodelphis*. In contrast with *Monodon*, however, the posterior basal portion of the pterygoid is spread laterally over the alisphenoid, and in most skulls there is an evident outer pterygoid reduplication like that present in *Stenodelphis;* though the teeth are tusk-like in manner of growth the general character of the dentition is normal, with several functional teeth of approximately equal size in each jaw; some of the hindermost teeth, especially in the upper jaw, show a distinct trace of a tricuspid crown structure when unworn (See True, Smithsonian Misc. Coll. Vol. 52, p. 329, April 28, 1909, and Lönnberg, Arkiv. för Zoologi, Vol. 7, pp. 2-4, fig. 1, July 5, 1910.). The cervical vertebræ, as in both *Monodon* and *Stenodelphis*, retain their primitive condition of distinctness, and the orbits are situated at a level in front of that occupied by the nasal passages. These characters, especially those of the teeth, have led Lönnberg to regard the genus as the representative of a distinct family. They appear, however, to be of no more than subfamily value.

Monodontinæ.—The genus *Monodon* has usually been associated with *Delphinapterus*, principally because in these two genera the cervical vertebræ differ from those of most other living dolphins in retaining their primitive separateness. Similarity between the two genera is also shown by the manner of growth of the teeth, by the conspicuous participation of the palatine in the formation of the

posterior orifice to the infraorbital canal, and by the situation of the orbits at a level decidedly in front of that of the narial passages. The orifice of the antorbital canal, as in *Delphinapterus,* lies distinctly behind the level of the anterior border of the orbit, a peculiar position as compared with ordinary mammals which would appear to show that special readjustment of the parts has taken place, either through a backward movement of the base of the rostrum which has carried the foramen with it, or by a secondary forward movement of the orbit after conditions had been established resembling those seen in the *Delphininæ.* On the other hand the posterior basal portion of the pterygoid of *Monodon* does not spread laterally over the surface of the alisphenoid in the peculiar manner seen in *Delphinapterus* and *Stenodelphis.* The relations of these two bones are of the ordinary dolphin type (No. 23,455, U. S. National Museum) except that there appears to be more of a tendency for the anterior basal portion of the pterygoid to expand outward in the direction of the optic canal. The anterior reduplication of the pterygoid is narrow and ridge-like, suggesting the conditions which occur in the ziphiids and in *Delphin-apterus,* but of a somewhat intermediate character. This combination of peculiarities taken in connection with a form of dental specialization which is unique among known cetacea appears to be sufficient to place the genus *Monodon* in a subfamily of its own.

Ziphiidæ.—The beaked whales have recently been regarded as near relatives of the sperm whales, often as members of the same family, chiefly because of similarities in the tusk-like manner of growth of the teeth and in the relationship of the hindermost ribs to the vertebræ. These characters now appear to be of little weight relatively to the type of skull-telescoping and the structure of the palatine and pterygoid. In these very important morphological features the beaked whales differ completely from the sperm whales and essentially agree with the delphinids. Telescoping is strictly of the delphinine type (see pl. 5, fig. 5, and pl. 7, fig. 4), the maxillary passing back horizontally over the eye even in such an excessively modified skull as that of *Hyperoodon.* Pterygoid greatly enlarged, covering almost the entire surface of the alisphenoid, its inner and outer reduplications present but low and ridge-like. Posterior orifice of infraorbital canal formed by maxillary, palatine, pterygoid and lacrimal, though the maxillary and pterygoid may be excluded (especially in the genus *Berardius*). It seems proper to consider the beaked whales as near relatives of the delphinids, though sufficiently characterized by the peculiarities of the skull, dentition and

ribs to form a distinct family. In general they appear to be more specialized than the dolphins; but the area formed by the palatine in the anterior wall of the narial passage as compared with that formed by the maxillary is narrower than in the dolphins, an apparently primitive feature which might indicate that the group originated from dolphin-like animals which were considerably less modified than any now living.

Platanistidæ.—The genus *Platanista* alone represents the family *Platanistidæ*. The type of telescoping shown by its skull is strikingly different from that seen in the recent genera *Inia, Lipotes* and *Stenodelphis,* and the fossil *Pontoplanodes* (as shown by Abel's photographs, Sitzungsber. k. Akad. Wissensch. Wien., Math.-Nat. Kl., Vol. 118, pt. 1, pl. facing p. 272, 1909), all of which, at one time or another, have been associated with it. In this character as well as in the anterior position of the orbit relatively to the narial passages it agrees with *Physeter* so far as general structure of the cranium is concerned; merely the lateral portion of the occipital has not advanced so far forward at the expense of the parietal as in the sperm whales. The resemblance of the frontal to that of a young *Physeter* is particularly noticeable (pl. 6, figs. 1, 2). In all other features the skull differs so widely from that of the sperm whale and its allies that the similarities in the type of telescoping cannot be regarded as indications of near relationship. On the contrary, among living odontocetes the total specialization of the skull is least of all in the physeteroids and greatest of all in *Platanista,* thus indicating the widest possible degree of separation between the two groups. Some of the more important of the special characters of the skull which show extreme departure from ordinary mammalian structures are: the great size of the pterygoid which spreads laterally to cover the alisphenoid and interlock with the squamosal and frontal, and which extends so far forward that about half of its area lies in front of the infraorbital foramen, into the formation of whose posterior and superior margins it largely enters; the development of the outer reduplication of the pterygoid as a heavy plate exceeding the original portion of the bone in both size and in density of structure (this plate is not homologous with the ectopterygoid of other mammals, an outgrowth from the alisphenoid which does not occur in modern cetaceans) ; the greatly reduced condition of the palatine, widely separated from its fellow of the opposite side and completely covered by the pterygoid except where it appears at the surface in the anterior wall of the narial tube; the backward forcing of the base of the

rostrum until the infraorbital foramen is brought to a position behind the orbit and wholly beneath the greatly elongated optic canal; the formation of the anterior orifice of the infraorbital canal by the pterygoid, frontal, and maxillary to the exclusion of the palatine and lacrimal.

Genera whose position is not clear.—Several extinct genera which have been carefully described so far as the known material would allow are still too incompletely understood to be assigned to a definite place in the present classification. Some of these have already been mentioned (see especially remarks on the *Agorophiidæ*, *Physeteridæ*, *Iniidæ*, *Delphininæ*, *Eurhinodelphininæ* and *Stenodelphininæ*). Others whose position is still more doubtful are those which have been described under the names *Cyrtodelphis, Diochoticus, Eoplatanista,* and *Squalodelphis;* also a remarkably long-beaked dolphin from the Calvert formation of Maryland, an account of which, by Mr. Remington Kellogg, is now in press.

EXPLANATION OF PLATES

In order to eliminate so far as possible the confusing influence of the great differences in size presented by the skulls of such animals as foxes, porpoises and baleen whales, most of the specimens have been photographed at a length of about 7-8 inches and then reduced to the dimensions required by the plates. Any attempt to indicate the scales of the various reductions would be contrary to the strictly morphological purposes of the illustrations.

The following abbreviations are used:

a. o. for. = Antorbital foramen.
a. pr. = Ascending process of maxillary.
a. sph. = Alisphenoid.
eth. = Ethmoid.
fr. = Frontal.
i. = Intermaxillary.
i. p. = Interparietal.
j. = Jugal.
l. = Lacrimal.
mes. = Mesethmoid.
mx. = Maxillary.
n. = Nasal.
occ. = Occipital.
o. pl. = Orbital plate of maxillary.
orb. = Orbit.
o. s. = Occipital shield.
o. sph. = Orbitosphenoid.
p. = Palatine.
par. = Parietal.
pt. = Pterygoid.
sq. = Squamosal.
v. = Vomer.
x. = Postero-internal angle of orbital plate of maxillary.
y. = Posterior termination of maxillary in median line.
+ = Position of anterior margin of occipital shield.
† = Position of narial orifice.

PLATE 1

Comparison between the skull of a toothed cetacean, fig. 1, and that of a baleen whale, fig. 2, to show the differences in method of telescoping described on page 4; dorsal and ventral aspects. (For comparison of lateral aspects see plate 6.)

FIG. 1. *Steno*. No. 49983, U. S. Nat. Mus. (The tympanic and periotic bones have been lost. The absence of the orbital plate of the maxillary is shown in fig. 1b by the exposed line of contact between the maxillary and the anterior border of the frontal.)

FIG. 2. *Balænoptera*. No. 236680, U. S. Nat. Mus. (The right tympanic bone and the left jugal have been lost. The great development of the orbital plate of the maxillary is shown in fig. 2b by the dotted line indicating the position of the anterior border of the frontal hidden in this view by the orbital plate.)
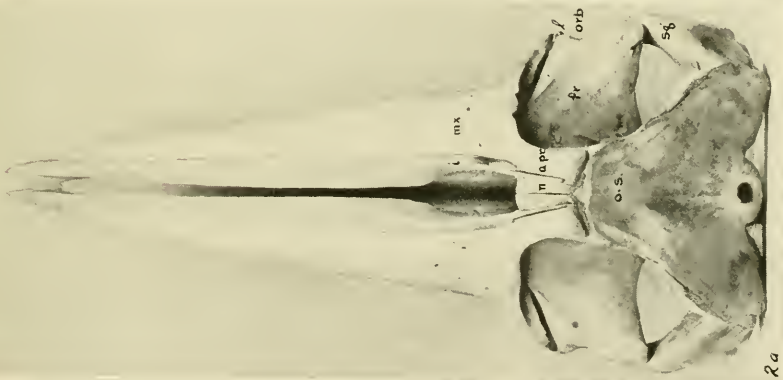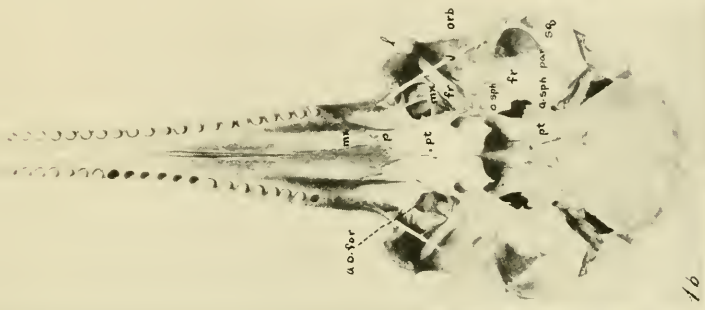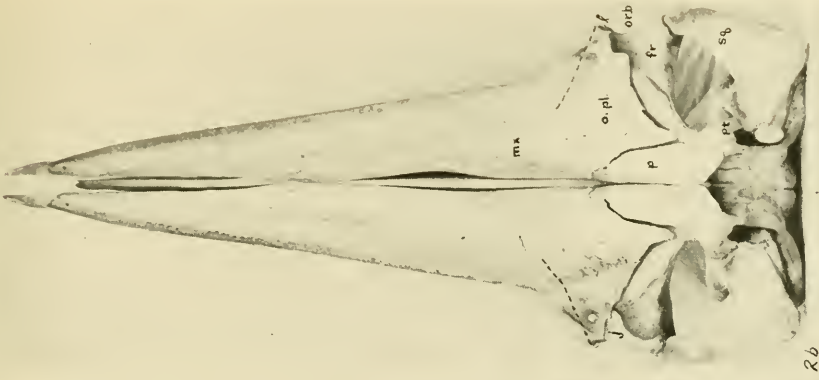
1. Toothed cetacean. 2. Baleen whale.

PLATE 2

Comparison between the skull of a young fox, fig. 1, and that of a young sea-lion, fig. 2; lateral aspect. Each skull has been photographed twice, from slightly different angles. The maxillary and occipital are disarticulated to show their differing mechanical relationships with the frontal and parietal respectively. In the fox the maxillary broadly overlies the frontal in the region of contact; the occipital and parietal are opposed. In the sea-lion the occipital broadly overlies the parietal in the region of contact; the maxillary and frontal are interlocked.

Fig. 1. *Vulpes.* .   No. 176017, U. S. Nat. Mus.
Fig. 2. *Eumetopias.*   No. 151534, U. S. Nat. Mus.
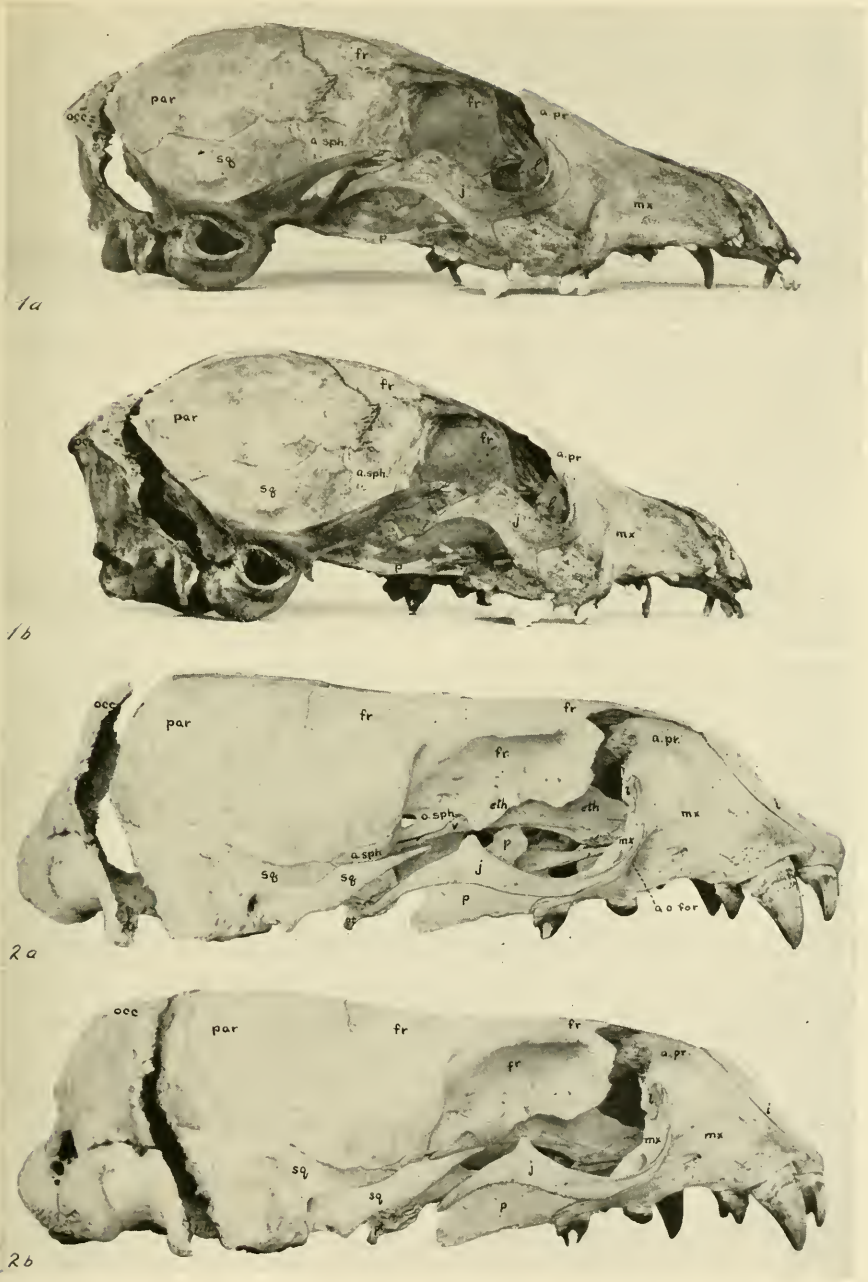
1. Fox.   2. Sea-lion.

PLATE 3

Left maxillary bone removed from skull and viewed from behind to show features of similarity between a sea-lion, fig. 1, a furseal, fig. 2, and a baleen whale, fig. 3, and those between a fox, fig. 4 and two toothed cetaceans, figs. 5 and 6.

FIG. 1.   *Eumetopias.*   No. 239330, U. S. Nat. Mus.
FIG. 2.   *Callorhinus.*   No. 239329, U. S. Nat. Mus.
FIG. 3.   *Balænoptera.*   20931, U. S. Nat. Mus.   (The missing lacrimal lay in the depression of the maxillary in front of the jugal, as may be seen in fig. 3 of plate 6.)
FIG. 4.   *Vulpes.*   No. 239333, U. S. Nat. Mus.
FIG. 5.   *Physeter*, very young.   No. 49488, U. S. Nat. Mus.
FIG. 6.   *Grampus.*   No. 15773, U. S. Nat. Mus.
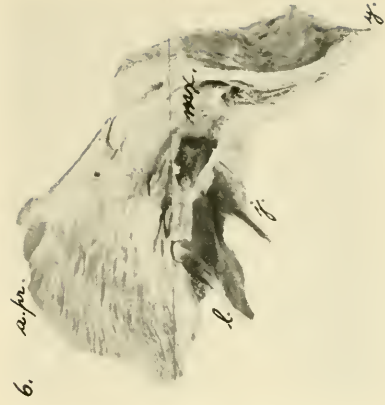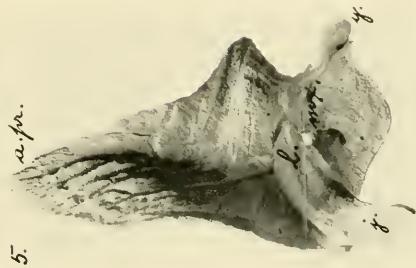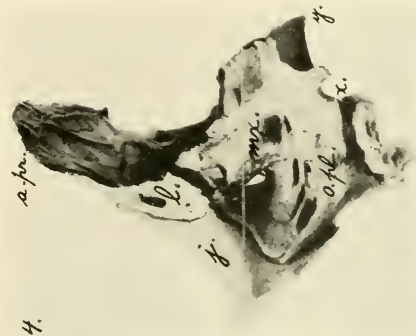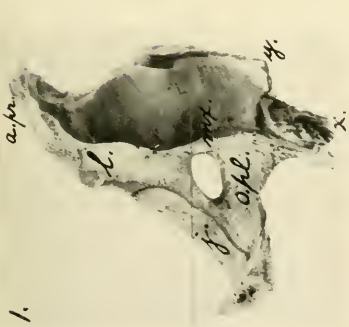
DETACHED MAXILLARY BONE VIEWED FROM BEHIND.

1. Sea-llon.
2. Furseal.
3. Baleen whale
4. Fox.
5. Sperm whale.
6. Grampus.

PLATE 4

Comparison between the lateral aspect of the maxillary of a zeuglodont, fig. 1, a toothed cetacean, fig. 2, and a baleen whale, fig. 3. The large orbital plate in the baleen whale is a structure which is absent in both the zeuglodont and the toothed cetacean.

FIG. 1. *Prozeuglodon* (from C. W. Andrews).

FIG. 2. *Grampus.* No. 15773, U. S. Nat. Mus.

FIG. 3. *Balænoptera.* No. 20931, U. S. Nat. Mus. (The missing lacrimal lay in the depression of the maxillary in front of the jugal, as may be seen in fig. 3 of plate 6.)
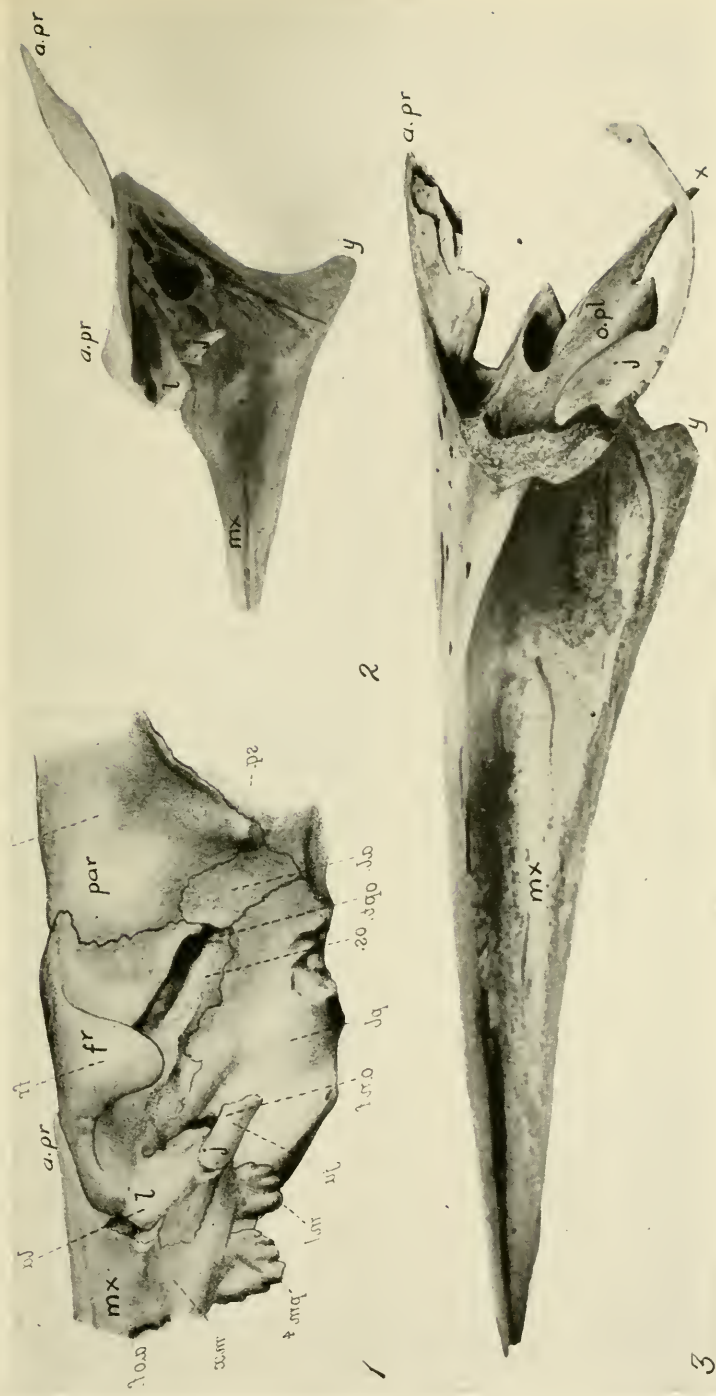
MAXILLARY VIEWED FROM THE SIDE.

1. Zeuglodont.
2. Toothed cetacean.
3. Baleen whale.

PLATE 5

Lateral aspect of skulls of zeuglodont, fig. 1 and toothed cetaceans, figs. 2-5.

FIG. 1. *Prozeuglodon* (from C. W. Andrews).

FIG. 2. *Agorophius* (from True).

FIG. 3. *Archæodelphis* (from G. M. Allen).

FIG. 4. *Delphinus.* No. 21525, U. S. Nat. Mus.

FIG. 5. *Mesoplodon.* No. 23346, U. S. Nat. Mus.

FIG. 6. *Xenorophus.* No. S. 402 W., Sloan Collection. (View of the type skull from slightly in front and above, to bring out particularly the terraced character of the maxillary, as shown by the level areas in the regions marked *mx* and *a. pr.* and the abruptly sloping area between them, and the wide overlapping of the maxillary and intermaxillary in the interorbital region; the upper dotted line indicates the original position of the maxillary border as shown on the opposite side of the specimen ; the lower dotted line indicates the approximate position of the lower border of the intermaxillary as seen in posterior view.) For other figures of *Xenorophus* see Kellogg, Smithsonian Misc. Coll., Vol. 76, No. 7, pls. 1-2, July 25, 1923.
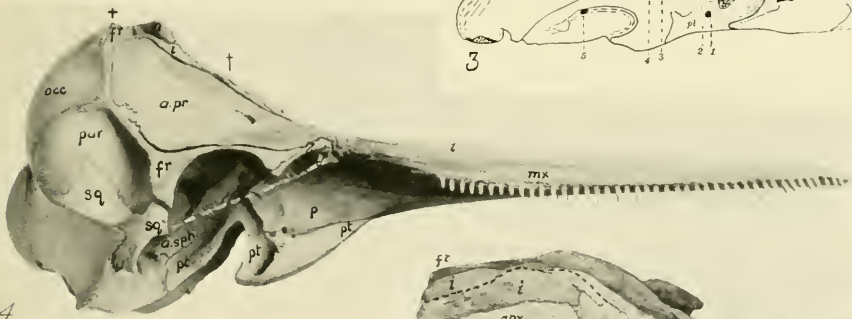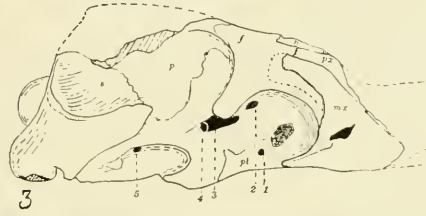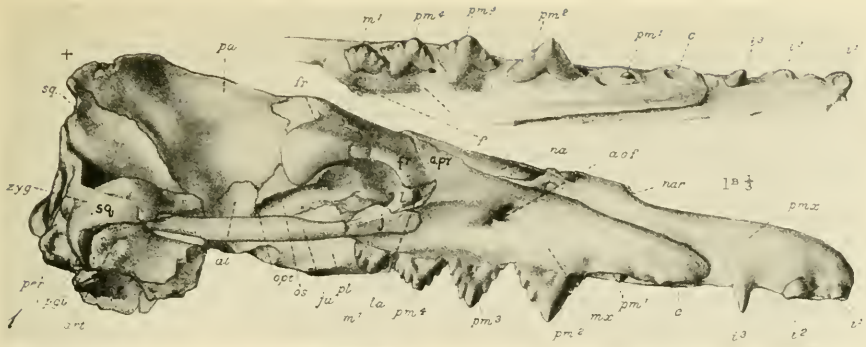
1. Prozeuglodon.   4. Delphinus.
2. Agorophlus.   5. Mesoplodon
3. Archæodelphls.   6. Xenorophus.

PLATE 6

Lateral aspect of skulls of toothed cetaceans, figs. 1, 2, and baleen whales, figs. 3, 4.

FIG. 1. *Physeter,* very young. No. 49488, U. S. Nat. Mus.

FIG. 2. *Platanista.* No. 172409, U. S. Nat. Mus. (The lacrimal and very short jugal are almost concealed beneath the overhanging edge of the orbit. The posterior orifice of the antorbital canal is visible above the edge of the zygomatic process of the squamosal in the region where the process comes in contact with the orbital portion of the frontal; above the orifice of the antorbital canal is a slit-like vacuity in the wall of the optic canal.)

FIG. 3. *Balænoptera.* No. 236680, U. S. Nat. Mus.

FIG. 4. *Eubalæna.* No. 23077, U. S. Nat. Mus.
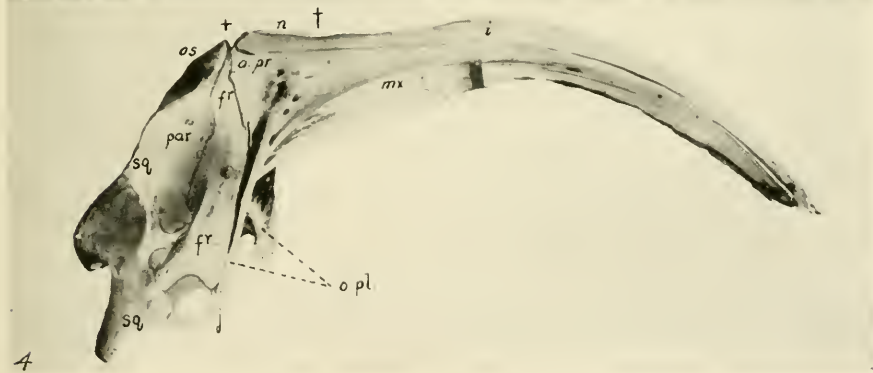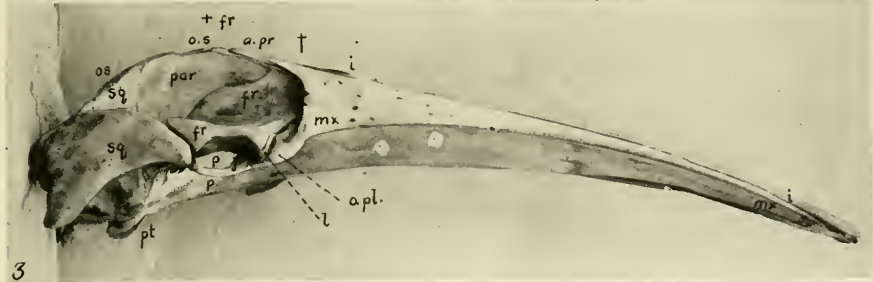
1. Physeter.
2. Platanlsta.
3. Balænoptera.
4. Eubalæna.

PLATE 7

Lateral aspect of skulls of highly modified toothed cetaceans, figs. 2, 3, 4, compared with that of a normal mammal, fig. 1.

FIG. 1. *Cynogale.* No. 145587, U._S. Nat. Mus.
FIG. 2. *Stenodelphis.* No. 49494, U. S. Nat. Mus.
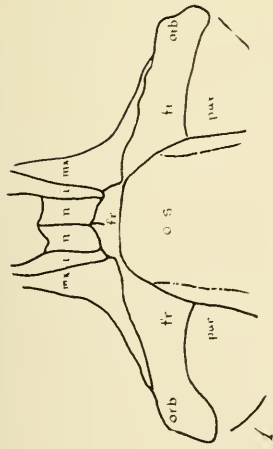FIG. 3. *Kogia.* No. 22015, U. S. Nat. Mus.
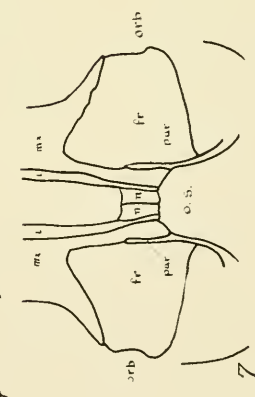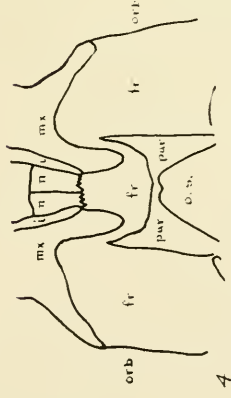FIG. 4. *Hyperoodon.* No. 14499, U. S. Nat. Mus.
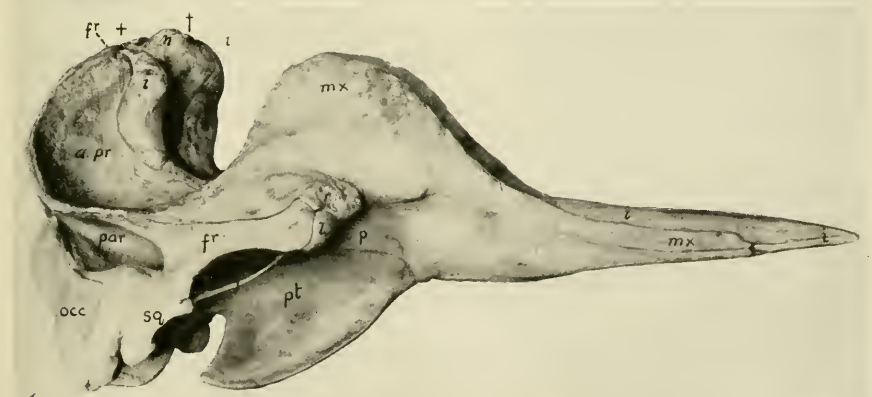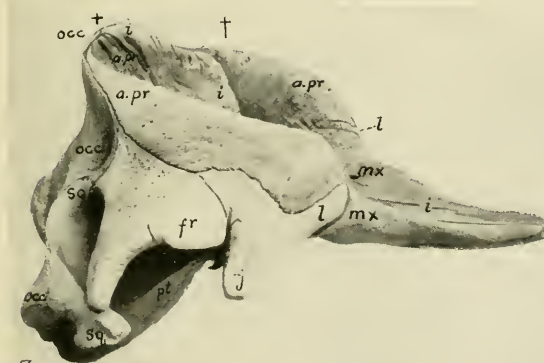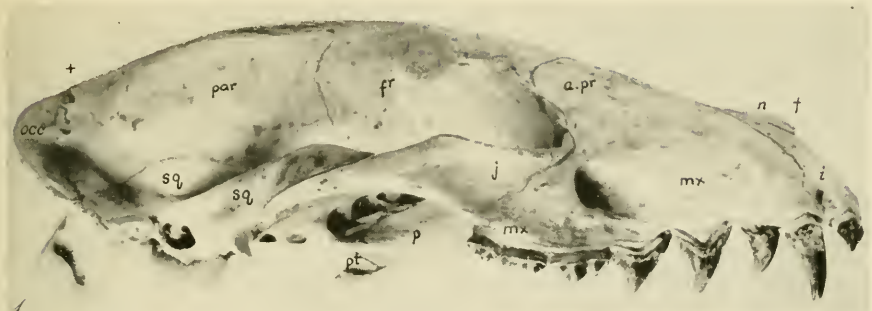
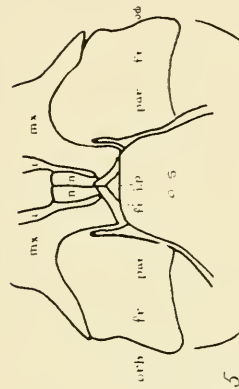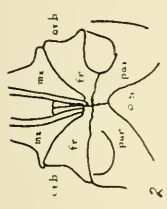1. Cynogale.　　3. Kogla.
2. Stenodelphis.　　4. Hyperoodon

PLATE 8

FIGS. 1-7 diagrams of telescoping in vertical region of mysticete skulls.

FIG. 1. *Eubalæna*. No. 23077, U. S. Nat. Mus.
FIG. 2. *Cetotherium* (from Van Beneden and Gervais).
FIG. 3. *Rhachianectes* (from R. C. Andrews).
FIG. 4. *Balænoptera,* young (from Eschricht).
FIG. 5. *Balænoptera* sp. No. 236680, U. S. Nat. Mus.
FIG. 6. *Balænoptera* sp. No. 16039, U. S. Nat. Mus.
FIG. 7. *Sibbaldus*. No. 49757, U. S. Nat. Mus.
FIG. 8. *Spalax* sp. (from Méhely). To show development of occipital shield
          and reduction of exposed area of parietals in a burrowing rodent.
FIG. 9. *Balæna* (from Eschricht). Longitudinal section of skull in frontal
          region to show presence of occipital, frontal and nasal at one
          vertical plane.

1. Eubalæna.
2. Cetotherium.
3. Rhachianectes.

4. Balænoptera.
5. Balænoptera.
6. Balænoptera.

7. Sibbaldus.
8. Spallax.
9. Balæna.