

SOME GENERAL FEATURES OF THE HISTORY OF THE CETACEANS (PART I)

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5/ FOREWORD

Interest in the cetaceans has grown considerably in recent years. This vast group of marine animals is one of the most important objects of recent investigations on the paleontology and zoology of the mammals, simultaneously engaging the attention of biologists, physicists, and members of several other specialties. Nevertheless many problems concerning the biology of the modern forms of the cetaceans, and also of the paleobiological history of the whole group, have as yet been insufficiently elucidated. They still need careful study or at least rigorous checking.

Naturally the leading role in the study of the phylogenetic history of the cetaceans, as of other animals, belongs to paleobiology, for only fossil material makes it possible to trace the main trends of the phylogenetic changes in an animal organism, if only in the broad features.

However, due to the incompleteness of the geologic record and, perhaps, of our knowledge, paleontology makes it possible to construct concrete phylogenetic series only in very rare cases.

Therefore, to set up investigations of the paleontological history of any group of animals properly, even when fossil material is abundant, it is absolutely necessary to bring in as many data as possible on the modern relatives of the fossil forms (if, of course, such exist). Moreover, it is of course understood that the present stage of evolution of the animals in itself is also a very important component part of their phylogenetic history as a whole.

It is natural therefore that in the proffered work, data from the special literature not only on fossil but also on recent cetaceans have been widely used in addition to paleontological data collected by us.

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6/ INTRODUCTION

On the Significance of the Investigation of Fossil Cetaceans

The cetaceans are one of the least studied groups of fossil mammals. The slight study of the paleobiological history of the cetaceans is due primarily to the scantiness of paleontological material and to the usually disjointed nature of occurrences of the remains of these animals. Also, the fact that investigators in the past, not attaching any importance to the cetaceans for the stratigraphic subdivision of sedimentary series, did not pay them due attention, has played a not unimportant role in this. Data on investigations of the cetaceans also have been used relatively rarely in working out theoretical problems of biology. Moreover, the paleobiological history of the cetaceans, which are secondary-aquatic animals, affords the possibility of studying the history of adaptations of terrestrial mammals to life in an aquatic environment, and thereby of explaining some general regularities of the evolution of organisms.

For example, the results of investigations of fossil cetaceans constitute rich material for the elucidation of the problem of evolutionary progression in biology, paths of ecogenesis of the mammals, the problem of extinction, and also a number of other theoretical problems.

The investigation of fossil cetaceans also is important in explaining the bionomic setting of ancient basins. Frequently the remains of these animals give an accurate picture of the facies nature of the formations containing them (W. Schäfer, 1955). Data from spectroscopic and chemical analysis of this material can be used to determine /7/ the saline regime of ancient seas (A. N. Kudrin, S. Sivkova et al., 1962), thus making it possible to establish the conditions of a given basin.

Up to the present time the value of fossil cetaceans for stratigraphy thus also been underestimated. Meanwhile one can hardly doubt that the study of such widely distributed and relatively rapidly evolving groups of cetaceans as the Zeuglodontidae, Cetotheriidae, Squalodontidae, and others might help in working out the complex problem of correlating geologic formations geographically remote from one another. Regrettably, the marine mammals have as yet been little used for such

purposes. This is explained partly by the difficulties which arise in constructing the fossil faunas of marine mammals. However, a no less important obstacle is the fact that investigators of these fossil forms usually limit themselves just to the description of the osteological material and do not pay enough attention either to the phylogenetic history of the animals investigated or to the organic forms associated with them and the nature of the enclosing sediments.

As is known, the cetaceans have an almost universal distribution at present, and although we have insufficient basis for believing that they enjoyed as wide a distribution in the past, nevertheless data accumulated in the last decade indisputably testify to their wide distribution in the seas of various geologic epochs from the Eocene to the present time.

There is no doubt that a more careful investigation of the faunas of fossil marine mammals already known to science will succeed in establishing the stratigraphic importance of many of them. We are even inclined to think that by virtue of their almost universal distribution and high rate of radiation, some groups of fossil cetaceans could be extremely important in intercontinental correlations.

However, it should not be forgotten that correct use of data on the fossil mammals in general and on the cetaceans in particular depends to a great extent on the extent of knowledge of their phylogenetic history, /8/ on a more detailed treatment of the problem of the genetic relationships of this or that group, refinement of the taxonomic composition and rank of the individual taxonomic units, and also clarification of the phylogenetic changes of the animals in relation to changes in exogenetic conditions, and a number of other things. Without careful preliminary analysis of the material, our conclusions could be inaccurate or even erroneous.

9/ REVIEW OF THE TAXONOMY AND GENERAL DESCRIPTION OF MODERN CETACEANS

The order Cetacea, according to the presently accepted taxonomy of the cetaceans, is divided into three suborders: the Archaeoceti, or ancient whales; the Mysticeti, or toothless whales; and the Odontoceti, or toothed whales. The first of these consists entirely of fossil forms, and the other two

include both living and fossil cetaceans. In the modern fauna, the toothless whales are represented by the following families: the Balaenidae Gray, 1825 (the right whales), comprising three genera; the Balaenopteridae Gray, 1864; (the rorquals), with two genera; and the Eschrichtiidae Gray, 1864 (the gray whales), represented by one genus.

The balaenids are relatively small or medium-sized whales (from 5 to 21 m long), clearly distinguished from the other toothless whales by the smooth belly and throat without longitudinal grooves and by the great length of the head, which constitutes a fourth and sometimes even a third of the total length of the animal.

The balaenopterids are very large forms, not only among present mammals but also among all the animals that ever lived. Their length varies from 11 to 33 meters, the belly and throat are covered with numerous longitudinal grooves, and the length of the relatively small head fits almost four times into the total length of the body.

The gray whales are animals of medium length (from 8 to 14 m long) with smooth belly (they have grooves only on the throat) and relatively short head comprising 1/5 of the total length of the animal. On the basis of a whole series of anatomical and also ecological features, they represent the most primitive group among all the modern toothless whales.

10/ Whereas the modern toothless whales, as is apparent from the very brief outline given above, are not distinguished by an abundance of forms, the toothed cetaceans, now in full flower, are characterized by a wide variety of both species and genera.

A number of investigators (G. Simpson, 1941; P. Grasse, 1955; and others) divide the modern toothed cetaceans into six families: Physeteridae Gray, 1821; Ziphiidae Gray, 1865; Delphinidae Flower, 1864; Delphinapteridae Weber, 1904 (→ Monodontidae Gray, 1891); Phocaenidae Brandt, 1885; and Platanistidae Gray, 1868. Some (A. G. Tomilin, 1957) divide this suborder into only four families, including the phocoenids and delphinapterids in the family Delphinidae. We are inclined to follow the

latter classification, as in our opinion it reflects to a greater extent the main stages in the phylogenetic history of this group of cetaceans.

The family of cachalots (Physeteridae) is represented by two genera comprising one species each. There are *Physeter catodon* L., the largest of the toothed cetaceans, which reaches 21 m in length, and *Kogia breviceps* (Blainville), the pygmy cachalot, not more than four meters in length. In contrast to all the other toothed cetaceans, the mouth of the cachalot is located on the lower surface of the head, and the perpendicularly truncated (in the large) or smoothly rounded (in the small) front of the head projects strongly beyond the front end of the very narrow mandible. The length of the skull in the large ones comprises $\frac{1}{3}$, and in pygmy ones $\frac{1}{5}$, of the total length.

The beaked whales (Ziphiidae) are large and medium-sized toothed whales (from 5 to 12 meters in length). Their head is small, sometimes comprising $\frac{1}{7}$ of the total length of the animal. The forward-tapering snout is extended in a relatively short beak. The lower jaws project somewhat beyond the tip of the rostrum at the front end, and are wider than the upper. Five genera are united in this family.

The dolphins (Delphinidae) are the largest family, embracing more than 20 genera of toothed cetaceans. The members of this family are small and medium-sized (from 1.60 to 10 m long). They are characterized /11/ by a tapered body, small head, and forward-elongated snouts of different shape and size. The lower jaws are as wide as the upper. Reduction of the dentition is noted only in rare cases.

The river dolphins (Platanistidae) are a unique group of small (2-3 m long) toothed cetaceans distinguished by a long extended snout and relatively large flippers. There are 4 genera in the family.

The cetaceans are animals very perfectly adapted to living in an environment. They have the torpedo-like body typical of marine vertebrates, laterally flattened tail stem, and horizontal tail fluke. Their body surface is smooth, without any projections which could retard their motion, the external *conchae auriculae* are reduced, the teats of the females are hidden in leathery pockets, the sex organs are located in the body cavity (S. E. Kleinenberg, 1956, p. 100). The skin is devoid of hair cover and of oil and sweat glands. The skin surface is covered with a special secretion of the epidermis, which increases the

slipperiness of the animal in the water. The upper layer of the epidermis is not subject to keratosis, which also promotes smoother gliding (B. F. Sokolov, 1955).

The skull in some cetaceans is very large, sometimes constituting 1/3 of the total length of the animal; in others it is relatively small. The facial part of the skull extends considerably forward due to elongation of the vomer, maxillae, and premaxillae. In the toothed whales the maxillae, widening proximally, completely overlap the facial surface of the skull; in the toothless whales they form only relatively narrow processes on the upper surface of the skull and in substantial part underlie the supraorbital processes of the frontal bones. The nasal bones are very much shortened. As a result of convergence of the pterygoid bones the bony palate is drawn back, thus causing displacement of the choanae in the larynx. The occipital bone, strongly developed in connection with the attachment of the powerful dorsal musculature and forcing the parietal bones to the sides, overrides the facial part of the skull to a different extent in the various forms. The mandibles are strongly extended, joined by ligaments (in the toothless) or fused together (in the toothed).

12/ The shoulder girdle is without a clavicle. The scapula has the shape of a triangular plate, with the spine considerably reduced and drawn toward the anterior edge of the bone. The proximal part of the limb is shortened. The hand is five-fingered (Odontoceti) or four-fingered (Mysticeti). The pelvis is reduced. A femur is present in the pelvic girdle only in the toothless whales.

There are four sections in the spine instead of the usual five of land animals: cervical, thoracic, lumbar, and caudal. The cervical section is very much reduced and the sacral is generally not formed due to reduction of the pelvis. The vertebrae are relatively reduced and sometimes even disc-shaped (in the dolphins). The transition to the caudal section is marked by the manifestation of hemapophyses.

The absence of tubular bones is typical. The forelimb bones, as are the other bones of the skeleton, are porous and saturated with a large amount of oil, which reduces the specific gravity of the skeleton to a considerable extent.

The respiratory canal, opening at the very top of the skull, ends either in one (in the toothed) or in two (in the toothless) external nostrils. Displacement of the nostril opening to the uppermost point of the skull permits the animals to breathe air without lifting the head from the water and remain unnoticed for a long time both by pursuing animals and by enemies. The complete separation of the respiratory and alimentary canals in the oral cavity (in the toothed) permits them to feed freely under water. The cetaceans are good divers. The development of this ability is related to the tolerance of their respiratory center to an accumulation of CO₂. What stimulates the act of breathing in the cetaceans is not the accumulation of carbon dioxide gas but the absence of oxygen, which permits the animal to utilize to the full the whole oxygen reserve of the inhaled air, thus increasing the duration of a dive. At the same time a complex and unique structure of the system of respiratory organs saves them from the bends.

The streamlined body shape, the structure of the skin, the powerful tail with strongly developed musculature, the asymmetrical skull (in the toothed), the flexible spine sometimes (in the dolphins) consisting of disc-shaped vertebrae, and other things guarantee /14/ rapid locomotion of these animals. However, not all the cetaceans have this ability to the same degree. Thus, for example, the toothless whales are relatively slow-swimming animals, with rare exceptions traveling at speeds of 7-8 kmph, while the toothed can work up a tremendous speed on the surface of the water--more than 50 kmph.

The main propulsive power of the cetaceans is the tail, although agitation of the animal's trunk itself apparently also plays a part in the forward motion of some toothed cetaceans (G. A. Mchedlidze, 1964).

Let us remember that as a rule the cetaceans give birth to one young. Births are facilitated by the presence of a diffuse epitheliochorial placenta. Also peculiar to the cetaceans is the position of the fetus at birth, which is unusual for other mammals: the fetus is born tail first. As a result, the body of the newborn one is lowered into the water head up, and because of its low specific gravity it stands up in the water like a buoy, permitting the newborn one to breathe air without hindrance. If the young occupied the opposite position at birth, it would inevitably suffocate upon its very first emergence.

Hearing is the most strongly developed of the sense organs. Sight is relatively well developed. The taste organs are weakly developed, and the organs of smell are completely (in the toothless) or partially (in the toothed) reduced.

The brain of the cetaceans is in the shape of a large oval hemisphere. Due to the intensive development of the temporal lobes of the hemispheres, the brain is strongly widened in the posterior part. Its width is markedly greater than its length, particularly in the toothed. The considerably developed frontal parts and strong curvature in the region of the diencephalon gives it a spherical shape as a whole. The cerebellum is intensively developed; its flocculi attain colossal size. The specific features of the cetaceans are: slight development (in the toothless) or complete absence (in the toothed) of olfactory nerves, bulbs, and stalks and relatively strong development of the V and VIII nerve pairs of the encephalon (A. Breathnach, 1961). Also typical is the strong development of the posterior tubers of the *corpore quadrigemina*, which in contrast to /14/ other mammals are considerably larger than the anterior, a fact which certainly is related to the intensification of the role of auditory perception in the orientation of these animals.

A whole series of similar morphofunctional features which the cetaceans have acquired during the long process of adaptation to life in an aquatic environment guaranteed the wide distribution of this group of mammals and their dominance in the present marine fauna.

Cetaceans are distributed in all regions of the world ocean. Some of them are even cosmopolitan, such as the blue whale, *Balaenoptera musculus* L., which seldom enters tropical seas but generally inhabits all the open seas and oceans from the Arctic to the Antarctic, or the white-flanked dolphin (*Delphinus delphis* L.), which is particularly numerous in regions of temperate waters but also does not shun the waters of tropical and northern latitudes.

Some cetaceans are typical Arctic animals (the Greenland whale, *Balaena mysticetus* L.; the narwhal, *Monodon monoceros* L.; and the beluga, *Delphinapterus leucus* Pallas). Others, for instance the southern whale *Eubalaena glacialis* (Bonaterre), are endemic to Antarctic waters. And others, like the

Japanese whale, *Eubalaena glacialis sieboldii* Gray, the Biscay whale, *Eubalaena glacialis glacialis* (Bonaterre), the gray whale, *Eschrichtius gibbosus* Erxleben, and others, live mainly in the waters of the temperate zone.

There also are endemics among the warm-water dwellers, such as, for example, the pygmy cachalot *Kogia breviceps* Blainv., which spends its whole life in this zone, and the cachalot (genus *Physeter*), the females of which enter higher latitudes only in the summer time (A. G. Tomilin, 1957). A small number of toothed cetaceans (members of the Family Platanistidae) live, as is known, in tropical rivers.

Having formed a considerable diversity of living forms in the course of intensive ecological expansion, the cetaceans utilize the very vast fishing resources of the littoral and pelagic zones of the world ocean: all the right whales are macroplanktophagous, the rorquals are microplanktophagous, the gray whales are benthophagous, the common dolphin and prodolphin are ichthyophagous, /15/ the porpoises, white whales, and bottlenose dolphin are benthichthyophagous, the sperm whales, beaked whales, bottle-nosed whales, and others are teuthophagous, and the pilot whales and pygmy sperm whales are teuthichthyophagous.

ON THE GENETIC RELATIONSHIPS OF THE VARIOUS GROUPS OF CETACEANS

The problem of the genetic relationships between the modern toothed (Odontoceti) and toothless (Mysticeti) cetaceans constitutes one of the most difficult pages in the history of the cetaceans.

On the basis of the substantial morphological differences between the two groups of cetaceans, W. Kükenhal (1891, 1900) and F. Beddard (1900) voiced the idea that the origin of this order possibly was diphyletic. However, looking at the essential similarity in the overall features of the morphology of the two groups of cetaceans, H. Winge (1921) later disputed the hypothesis advanced by Kükenhal and Beddard and subjected it to thorough criticism. From that time and almost until now, the order Cetacea has been regarded as a monophyletic group.

However, in recent years this problem has again been included in the order of the day. At the XV International Zoological Congress in London in 1958, S. E. Kleinenberg put forward the idea developed in the past by Kükenthal concerning the independent origin of the suborders Odontoceti and Mysticeti. As a result of a comparison of the morphological features of several systems of organs in the toothed and toothless cetaceans, he demonstrated an essential difference between these suborders. Thus, for instance, that author (S. E. Kleinenberg, 1958) noted that in contrast to the toothless, in the toothed there is always only one external blowhole, giving entrance to a single nasal passage, and in addition to an external skin-and-muscle valve, they always have a ramified and complex system of air sacs which are never present in the toothless. On the other hand, the toothless characteristically still retain the ethmoturbinal conchae which as a rule are absent in the toothed. Also demonstrated were differences in the principle of structure of the throat, pharynx (complete separation of the respiratory and alimentary canals in the toothed /16/ and only periodic [separation] in the toothless), trachea (with closed rings in the toothed and open in the toothless), lungs, and also of the alimentary system. Differences in the structure of the skull (asymmetrical in the toothed and symmetrical in the toothless) and flippers (four-fingered hand in the toothless and five-fingered in the toothed) were also mentioned, and attention was also directed to several ecological differences between the members of these suborders.

While S. E. Kleinenberg paid attention mainly to the differences between members of the suborders being compared, A. V. Yablokov (1964), dealing with the problem of the evolution of the suborders of the cetaceans, dwelt both on the differences and on the marks of resemblance of members of both groups of modern cetaceans.

To determine the nature of the evolution (convergence or parallelism?), that author proposed the following criteria: 1) a continuous series of changes in the organs over a long period of evolution of the group (this he considered to be the most reliable, but in practice diminished in value by virtue of the incompleteness of the "paleontological record"), 2) morphological differences in outwardly similar structures being examined, which have considerable value; and 3) independent origin of a structure

similar to the structures being examined, in a group (or groups) to be unrelated by distant or close kinship (A.V. Yablokov, 1961).

Using only the last two criteria for his analysis, the author shows that all the fundamental criteria characterizing the order Cetacea as a whole are also characteristic of other groups not related by close kinship. Therefore he came to the conclusion that the presence of the abovementioned features common to different representatives of the cetaceans is not a reliable basis for uniting them in one order; that is, it does not indicate their common origin.

In establishing the relationship of the early cetaceans (Archaeoceti) to the other groups of the Cetacea, A. V. Yablokov came to the conclusion that the Archaeoceti cannot be regarded as the ancestors of the modern cetaceans. He pointed out the following differences between the archaeocetes and the other cetaceans: snake-like body shape, small head, movable thorax, /17/ movable elbow joint, unique histological structure of the humerus, crests on the skull, differentiated dentition, lower jaw halves movable with respect to one another, etc. As for those characteristics of the archaeocetes which are seemingly common to other representatives of the order Cetacea, in the author's opinion those were different in principle in the archaeocetes: "their body was snake-like, not torpedo-shaped," as in the other cetaceans. He also doubted the possibility that a two-fluked tail fin, postulated on the basis of the presence of lower hemal arches, was present in the archaeocetes inasmuch as chevron bones are typical of all living forms which have carinate tails (for instance, the crocodiles). Finally, according to Yablokov, the elongation of the facial section of the skull common to all cetaceans and the supposedly identical structure of the fore limbs are of absolutely different nature in the archaeocetes

On the basis of these considerations the author came to the conclusion that as yet there are insufficient grounds for denying the convergent character of the evolution of the group Archaeoceti, and consequently for retaining this group as a subgroup of the order Cetacea.

While thus excluding the archaeocetes from the order of the cetaceans, the author further points out the essential differences in structure between the modern toothless and toothed cetaceans and also the superficial nature of their similarity, which indicates convergent evolution.

Without objecting in principle to the suggestion of a diphyletic origin of the Odontoceti and Mysticeti (which, however, in our opinion needs more substantial proof than has yet been offered) we find it relevant to report some additional data on the taxonomic position of the Archaeoceti and also to make some remarks of a methodological nature.

It seems to us that to elucidate the nature of the evolution (convergent or parallel?) of the suborders of the cetaceans, a morphological study (Yablokov's criterion 2) of only the marks of resemblance is not enough. For this it is necessary to resort not only to a thorough anatomical study but also, where possible, to histological and embryological investigations which to some extent reflect the trend of the phylogenetic changes of this or that structure of an animal organism. Thus, for instance, one of the main features of the modern toothed cetaceans which distinguishes them from the toothless, which have paired nasal openings as Kleinenberg (1958) points out, is the presence of one external blowhole giving entrance to a single nasal passage.

However, as investigations by M. M. Bleptsov (1955) show, in the toothed cetaceans (for instance the dolphins) the unpaired nasal opening forms only in the relatively late stage of embryological development; in the early stages (up to one and a half months) they retain a double opening, a fact which can fully serve as the basis for disputing the suggestion of a profound difference in the structure of the nasal opening of the toothed and toothless cetaceans.

Furthermore, concerning such an essential feature of the modern toothed cetaceans as the asymmetry of the skull (in contrast to the symmetrical one in the toothless) it should be noted that the Late Miocene and possibly even some Early Pliocene members of this group of cetaceans (for instance, such representatives of the delphinoids as *Kentriodon*, *Iniopsis*, *Cyrtodelphis*, *Delphinus*, *Anacharsis*,

and others) also have a symmetrical skull, and others (for example the fossil cachalot of the genus *Orycterocetus*) already had an asymmetrical skull in Miocene time (R. Kellogg, 1965).

However, these data do not contradict the idea of a diphyletic origin of the groups in question. They show that each feature under detailed discussion should be verified so far as possible by evidence on its phylogenetic development. In that case it will become possible to eliminate relatively unconvincing comparisons, which still further supports the standpoint of the diphyletic theory.

In our opinion a hardly very unimportant feature which shows the profoundest difference of all between the suborders Odontoceti and /19/ Mysticeti, and not only between their modern representatives but the ancient ones too, is the unique type of reorganization of skull construction peculiar to each of them which is traced during the course of their phylogenetic history beginning from Eocene time. This feature meets A. V. Yablokov's first criterion in the best way possible. During the phylogenetic history of the Odontoceti there is observed a gradual intensification of the caudal overriding and widening of the rostral elements, namely: their maxillae and premaxillae are overridden more and more strongly and, widening, overlap the skull bones situated caudally with respect to them, ultimately coming against the supraoccipital bone. We do not observe a similar process among the toothless cetaceans. In the latter, expansion of the rostral elements is limited by the fact that the maxillae and premaxillae form only relatively narrow and short processes on the dorsal surface of the marginal part of the skull, and for the most part the maxillae lie beneath the overriding processes of the frontal bones.

On the other hand, in contrast to the toothed, in the phylogenesis of the toothless there is observed an intensive increase in the size and gradually increasing overriding of the supraoccipital bone, peculiar only to them, which in some forms reaches the proximal ends of the maxillae.

Consequently, while in the toothed cetaceans the approach of the maxillae and supraoccipital bones is brought about by widening and overriding of the maxillae, in the toothless an intensive overriding of the supraoccipital bone plays the main role in this.

The common feature arising in the course of evolution of both these groups of cetaceans-- approach of the supraoccipitale-maxillaria leading to a distinct strengthening of the skull construction due to strengthening of the connection of the facial and cranial elements-- was developed in completely different ways in the Odontoceti and Mysticeti, which positively indicates the convergent character of this mark of resemblance.

Particulars indicating the relative antiquity of the one group or the other probably constitute the same kind of feature. From this point of view, the fact merits attention that /20/ the common features of skull structure (except asymmetry) inherent in the modern representatives of the toothed cetaceans, for instance the Delphinidae, had already formed in them at the end of Oligocene time; that is, the main process of reorganization of the skull construction was already completed toward the end of the Paleogene. Thus, while the relatively slightly diverging maxillae only partly override the supraorbital processes of the frontal bones in the Eocene *Archaeodelphis* (C. Dechaseaux, 1961), in the Oligocene *Oligodelphis* (S. M. Aslanova and G. A. Mchedlidze, 1968) the same bones, strongly diverging completely override not only the corresponding processes of the frontal bones but also the temporal fossa; and already come in contact with the supraoccipital region. At the same time an Oligocene representative of the toothless whales, *Mauicetus* (C. Dechaseaux, 1961), in its strongly elongated parietal part of the skull (see Fig. 1) and very slightly caudally displaced nasal opening (the nasal opening in this form is situated in the middle of the length of the rostrum), is closest of all to the presumed terrestrial ancestor and from the point of view of development of skull construction stands on a much lower level of evolution.

Probably the common features of skull construction inherent to each individual group of modern cetaceans formed very much later, in the geologic sense, in the suborder Mysticeti than in the suborder Odontoceti (in some cachalots, as has been mentioned, even the asymmetry had already been developed in Eocene time). In our opinion this should indicate the relative antiquity of the second of these groups.

In this section of the work we do not intend to dwell in detail on problems of the phylogenetic history of the Archaeoceti, as they will be examined mainly in subsequent chapters, but nevertheless we find it not superfluous to touch briefly upon some ideas put forward by A. V. Yablokov in connection with the early cetaceans.

21/ Among the features which distinguish the archaeocetes from the other members of the cetaceans, A. V. Yablokov points to the snake-like body shape supposedly present in all the archaeocetes, (or at least most of them), and considers that the character of the streamlining of the body of the archaeocetes is different in principle from that of the other cetaceans, inasmuch as their body "as a rule is snake-like, not torpedo-shaped" (A. V. Yablokov, 1964, p. 101). As a matter of fact not all the archaeocetes are characterized by a snake-like body, only members of the genera *Basilosaurus* and possibly *Eocetus*; most of the forms (for example, members of such genera as *Protocetus*, *Pappocetus*, *Zygorhiza*, *Dorudon*, and *Prozeuglodon*, have a relatively short and not at all snake-like body. Consequently a snake-like body is not typical of the archaeocetes. It might be, and not by chance, that precisely the forms with a relatively short torpedo-like body were longer-lived phylogenetically (for instance, members of the family Dorudontidae, which lived until the Lower Miocene) than the snake-like basilosaurs which, however, had more highly developed dentition. But that is another problem, meriting special attention. As for the presence of a small head in the archaeocetes, distinguishing it from the other cetaceans, that feature also demands some clarification.

It is fully evident that the large head characteristic of modern toothless cetaceans, for example, could not have originated right after the terrestrial ancestors, which as is known had a relatively small head, took to the aquatic medium. The increase in size of the skull took place in the course of a long process of adaptation to life in the aquatic medium, in connection with the development of the unique way these animals feed (straining a large amount of water for food). Furthermore, concerning the existence of a head small in comparison to the body, again one can speak only with respect to members of the genus *Basilosaurus*, which in absolute head size do not in any way exceed the other archaeocetes,

which are characterized by a medium relative head size. Evidently there is here a lengthening of the body and tail, peculiar to members of the genus *Basilosaurus*, alone, which is caused by a lengthening /22/ of the bodies of the vertebrae. In forms with short vertebrae, such as *Zygorhiza kochii* for example, the length of the skull amounts to 1/6 the total length of the animal, which is not small even for some modern cetaceans.

As for the presence of a movable elbow joint in the archaeocetes, distinguishing it from modern cetaceans, it should be noted that so far there are no adequate grounds for denying that this joint was movable in fossil representatives of the Odontoceti and Mysticeti. Rather, paleontological data tell us that mobility of that joint was still possible in fossil Odontoceti and Mysticeti. The reduction of movement of the elbow joint was related to perfection of the steering function of the flippers, which in turn was related to the gradual increase in the propulsive function of the tail. Therefore it is difficult to conceive that from the beginning the flippers would have fulfilled a steering function alone, before the perfection of these animals namely main propeller of the tail. It is fully evident that an initial stage of mobility must first have preceded the immovable state in them. This is the more probable, as even in modern toothless cetaceans, in contrast to the toothed, the muscles of the free limbs are still retained and their elbow joint does not have a cartilaginous union (A. N. Druzhinin, 1924). As for the unique histological structure of the humerus of the archaeocetes (presence of two sharply different layers of bone tissue and weak development of marrow cavity), that indicates only the archaic nature of the structure of the limb bones inasmuch as to some extent they, together with other features of the skeleton, resemble the terrestrial ancestors which certainly had hollow leg bones. The archaeocetes, as the forms closest to the terrestrial ancestors, naturally still retained this ancestral feature. However it is noteworthy that not only do the earliest cetaceans retain this archaic feature, but so also do some Oligocene dolphins (S. M. Aslanova, 1968) and squalodonts. It is not impossible that a similar structure will also be discovered /23/ in well preserved fossil material in the earliest fossil toothless whales too, although possibly less clearly manifested than in the archaeocetes.

As for those features which distinguish them from the other cetaceans such as the presence of a crest on the skull related to the development of the jaw musculature, the process of their gradual disappearance, and likewise the simplification of the dentition to its complete reduction, is very clearly traced in the phylogenetic history of the Archaeoceti, which will be gone into more thoroughly in the ensuing chapters of this part of the work. In our opinion the presence of movable halves of the lower jaws does not contradict their convergence with the toothless whales.

We believe that to solve the problem posed (parallelism or convergence in the evolution of the cetaceans) it is impossible to proceed from a comparison only of the features of the modern Odontoceti and Mysticeti. If such a point of view is adhered to, it would be difficult to find a place for some fossil members of the Odontoceti and Mysticeti in these suborders. All the more unwarranted methodologically is a comparison of the completely extinct Paleogene groups of Archaeoceti only with modern representatives of the groups of the toothed and toothless cetaceans.

As will be evident from what follows, a comparative morphofunctional analysis of the particulars of the archaeocetes and, even more, their comparison with fossil representatives of the Mysticeti, makes it possible in a number of cases to bring out a continuous series of changes in features which indicate a distant relationship between these groups.

As for the question of a possible relationship of the archaeocetes with the Odontoceti, recently brought up again by Van Valen (1968), we believe it desirable to examine this in the second part of the work after a review of the main features of the history of the toothed cetaceans. However, let us remark nevertheless that a genetic relationship between the Middle Eocene archaeocetes (*Protocetus*, *Pappocetus*) and toothed cetaceans (Van Valen, 1968, p. 64) seems to us unlikely.

REVIEW OF THE TAXONOMY AND BRIEF DESCRIPTION OF THE FOSSIL CETACEANS

The fossil members of the cetaceans known to science at the present time are distributed in three suborders. The geologically earliest, which have the greatest similarity to terrestrial mammalian forms,

comprise the suborder of ancient cetaceans, the Archaeoceti, consisting of three families: Protocetidae Stromer, 1908; Dorudontidae Miller, 1923, and Basilosauridae Cope, 1867.

The family Protocetidae has both short-bodied and long-bodied forms. *Protocetus* does not exceed 2.5 meters in length and *Eocetus*, characterized by markedly long vertebrae and relatively large (120 cm) skull, evidently was a very large animal. The protocetids as a whole are characterized by a nasal opening located near the front end of the skull, a tritubercular-secodont type of dentition with unreduced M^3 , the presence of a crest on the skull, very large temporal fossae, strongly elongated parietal bones, caudally recurved occipital part of the skull, sacral vertebrae different from the lumbar indicating the presence of a well developed pelvis, etc.

In the opinion of some investigators, the members of the Basilosauridae originated from *Eocetus* with its long vertebrae and the members of the Dorudontidae from the short-bodied *Protocetus* and *Pappocetus* (C. Dechaseaux, 1961, p. 846). Therefore some objections arise against the inclusion of the short-bodied prozeuglodon (genus *Prozeuglodon*), apparently referred to the Basilosauridae only on the basis of the absence of M^3 , in the composition of the basilosaurids. According to the latest data there are 4 genera in the family Protocetidae

Members of the Dorudontidae are medium-sized animals (8-9 m long) with long flexible cervical part of the spine and sacral vertebrae not different from the lumbar, and relatively short vertebrae connected by zygapophyses. The flattened serrated cheek teeth sharply /25/ differentiate the dorudontids from members of the family Protocetidae. In some members of the family, M^3 is absent (*Zygorhiza minor* Kellogg). There are 4 genera in the family. The Basilosauridae (see p. 49) are medium-sized or larger (from 8 to 22 m long) cetaceans, corresponding to a higher degree of evolution of the archaeocetes on the basis of the level of development of some features of the skeleton (A. S. Romer, 1966, p. 297).

According to Simpson (1945) the Upper Oligocene *Patriocetus* Abel, *Agriocetus* Abel, and *Microzeuglodon stromeri* and the Eocene *Archaeodelphis* Allen, 1921, comprise a unique group of early cetaceans, "Archaeoceti incertae sedis."

As is known, *Microzeuglodon* was set apart by Abel¹ in his time in the special family Microzeuglodontidae (O. Abel, 1913, p. 220)² but several years ago we demonstrated that this separation is not appropriate (G. A. Mchedlidze, 1964).

O. Abel (1913) united *Patriocetus* and *Agriocetus* in the family Patriocetidae, which he believed to be an intermediate link between the archaeocetes and the toothless cetaceans. In the new edition of "Vertebrate Paleontology," A. Romer (1966) confirms anew the independence of the family Patriocetidae, including it in the suborder Mysticeti.

Results of our investigations on the Upper Oligocene archaeocetes also bring us to the idea that there is a close kinship, between the members of this group of archaeocetes and the toothless cetaceans. However, contrary to the opinion of A. Romer, it does not seem correct to, us to include in the family Patriocetidae the genus *Archaeodelphis*, which belongs to a completely different branch of evolution of the cetaceans in general (preferably to the odontocetes). Besides, it can hardly be considered acceptable to refer these cetaceans, which have toothed jaws, to toothless--to the whalebone whales (suborder Mysticeti).

The suborder Mysticeti is represented in the fossil cetacean fauna by the following families: Cetotheriidae Cabrera, 1926, /26/ consisting exclusively of fossil forms (more than 25 genera), Balaenopteridae Gray, 1864, represented by nine genera (two of which are also found in the modern fauna), and Balaenidae Gray, 1825--seven genera, two of which are found at the present time.

Five of the 10 known families of the suborder Odontoceti consist entirely of extinct forms. Those families are: Agorophiidae Abel, 1913; Squalodontidae Brandt, 1873; Eurhinodelphidae Abel, 1901, Hemisyntrachelidae Slijper, 1936, and Acrodelphidae Abel, 1905. As for the rest, they are represented in

¹ Printed "Stromer," corrected via an errata inserted in the volume

the modern fauna by a smaller number of genera than in the geologic past. Thus, for example, of the 30 known genera of the family Platanistidae Gray, 1963, only three are found at the present time. Of the 16 genera of the family Ziphiidae Gray, 1865, one (the genus *Mesoplodon*) is found both in the fossil and in the modern fauna, four are exclusively modern genera, and most of the genera (11 genera) are known only from fossil remains. The family Physeteridae was characterized by great diversity in the geologic past (about 15 fossil genera are known).

The family Delphinidae Gray, 1821, comprising more than 39 genera (including the phocenids) in its composition as a whole, is represented by 30 genera in the fossil fauna, 6 of which are also living at the present time. As for the family Monodontidae, it is represented the same genera (*Monodon* and *Delphinapterus*) both in the fossil and in the modern faunas.

MOST IMPORTANT LOCALITIES OF FOSSIL CETACEANS

The usual disjointed and sporadic nature of occurrences of fossil cetaceans substantially hampers the recovery of the assemblages of fossil forms typical of the various geologic epochs. Nevertheless the data already amassed make it possible, as we will show, to designate the main stages of the history of formation of the cetaceans and to elucidate the corresponding sequence of changes of the fauna of these marine mammals.

Thus, for example, /26/ the Fayum assemblage of early cetaceans discovered in 1879 by G. Schweinfurth in the Eocene formations of the Fayum basin of Egypt Qasr el Sagha beds referred to the Middle Eocene and the Qasr el Sagha Formation, Upper Eocene), which in addition to cetaceans contain numerous remains of crocodiles, dugongs, sea turtles, and land vertebrates (Rushdi Said, 1965), can be considered typical of Middle-Upper Eocene time.

The most complete picture of the cetacean fauna of Oligocene time is given, in our opinion, by the so-called Perekishkyul fauna (near the settlement of Perekishkyul, Azerbaijan, in the Caucasus),

² Printed "(Stromer, 1904, p. 89)," corrected via an errata inserted in the volume

distinguished by an exceptional diversity of forms not only of cetaceans but also of pinnipeds, sea turtles, and birds (S. M. Aslanova, 1963).

Typical Lower Miocene forms are represented in the cetacean fauna of the Lang [?] group in Italy (vicinity of Beluno); the group of Helvetian cetaceans of France might be taken as typical of the Middle Miocene. The Upper Miocene might be characterized by the fauna from the Calvert formation of Maryland, U.S.A., and the Antwerp group of Belgium (R. Kellogg, 1925).

In the U.S.S.R. the main fossil cetacean localities are concentrated in the south of its European part, in the belt once covered by Tethys seas. Without dwelling on individual finds of cetacean remains, we think it desirable to describe briefly those localities from which more or less substantial accumulations of the remains of these animals are known.

Such individual localities are the North Caucasus, Azerbaijan, Moldavia, the Mangyshlak, and Western Georgia.

Particularly distinguished by the richness of the fossil material and abundance of forms is the Apsheron Peninsula (Azerbaijan), where the remains of cetaceans are found almost throughout the section of Tertiary formations from the base of the Eocene to the Apsheron inclusive (S. M. Aslanova, 1963; V. V. Bogachev, 1938; N. M. Gubkin, 1950; R. Lydekker, 1892; A. N. Riabinin, 1938).

In the North Caucasus and Western Georgia, groups of Middle Miocene (Chokraskoye, Karaganka, and Konka) and Upper Miocene (Sarmatian) forms are mainly represented (G. A. Mchedlidze, 1964). As for the localities in Moldavia and the Mangyshlak, they contain the remains only of 128/ Sarmatian cetaceans (V. S. Bazhanov, 1968; A. A. Kirpichnikov, 1954; N. Macarovici and S. V. Oescu, 1942; N. F. Sintsov, 1883).

PALEOBIOLOGICAL HISTORY OF THE FAMILY ZEUGLODONTIDAE

The Zeuglodontidae Bonaparte, 1849 (= Basilosauridae Cope, 1867) are the most interesting of the ancient cetacean families. Members of this family have wide geographic distribution and very

unusual morphological features which suggest that they are the most highly evolved of the archaeocetes (A. S. Romer, 1939).

The particular interest of the archaeocetes, and of the zeuglodontids in particular, to a paleobiological investigations is due to the fact that the inadequate state of study of these marine mammals is the main reason for the differences of opinion which have long existed concerning the problem of the genetic relationships of the suborders of the cetaceans (S. E. Kleinenberg, 1958; R. Kellogg, 1928, 1936; A. V. Yablokov, 1964; and others).

The remains of representatives of the zeuglodontids were first found in 1834 in the Upper Eocene of North America, in Louisiana. Mistaking them for reptile remains, R. Harlan named this animal *Basilosaurus*, but later (in 1839) R. Owen established that they belonged to a gigantic mammal, which had several features in common with modern cetaceans. He suggested the name *Zeuglodon cetoides* (Owen) for it.

Later on, the remains of zeuglodons were found repeatedly in the Upper Eocene and Lower Oligocene formations of North America [*Zeuglodon serratum* Gibbes (F. True, 1908), *Zeuglodon brachyspondylus* Muller 1849]. A vast accumulation of the remains of these animals was discovered in the Middle Eocene and Upper Eocene deposits of Egypt (Fayum basin), whence such types as *Z. osiris* Dames (V. Dames, 1894, *Z. zitteli* Stromer, (E. Stromer, 1903), *Z. isis* Beadnell (N. Beadnell, 1905), *Z. cf. brachyspondylus* Muller (Dames, /29/ 1894; E. Stromer, 1908) are known. The remains of zeuglodons are also known from the Upper Eocene of South Australia [*Zeuglodon harwoodi* -- *Microzeuglodon harwoodi* Sanger (E. V. Sanger, 1881)], the Upper Eocene of England [*Z. wanklyni* Seeley (F. Seeley, 1876)], the Lower Oligocene of Russia [*Z. cetoides* Owen (O. Paulson 1876)], *Z. rossicum* (= *Z. paulsoni*) A. Fedorovskiy, 1912)], and also from the Middle and Upper Oligocene of Azerbaijan [*Zeuglodon caucasicum* Lyd. (= *Microzeuglodon caucasicum* Lyd. (R. Lydekker, 1892) and *Microzeuglodon aff caucasicum* Lyd. (A. N. Ryabinin, 1938).

Zeuglodon remains have often been found also in the Eocene formations of the North Caucasus, in the vicinity of the city of Pyatigorsk (Orbel 'yanov Village Soviet, left bank of the Kuma River).

As this brief review shows representatives of the zeuglodons had very wide distribution in the seas of the early Tertiary Epoch.

According to the data of some authors (C. Dechaseaux, 1961; V. I. Gromova and B. A. Trofimov, 1962; R. Kellogg, 1936) the following genera are united in the family Zeuglodontidae: *Basilosaurus* Harlan, 1834 (= *Zeuglodon* Owen, 1839), *Prozeuglodon* Andrews, 1906, and *Platyosphys* Kellogg, 1936. According to others (A. S. Romer, 1966) *Mammalodon*, *Pontobasileus*, and *Pontogeneus*, about whose independence Romer himself, however, are still included in this family. Here we accept the first of these schemes, although we find it expedient also to include in this family, in addition to those listed above, the genus *Microzeuglodon*, the question of whose taxonomic position will be examined specially in a later chapter of this book.

The taxonomic composition of the family Zeuglodontidae has been examined by many investigators (O. Abel, 1913; R. Kellogg, 1928, 1936; E. Stromer) 1903, 1908; I. Brandt, 1887; C. Dechaseaux, 1961; V. I. Gromova and B. A. Trofimov, 1962; and others). Frequently some representatives of the archaeocetes which actually are related to other families have been combined with the zeuglodontids. More often, the general affinities of the individual forms frequently are unclear. In many cases criteria for distinguishing the members of one family from another are not indicated. Even in such a fundamental work as the "Traité de Paléontologie" /30/ (1961), diagnoses of the individual families of the archaeocetes are not given.

Analysis of the data in the literature leads us to the conclusion that the taxonomy of the family Zeuglodontidae, like that of the family Dorudontidae also, is artificial. As for the Protocetidae, their position in the system is clearer.

O. Abel (1913) included the following forms in the family Zeuglodontidae: *Protocetus atavus* Fraas, *Eocetus schweinfurthi* Fraas, *Prozeuglodon atrox* Andrews, *Zygorhiza minor* Muller, *Zeuglodon*

cetoides Owen, *Zeuglodon serratum* Gibbes, *Zeuglodon brachyspondylus* Muller, *Z. osiris* Dames, *Z. isis* Beadnell, *Z. zitteli* Stromer, *Z. wanklyni* Seeley, *Z. rossicum* Paulson, *Kekenodon onamata* Hector, and *Phococetus vasconom* Delfortrie. However, only a few of those enumerated above can be referred with confidence to the family Zeuglodontidae.

Protocetus and *Eocetus*, together with *Pappocetus*, are now united in the family Protocetidae Stromer (R. Kellogg, 1936). In this let us remember that without adequate grounds for it, E. Fraas (1914) included the *Zeuglodon zitteli* described by Stromer (Stromer, E., 1903, p. 82) in the composition of the family Protocetidae (E. Fraas, 1914, p. 21). *Zygorhiza* True (1908), *Kekenodon* Hector (1881), *Phococetus* Gervais (1876), and *Dorudon* Gibbes (1845) are now united in the family Dorudontidae Muller, 1923 (C. Dechaseaux, 1961). As for *Prozeuglodon atrox* described by C. Andrews, Stromer identified the remains of this animal, figured in that work under Number 83 (C. Andrews, 1906, p. 252-256, Fig. 83) with *Z. osiris* Dames from the Eocene described by him (E. Stromer, 1908, p. 110), and part of the material on *Prozeuglodon atrox* (Nos. 80-82) he referred to a young specimen of *Z. isis* (C. Andrews, 1906, p. 243, Fig. 80-82, Table 21). As is known, R. Kellogg subsequently (1936) combined *Z. isis* Andrews and *Prozeuglodon atrox* Andrews under *Prozeuglodon isis* (Andrews).

The taxonomic position of such members as *Z. serratum* and *Z. brachyspondylus* is not clear. Stromer identified the latter with *Dorudon serratum* Gibbes (E. Stromer, 1908, p. 118), R. Kellogg referred it to *Zygorhiza kochii* (R. Kellogg, /31/ 1936), Consequently this form too drops out of the composition of the family Zeuglodontidae.

In our opinion, at present it is possible to state with confidence that only a few forms, in particular *Basilosaurus cetoides*, *Pr. isis* (Andrews), and *Z. caucasicum* Lyd., be long to the family Zeuglodontidae. As for *Platyosphys*, supposedly similar to this family, separating it is a special genus still raises some doubts: the type, and apparently only, species of *Platyosphys* is known only on the basis of vertebrae.

We do not believe that it is relevant to give a description here of the individual members of the family in question, but for further discussion we think it necessary to give a brief osteological description of the family Zeuglodontidae as a whole.

The skull of the zeuglodontids retains the ratio of individual skull parts which is typical of terrestrial mammals. However, the facial section of the skull is somewhat longer than in terrestrial forms, although it still does not overlap the other sections. The brain case is low. It is usually thought that the brain case of the zeuglodons is not shortened in the anteroposterior direction as in typical cetaceans (R. Kellogg, 1928). Nonetheless, a detailed investigation of material on both the basilosaurs and the /32/ prozeuglodons shows that the brain case of the skull, sharply demarcated from the intertemporal constriction, is to some extent transversely elongated. Elongation of the intertemporal constriction and considerable elongation of the temporal fossae are typical of all members of this family.

The parietal bones comprise a large part of the roof of the skull. The dorsal surface of the intertemporal constriction is formed exclusively by the parietal bones, is clearly separated from the broadened part of the brain case, and has almost parallel margins. In the prozeuglodon it is less constricted and not inflated at the contact with the frontal bones, while in the basilosaur the parietal part is relatively narrow and strongly inflated at the contact with the frontal bones. The temporal fossae usually are long but do not have the same shape in different members of the family: in the basilosaurs they have obtuse posterointernal angles and in the prozeuglodons the same angles are nearly right angles (see Fig. 2 and 3). The sagittal crest is well developed in all. The lambdoid crest, which sometimes is slightly curved caudally, is well developed. The skull of the zeuglodontids has a plane frontal section. The supraorbital process of the frontal bone is strongly broadened, extending laterally behind the zygomatic part of the zygomatic arch and curved at the end. The preorbital constriction is not manifested. The supraorbital plates of the frontal bone are formed only of the frontal bones; the maxillae do not enter into the composition of the plate. The proximal end of the maxilla abuts anteriorly against the supraorbital /33/ process of the frontal bone and, dropping below the latter, leaves room for the back

molars. The premaxillae have ascending processes which do not reach the frontal bone and terminate behind the preorbital notch, above P² and P³ (see Fig. 4). They project forward considerably and terminate beyond the maxillae. The *foramen incisivi* is reduced to a narrow slit. The squamosal bone takes part in the formation of the outer wall of the brain case. The occipital shield is high, set perpendicular to the long axis of the skull, has a quadrangular shape in its general lines, and is considerably elongated transversely in the lower part. Its upper edge is arched and relatively wide. The lateral edge of the shield sometimes curves backward somewhat (for example, in the *Prozeuglodon*) but does not form the tubular projection typical of the protocetids.

One feature of the zeuglodontid skull, which is discovered upon comparison with the protocetid skull, calls attention to itself. The terminal point of the sagittal crest in the protocetids is situated far back behind the occipital condyles. In the zeuglodontids the arched upper edge of the shield and the terminal point of the sagittal crest are thrust forward (ratio of length to the distance from the condyles to the end point of the sagittal crest to the total length of the skull in the zeuglodonts is 10). *Prozeuglodon isis* (Andrews), in which the occipital shield is thrust very considerably forward (see Fig. 3), is particularly distinctive. The nasal bones in the zeuglodontids do not intrude between the frontals and are situated entirely at the level of the anterior edge of the supraorbital processes of the frontal bones. The nasal bones are relatively long but markedly shortened in comparison with the protocetids, comprising 1/5 of the total length of the skull (in the protocetids the length of the nasal bones is 1/3 of the skull length). The external nasal opening in the zeuglodontids is moved back. Whereas in the protocetids the posterior edge of the nasal opening is situated at the level of the posterior edge of C, in the zeuglodontids this line is situated behind P².

The size of the snout is a feature characteristic of the individual genera. Thus, in the prozeuglodonts it is relatively longer than in the basilosaurs. The zygomatic arch in the basilosaurs is relatively thinner and longer than in prozeuglodonts. 34/ The basioccipital and basisphenoid bones are firmly united with each other and in the anterior part are bounded on the sides by (the?) low(er)? plates.

The palatine bone has a posterior edge which protrudes in a wedge above the triangular vomer, and is very thick. Anteriorly the palatine bone does not go beyond the posterior edge of the last premolar. Posteriorly the palate is somewhat elongated due to prolongations of the palatinum and pterygoideum. The petrous temporal bone is in a closed fossa and the foramen lacerum posterius is situated to the side on the inner side of this bone. The mastoideum is united with the petrous temporal bone along a small segment; the squamosum and exoccipitale are firmly fused and form pr. mastoidea (while in modern cetaceans the place of union with the petrous temporal bone is far wider and is separated from the squamosum by a suture which is very much more sharply expressed than in the zeuglodon). The basilosaur skull comprises 1/10 of the total length of the body, in the *Prozeuglodon* only 1/5.

Teeth. The dental formula of the zeuglodontids is I3/3, C1/1, P4/4, M2/3. The incisors are conical in shape. The first upper premolar is conical, like the teeth situated in front of it. Sometimes this tooth (Fig. 4) has a weakly developed accessory denticle in the basal part of the posterior cutting edge (*Basilosaurus cetoides*) which is not usually mentioned in the literature (C. Dechaseaux, 1961; V. I. Gromova and B. A. Trofimov, 1962). P² is already sharply different from the incisors. The crown of this tooth is considerably elongated and flattened laterally; accessory denticles are not always present on both cutting edges. P³ is larger than all the molars but not always larger than P² (for example, in the prozeuglodon). P⁴ is considerably smaller, M¹ and M² are strongly reduced in size. The molars [literally "root teeth"--Translator] in the P³-M² row have accessory denticles on both cutting edges. The number of denticles is not constant (it is more or less constant only on P⁴, where their number reaches 3-4 not counting the cusps).

P²-M² are two-rooted. However (in the *Prozeuglodon*) there are traces of a posteriorly extended cone on DP³ and DP⁴ which evidently was supported by third root (R. Kellogg, 1928, /35/ 1936). P² and P³ in the *Prozeuglodon* are separated by a wide diastema (E. Stromer, 1908, Plate VI, Fig. 9). In other forms they abut closely against one another. The cheek teeth of the maxilla sometimes form a broken

row, sometimes a closed row, and this closed row is represented by either the P³-M² the P²-M² series. The row of molar teeth always extends forward beyond the center of the orbit.

The teeth of the mandible (molars and premolars) are distinguished from those of the maxilla by a higher crown and sometimes by the fact that they are set less deeply in the jaws (see Fig. 5). P₁ is conical in shape, with one root and one cone and no accessory denticles. But sometimes there are two crenulations in the base of the anterior edge (*Basilosaurus cetoides*). P₂ is elongated in an anteroposterior direction, the crown of this tooth is laterally flattened, and accessory denticles are present on both cutting edges. The number of denticles on the anterior and posterior /36 edges is not always the same. Usually there are fewer of them on the anterior edge. P₃ is always separated from P₂ by a wide diastema. P₃ more often yields to P₄ in size, but sometimes it reaches the same size as the latter (*Z. isis*, Stromer, 1908). The number of accessory denticles is variable (more often 5, not counting cusps). P₄ usually is the largest tooth in the mandible. P₃ and P₄ touch one another but sometimes (for instance in *Microzeuglodon caucasicum* Lyd., s. *Z. caucasicum* Lyd.) they are separated by a rather wide diastema (R. Lydekker, 1892, 1892 Plate 36, Fig. 1). Sometimes there is a triangular cingulum with a shallowly crenulated edge on the labial surface of P₄, M₁, M₂ and M₃. : M₁, M₂ and M₃ are usually very small and on these teeth accessory denticles are present only on the posterior edge. However, there also are those among the zeuglodontids (for instance, *Microzeuglodon caucasicum* Lyd.) in which M₂ and M₁ are relatively slightly different from the premolars (P₃ and P₄) both in height and in degree of development of accessory denticles, which are present on both edges. A cingulum is well developed on these teeth also. The cheek teeth of the mandible of the zeuglodontids are more often closed, but sometimes they are completely separated as, for example, in *M. caucasicum* Lyd., and where the row is closed it usually is formed by the P₃ - M₃ series (see Fig. 5).

M₁- M₃ are always set in the ascending part of the alveolar edge of the jaw. The molar teeth of the mandible of the zeuglodontids have a relatively high crown compared to the upper molars. As for the projection of the root above the edge of the jaw, that is manifested more clearly in the mandible than in

the maxilla. The inclination of the upper molars to the alveolar edge of the jaw, manifested in some specimens, is possibly an indication of age.

The presence of a diastema between the molars is generally an extremely variable feature. In members of the family Zeuglodontidae, both closed and separated molars are found. For example, there are separated upper molars in *Prozeuglodon isis* (Andrews) (Stromer, 1908, Plate VI, Fig. 9), *Basilosaurus cetoides* Owen (the specimen in the Leningrad Mining Institute), and others. At the same time the lower molars of these forms may be closed [molars without diastema in *Prozeuglodon isis* (Andrews)]. /37/ Among the zeuglodontids there also are forms in which both the lower and upper molars form closed rows (*Basilosaurus cetoides*, see Fig. 4, 5). However, in addition to these there also are forms in which the row of upper molars is closed and the lower molars are separated by wide diastemata (*Microzeuglodon caucasicum* Lyd., G. A. Mchedlidze, 1963, Plate I, Fig. I,4). Thus the molar teeth in the zeuglodontids can be both closed in the upper jaw and separated in the lower, or closed in the lower and separated in the upper, and also closed in both jaws. Therefore it does not seem to us to be expedient to distinguish a special family of Microzeuglodontidae mainly on the basis of this feature.

In other words, for the taxonomy of the early cetaceans (in particular for the Zeuglodontidae and Dorudontidae), such features of the dentition as the presence of a diastema between the back molars, the number of accessory denticles on the cutting edges, and the presence of these formations on this or that edge of a tooth have no particular significance. In our opinion, exaggeration of the role of these features, which to a considerable extent are variable, leads to erroneous conclusions on the taxonomic position of these or those forms.

The fact is that the dentition of the cetaceans, in contrast to that of other mammals, does not fully reflect the most typical features of their form of life. In the cetaceans the evolution of this system tended toward simplification, toward homonomous structure and loss of active participation of the teeth in the feeding process. Thus completely different variants could exist even within closely related units. On the

other hand some similarity in the abovementioned features could exist between members of groups which were very remote from one another (even the Zeuglodontidae and Squalodontidae), arising convergently in connection with life in the same environment.

However, it is impossible to ignore completely the significance of such features as the reduction of M^3 or the presence of a postero-internal cone on DP^3 and DP^4 , although these features were subject to /38/ some variability not only in the zeuglodontids but even in the most primitive member of the archaeocetes, the protocete.

The phylogenetic history of the zeuglodontids shows that the incisors and anterior cheek teeth increase in size, the premolars become higher and acquire a high main cone, and the molars are gradually reduced. The cheek teeth of the later forms have several accessory denticles on the anterior and posterior edges, and rudiments of a posterointernal cone are rarely retained. The premolars and molars of the early zeuglodons, are also characterized by the presence of a rudimentary internal part of the crown and slightly developed but constant posterointernal cone.

Cervical section of the spine. Atlas with one strong apophysis directed backward. Epistrophei with one neural arch and high neural process which projects forward above the atlas, and backward over the third and sometimes over the fourth vertebra. However, the shape and size of this process are rather variable. *Prozeuglodon*, for example, has a relatively short, blunt, and rounded process, while in the basilosaur it is high and strongly flattened in the posterior part (see Fig. 6). The body of the vertebra is relatively shortened, as are its lateral processes also. In descriptions of the zeuglodontids it is frequently stated that the cervical part of the spine is strongly shortened in members of this family (R. Kellogg, 1928; C. Dechaseaux, 1961; V. I. Gromova and B. A. Trofimov, 1962. Actually if we compare the length of the neck of a basilosaur with the length of the thoracic section of the spine, it appears that the neck is 1/6 of the length of the thoracic section. On other hand, in a member of the family such as the prozeuglodon, the length of the cervical section is only half that of the thoracic. Evidently the relative length of the neck noted in the basilosaur is caused to a certain extent by elongation of the other parts of

the spine: thoracic, Lumbar, and caudal. Although there certainly is also /39/ some shortening of the body of the cervical vertebrae and, in particular, of the epistrophei.

In comparison with the protocetids, in which the second cervical vertebra is elongated as in the creodonts, the neck in the zeuglodontids is decidedly short. However, their short neck appears not to be due to shortening of the cervical vertebrae (only the length of the epistropheus is shortened) but is a result of lengthening of the body of the vertebrae of the rest of the spine. This is particularly conspicuous if we take into account the fact that in absolute length of neck the long-bodied and short-bodied forms differ very little from each other.

Thus, if shortening of the neck is taken as a diagnostic criterion for the Zeuglodontidae (V. I. Gromova and B. A. Trofimov, 1962), that excludes from its composition the genus *Prozeuglodon* which, however, undoubtedly belongs to this family.

We believe that the lengthening of the body of the vertebrae, beginning from the fifth thoracic vertebra, and consequently the relative shortening of the cervical section, is a generic feature typical only of the basilosaur.

The thoracic vertebrae of various members of the zeuglodontids differ from one another in shape and in some details of structure. The vertebrae of the thoracic section of the short-bodied forms (the *Prozeuglodon*), in contrast to the vertebrae of the long-bodied forms (the basilosaur) are short; however, the former are distinguished from the latter by the very high and thick spinous process whose height abruptly decreases beginning from the tenth vertebra, and also by the long articular processes--zygapophyses (resembling those in the dorudontids). In the long-bodied forms the vertebrae of the thoracic section are strongly elongated beginning from the fifth, and the spinous processes and zygapophyses are strongly shortened. The lateral processes of the X-XV vertebrae are without articular surfaces for the ribs. The last two vertebrae are hardly different from the vertebrae of the lumbar section.

There are 15 lumbar vertebrae. In the *Basilosaurus* they are strongly lengthened, in *Prozeuglodon* relatively slightly lengthened and the well developed spinous processes and zygapophyses resemble those of members of the dorudontids.³

40/ The neural processes, like the lateral processes also, are strongly shortened in the basilosaurs. The zygapophyses are reduced and separated by wide intervals. The distal ends of the lateral processes of the last two sacral vertebrae have roughened surfaces for connection with the pelvis. In the *Prozeuglodon* the neural process is almost unreduced, the zygapophyses also are not reduced, and the sacral vertebrae are not different from the lumbar. No modification of the distal ends of the lateral processes for connection with the pelvis is noted in them (the latter is unknown in the *Prozeuglodon*).

The caudal vertebrae comprise about 1/3 of the total length of the spine. The body of the vertebrae is long. The neural arch is very low. The zygapophyses are strongly reduced. The lateral processes are short and flattened, slanted downward and outward.

The scapula of the zeuglodontids is large and strongly broadened. Its width in most cases is considerably greater than the height. Acromion process well developed, curved forward and downward, giving rise to a weakly developed crest. The crest of the scapula sometimes is in the form of a drum-like projection in its lower part. Preglenoid part considerably smaller than the postglenoid.

The humerus is medium sized (see Fig. 7). Diaphysis of the bone relatively flattened. Well developed *crista deltoidea* on anterior edge of the bone. Posterior edge of diaphysis 41/ relatively flattened. Diaphysis strongly broadened in the middle of its height. Head of humerus rounded-oval in shape and turned caudally, but inclination of the articular head very weakly expressed in some forms (*Basilosaurus cetoides* Owen). *Tub. major* well developed but naturally much more weakly than in modern predators. *Tub. minor* very weakly developed. *Sulcus bicipitalis* rudimentary. Distal end

³ The dorudontids as a whole are so similar to the prozeuglodon in skull construction and in a number of features of the vertebrae that it appears fully appropriate to raise the question of uniting them in one family. Only the reduction of M³ in the prozeuglodon contradicts such affinity. To solve this problem, however, more factual material is needed than we have at our disposal.

somewhat resembles that in terrestrial forms, but still its angle of rotation is very like that typical of the cetaceans. Forearm bones strongly widened and lie close to each other at their medial edges. Ulna with well developed olecranon.

Pelvis reduced. Symphysis absent. The single acetabulum is situated on the outside and has a depression for the *ligamentum teres*, but the femur evidently was not functional.

The zeuglodontids are distinguished from members of the protocetids by very essential structural features of both the skull and dentition and of the spine. The snout in the protocetids is long and narrow, constituting more than half the length of the skull, while in the zeuglodontids the length of the snout is half the length of the skull. The profile of the snout is straight in the protocetids, but drops sharply at the level of the middle of the orbit in the basilosaurids. The external nasal opening in the protocetids is situated nearer the anterior edge than in the zeuglodontids (E. Fraas, 1914, Plate I). The posterior edge of the nasal opening in the protocetids is at the level of the posterior edge of C, while in the zeuglodontids it is pulled back to the posterior edge of P¹. The nasal bones of the former constitute 1/3 of the length of the skull, in the latter 1/5. In each of these families there is a special shape of the suture between the frontal bones and maxillae: in the protocetids it is more or less rectilinear, in the basilosaurids the supraorbital process of the frontal bones is united with the maxillae by means of an undulating or jagged suture. The brain case of the protocetids is small, slightly convex and like a triangle in shape, but not transversely broadened. Its anterior edge is curved arcuately. In the basilosaurids the brain case is relatively widened, transversely elongated, and the anterior edge is convex; in the protocetids the supraoccipital bone is high, constricted in the upper part, and its laterally recurved edge forms an almost tubular excrescence. The upper edge of the occipital shield is situated considerably behind the occipital condyles. In the zeuglodontids, as has been mentioned, the supraoccipital bone is strongly widened in the upper part, its lateral edges are not recurved, and the dorsal edge of the shield is found at the level of the posterior edge of the condyles; thus some overriding of the occipital elements is already noted in them. The premaxilla bones in the protocetids extend to the frontal bones, in the zeuglodontids they

terminate behind the preorbital opening, above P²-P³. The intertemporal constriction in the protocetids is triangularly tapered, in the zeuglodontids it is relatively wider and has more or less parallel side margins; moreover this region is somewhat inflated at the boundary with the frontal bones. The row of molars reaches to the anterior edge of the orbit in the protocetids and to the posterior third of the eye socket in the zeuglodonts.

It is natural to pay particular attention to the comparison of the zeuglodontids with the protocetids inasmuch as the latter are characterized by archaic features of skeleton structure and dentition which bring them close to terrestrial mammals. The zeuglodontids are the most progressive of the archaeocetes, and in our view comparing them with the protocetids makes it possible to ascertain the most essential adaptational features acquired by the ancient cetaceans in the course of evolution.

The nature of the heterodont dentition (secodont teeth, dental formula of primitive eutherians, tritubercular molars and P⁴), the structure of the second cervical vertebra with long body resembling that of the creodonts, and the particulars of the structure of the lateral processes of the sacral vertebrae indicating the presence of a well developed pelvis, sharply distinguish the protocetids from the zeuglodontids.

However, it is not possible to say the same with confidence the with respect to the dorudontids, as members of that family are not so sharply different from some zeuglodontids. If members of these two families are compared on the basis of the fundamental features of skull structure, dentition, and spine, then their similarity becomes obvious. The snout in the dorudontids is not unusually long but as in some members of the zeuglodontids (in the *Prozeuglodon*) it is more than half of the total length of the skull (Fig. 8). The profile of the snout also drops relatively abruptly at the level of the middle of the orbit (see Fig. 9). The nasal bones of the dorudontids, as in the zeuglodontids, comprise 1/5 the total length of the skull. The suture between the supraorbital plate and the maxillae /43/ is of zeuglodontid type (jagged or undulating). The almost identical shape of the transversely elongated brain case, the development of lambdoidal and sagittal crests, the similar outline of the occipital shield and the position of the upper

edge of the shield with respect to the condyles, not reaching the frontal bones; the short premaxillae, the tooth row is thrust farther forward than the middle of the orbit (see Fig. 8), the configuration of the configuration of the temporal fossa, and a number of other features make it a close affinity between these two families.

The absence of M^3 in the zeuglodontids might be considered the only essential distinguishing feature. However, as has already been mentioned, forms with reduced M^3 (*Zygorhiza minor* Kellogg) are also found among the members of the dorudontids.

The presence of a cingulum P^2 , P^3 , and P^4 is often taken as a feature diagnostic of the dorudontids. But as is clear from our observations, the cingulum is not typical of all members of the family Dorudontidae (species of the genus *Dorudon* have no cingulum). In addition, a cingulum on the molar teeth is present in some protocetids and zeuglodontids (in *Pappocetus* on P_3 and M_3 and in *M. caucasicum*.) on P_3 - M_3). Thus this feature cannot be diagnostic of the whole family of Dorudontidae. As for the aforesaid occasional presence of accessory denticles on the cutting edges of the teeth, their presence and number are even more variable in both families.

44/ It is noteworthy that the differences between the dorudontids and zeuglodontids in structure of the cheek teeth hardly exceed the limit of variability of their features in such genera of the family Dorudontidae as *Dorudon* and *Zygorhiza*.

A difference in size is of course indisputable, particularly if the dorudontids are compared only with the genus *Basilosaurus* (body length of the dorudontids is 5-8 m, of the basilosaurs up to 22 m). However, members of other genera of the zeuglodontids (for example *Prozeuglodon*) are similar in size to the dorudontids. The short body of the vertebrae, the well developed spiny processes, and the more or less, well developed zygapophyses also liken *Prozeuglodon* to the dorudontids. The dorsal vertebrae of the dorudontids have a high and wide neural arch and also well developed lateral processes and zygapophyses, which distinguish them from the basilosaurs and liken them to the *Prozeuglodon*. In the dorudontids the zygapophyses of these vertebrae in the posterior part of the series of lumbar vertebrae

are free. The sacral do not differ from the lumbar vertebrae and, as in the zeuglodontids, have a slight roughness on the ends of the lateral processes.

In the description of the archaeocetes given by C. Dechaseaux (1961), the existence of a long neck is reported for the dorudontids, and for the basilosaurids a considerable shortening of that part of the animal's body. But as has already been noted, the shortening of the neck in the basilosaurs is relative, a result of lengthening /45/ of their thoracic, lumbar, and caudal vertebrae. But in absolute length of the neck these animals differ little from one another.

Here it is fully appropriate also to touch on the problem of the taxonomic position of *Microzeuglodon caucasicum* Lyd., s. *Z. caucasicum* Lyd., and clarify its relationship to a unique representative of the archaeocetes described by A. N. Ryabinin (1938), *Microzeuglodon* aff. *caucasicum* Lyd. *Microzeuglodon* was first described by R. Lydekker as a new species of the genus *Zeuglodon* (*Z. caucasicum*) and the author thought that the main feature of this species was its small size (R. Lydekker, 1892, p. 507). Then E. Stromer put the Caucasian zeuglodon into a special species *Microzeuglodon*, mentioning the presence of a diastema between the back molars of the mandible as a typical feature in addition to the small size (E. Stromer, 1903, p. 89). On the same basis O. Abel deemed it possible to separate the new family Microzeuglodontidae, including in it in addition to the Caucasian form *M. harwoodi* Sanger from the Upper Oligocene of Australia (O. Abel, 1913, p. 220), the accuracy of those determination, however, is open to doubt because of the extreme poverty of the material (only one tooth). Later the features of *M. aff. caucasicum*, referred by A. N. Ryabinin without sufficient grounds to the genus *Microzeuglodon*, were included in the description of the family Microzeuglodontidae (V. I. Gromova and B. A. Trofimov, 1962).

In separating the family Microzeuglodontidae, O. Abel went on the basis of the fact that the presence of a diastema between the molars of the mandible in *Microzeuglodon* should be considered an important taxonomic feature making it possible to separate the family. However, upon becoming familiar with the features of the structure of the dentition of the different members of the zeuglodontids

and of the archaeocetes as a whole, we have come to the conclusion that the taxonomic significance of this feature, the rather considerable variation of which has been discussed in the descriptive part of this work, has clearly been exaggerated.

As for *M. aff. caucasicum* described by A. N. Ryabinin, its supposed affinity to *M. caucasicum* is not supported by our investigations.

The development of a diastema between the molars of the maxilla in *M. aff. caucasicum* Lyd. permitted Ryabinin to assume its probable affinity and even identity with *M. caucasicum* A. N. Ryabinin, 1938, p. 152). However, /46/ the Caucasian microzeuglodons have diastemata between the back molars only in the mandible, the features of which we were not investigated in *M. aff. caucasicum*. Evidently the author assumed that inasmuch as there were diastemata between the molars in the maxilla of *M. aff. caucasicum*, there must also have been in the mandible. Meanwhile, data on the dentition of various zeuglodontids have shown that the arrangement of the back molars in their upper and lower jaws is subject to very considerable variation (see p. 35).

However, the differences between these animals in the structure of other parts of the skeleton are no less essential. The vertebrae in *M. caucasicum* are more elongated than in *M. aff. caucasicum* (index of length to width of the lumbar vertebrae about 1.50 for the former, about 1.00 for the latter); in the former the head of the humerus is strongly developed and the greater tubercle is relatively weakly expressed, while in the latter the greater tubercle is very strongly developed and more massive than the head (A. N. Ryabinin, 1938, p. 165); the articular area for the olecranon in *M. caucasicum* is 1/3 and in *M. aff. caucasicum* only 1/5 of the bone.

Thus it is fully apparent that there are no adequate grounds for genetically connecting these forms of the archaeocetes. Judging only on the basis of the development of a diastema in the maxilla, the zeuglodon described by A. N. Ryabinin should rather have been assigned to *Prozeuglodon isis* (E. Stromer, 1908).

Consequently, at present it is necessary to think that the only representative of the genus *Microzeuglodon* is *M. caucasicum* Lyd., whose separation into a special family of archaeocetes cannot yet be fully substantiated until additional information on it has been accumulated.

On the other hand, the features of the structure of the occipital part of the skull of *M. aff. caucasicum* Lyd. (horizontal, triangular shape, occipital shield prolonged strongly forward) which distinguish this animal from almost all known representatives of the early cetaceans, cry out for attention. At the same time these features liken it to a decided extent to the unique archaeocetes united in the family Patriocetidae Abel. The presence of the aforementioned skull features of *M. aff. caucasicum* may constitute sufficient grounds for separating it into an independent genus. This new genus, for which the name *Mirocetus* is hereby proposed, can be described as follows:

Family PATRIOCETIDAE Abel, 1913

Genus *MIROCETUS* gen. nov.

Type of genus, *Mirocetus ryabinini* sp. nov. (= *Microzeugodon* aff. *caucasicum* Lyd. A. N. Ryabinin, 1938).

Diagnosis of the genus: Size medium or small. Trunk relatively short. Cranial part of the skull relatively short and wide. Supraoccipital bone triangular in shape, with strong forward slant (its anterior end reaches the level of the middle of the zygomatic arch). Parietal part of the skull considerably broadened, parietal bones form a wide band on the dorsal surface of the skull. Supraorbital processes of the frontal bones also considerably broadened. Width of the skull in the orbital region almost equal to the maximum width in the cerebral part. Preorbital constriction well expressed. Temporal fossae narrow and short. M^3 reduced. Vertebrae slightly elongated, zygapophyses well developed. Second cervical vertebra with short body and long toothlike processes.

Comparison: Structure and position of the maxillae, their relationship to the supraorbital processes of the frontal bones, the location of the nasal opening, the number of molars, the structure of

the forelimbs and a number of other features of the skeleton indisputably relate *Mirocetus* to representatives of the other families of the archaeocetes, from which at the same time it is distinguished by very essential features of skull structure. Thus, for example, whereas in all representatives of the archaeocetes so far known, the preorbital part of the skull passes gradually to the orbital region without abrupt widening and development of notches at the boundary, in *Mirocetus* the facial part widens abruptly as it approaches the orbit, forming relatively well expressed notches. Furthermore, the parietal part of the skull, which is considerably narrowed and elongated in the Protocetidae, Dorudontidae, and Zeuglodontidae, is wide and relatively very short in *Mirocetus*. *Mirocetus* also is distinguished from the other archaeocetes by the shortened and narrowed temporal fossae and wide and short zygomatic arches. The supraoccipital bone, which in the archaeocetes described earlier has a nearly rectangular /48/ configuration, is triangular and slants strongly forward in *Mirocetus* (in the protocetids it is bent back caudally, in the dorudontids and zeuglodontids it is set almost vertically), relating it to the patriocetids on the basis of this feature.

Composition of the genus: One species, *Mirocetus riabinini* sp. nov.

Geologic age and locality: Upper Oligocene, Azerbaijan, western part of the Apsheron peninsula, village of Dzhangi.

Holotype: VSEGEI, Monographic Museum, coll. no. 51.73 (skull without mandible, 35 bones, limbs and ribs, belonging to one individual),

Remarks: Detailed description of the holotype given by A. N. Ryabinin (1938). Generic name - *Mirocetus* -Latin, amazing whale; species name *-riabinini* - in honor of the famous Russian paleontologist A. N. Ryabinin who first described the remains of this animal.

As already mentioned above, the diagnostic features of the family Zeuglodontidae are not presented completely accurately in the recent literature (C. Dechaseaux, 1961; V. I. Gromova and B. A. Trofimov, 1962). C. Dechaseaux generally gives diagnoses of neither families nor genera. Diagnoses of the family Zeuglodontidae and some of its genera are given in "Fundamentals of Paleontology" (V. I.

Gromova and B. A. Trofimov, 1962), but they are compiled on the basis of earlier-existing criteria for this family. As is apparent from what has been said (see p. 36), some features of skeleton structure which are as diagnostic criteria in that work either are subject to considerable variation, or are characteristic not only of the zeuglodontids but of all the archaeocetes as a whole.

According to Gromova and Trofimov (1962) the diagnosis of the family Zeuglodontidae runs: "Size very large (body length up to 12-15 m, skull up to 1.5). Preorbital constriction not manifested. Parietal region of the skull very constricted, plate of temporal bone forms a large part of the outer wall of the brain case; temporal fossa very large. Large pterygoid fossa forms an additional air sinus connected to the middle ear cavity. $M^2/3$, P^1 small, almost conical, /49/ the rest with a flattened main cone and supplementary denticles on its flanks; on P^2-M^2 and P_2-P_4 on front and back, on M_1 and M_3 on back only. Back molars in closed row, no rudiment of a protocone. Cervical vertebrae short, the rest long, with low neural arches. U. Eocene of America and Africa, L. Oligocene of Europe, Ukraine)."

However, the absence of a preorbital constriction is typical not only of members of the family Zeuglodontidae, but also of the dorudontids and protocetids. The same can be said of the constriction of the parietal region of the skull, the participation of the temporal bones in the formation of the outer wall of the brain case, and the size (but not the shape) of the temporal fossa.

As for the size and structure of the P^1 and M^2 molars, it should be pointed out that these teeth do not have a conical shape and are considerably flattened laterally; although the second upper molar is sometimes smaller than the first, more often it is the same size. (in the basilosaur -- see Gromova and Trofimov, 1962, p. 175, Fig. 176; W. K. Gregory, 1951, p. 891, Fig. 4). As a matter of fact, in the basilosaur M_3 is smaller than the rest of the molars, but in *Prozeuglodon* it is the same size or even somewhat smaller than M_1 and M_2 (E. Stromer, 1903, Plate IV; W. K. Gregory, 1951, p. 891; V. I. Gromova and B. A. Trofimov, 1962, p. 175, Fig. 176c). Denticles are not always present on both sides of the crown on P^2 . In the *Prozeuglodon* (E. Stromer, 1903, Plate IV) there are no accessory denticles on the front edge of P^2 . In the P_2-P_4 series there are accessory denticles on the front and back edges not only

in the zeuglodontids but also in the dorudontids --in *Zygorhiza* (C. Dechaseaux, 1961, p. 848; W. K. Gregory, 1951, p. 893, Fig. c). The back molars do not always form a closed row. In *Prozeuglodon isis* (Andrews) the upper molars are distinctly separated. The back molars are also separated in the zeuglodon preserved in the museum of the Mining Institute in Leningrad.

50/ Below are given diagnoses of the family Zeuglodontidae and of the genera entering into its composition, compiled by us on the basis of a revision of the material at our disposal and an analysis of the data in the literature.

Order CETACEA Brisson, 1762

Suborder Archaeoceti Flower, 1887 (= Zeuglodontia Gill, 1871)

Family Zeuglodontidae Bonaparte, 1849 (= Basilosauridae Cope, 1867)

Diagnosis: Large archaeocetes (length 18-22 m). Length of snout a little greater than that of the rest of the skull. Lumbar vertebrae with long or short body. Neural processes and zygapophyses not always reduced. Body of second cervical vertebra shortened, M³ absent. DP³ and DP⁴ sometimes with rudimentary posterointernal cone. P¹ conical, rest of the cheek teeth with laterally flattened crown and accessory denticles. Presence of denticles on anterior and posterior edges and also their number, not a constant feature.

Genus *Basilosaurus* Harlan, 1834 (= *Zeuglodon* Owen, 1839)

Type of genus, *Basilosaurus cetoides* Owen, 1839.

Diagnosis of genus: Body long and snake-like. Head relatively small. Facial section only slightly longer than the remaining part of the skull. Ratio of length from the posterior edge of the condyles to the acrocranium to total length of the skull, 11%. P¹ somewhat molarized. Second cervical vertebra with relatively short body and flattened neural process. Humerus with large head, the axis of which prolongs the axis of the long diaphysis. Five thoracic vertebrae and also all the lumbar and sacral with strongly elongated bodies and with short and wide neural and short and narrow transverse processes.

51/ Genus *Prozeuglodon* Andrews, 1906

Type of genus: *Prozeuglodon atrox* Andrews, 1906

Diagnosis of the genus: Body considerably shorter than in the basilosaurs. Facial section of the skull relatively long. Frontal bones wedged in by long processes in the nasal region. Lambdoid crest has the shape of a semicircle. Occipital shield relatively low. DP³ and DP⁴ with vestige of a protocone. Second cervical vertebra with short blunt and rounded toothlike process. Body of the vertebrae not elongated. Acrocranium thrust markedly forward. Index of ratio of length from posterior edge of the condyles to acrocranium to total skull length, 9%.

Genus *Platyosphys* Kellogg, 1936

Type of genus, *Zeuglodon paulsoni* Brandt, 1873 (= *Zeuglodon rossicum* Paulson, 1873).

Diagnosis of the genus: Lumbar vertebrae long. Transverse processes of the lumbar vertebrae wider than in other genera. Their length at the base is almost equal to the length of the body of the vertebra.

Remarks: Only vertebrae alone are known.

Genus *Microzeuglodon* Stromer, 1903

Type of the genus, *Microzeuglodon caucasicum* Lyd., (= *Z. caucasicum* Lyd.)

Diagnosis of the genus: Size small. Skull relatively short (length of mandible about 28-30 cm). Index of length to width of body of the thoracic vertebrae 0.8-1, of lumbar and anterior caudal vertebrae 1.5. All molar teeth of the mandible are flattened leaf-like, with notched cutting edges. Vestige of posterointernal cone lacking. Humerus with strongly slanted head, with weakly developed deltoid crest and more or less sharply manifested greater and lesser tubercles.

52/ON THE HISTORY OF THE ORIGIN AND DISPERSION OF THE EARLY CETACEANS

The origin of the cetaceans from archaic land mammals is indubitable. This is attested by the multitude of features in common with land mammals observed in both modern and, in particular, fossil cetaceans. The ancient cetaceans, like the land mammals, had a narrow elongated brain case, an external nasal opening situated not as far back as in modern cetaceans, maxillary and occipital bones which did not override the parietal and frontal bones, small ethmoturbinal conchae and sagittal crest, molars with three and sometimes two roots. In some of them there was also the rudiment of a protocone, the mandible had a well developed coronoid process, the elbow joint was movable, and the cervical vertebrae were free. The presence of vestiges of the hind limbs and hair cover in the newborn of most of the now living members of the order Cetacea, together with some other particulars of body structure, also indicate their affinity. Interesting data indicating a relationship of the ancient cetaceans to the terrestrial mammals have also been obtained as a result of paleohistological investigations of the limb bones of some archaeocetes (G. A. Mchedlidze, 1964).

But the problem of which group of ancient mammals should be considered their ancestor still remains unsolved. The archaeocetes have been connected with very different groups of terrestrial mammals: Marsupialia, Triconodonta, Insectivora, Edentata, Carnivora, Artiodactyla, Perissodactyla. The most popular hypothesis is that the cetaceans originated from primitive carnivores and insectivores (C. Dechaseaux, 1961).

The remains of the earliest cetaceans are known from the Lower Eocene formations of England, Africa, and the Caucasus. We have in mind *Anglocetus beaumonti* Tarlo (L. Tarlo, 1964), described recently from the Londinian suite of England (Sheppey Island), the African *Pappocetus lugardi* Andrews (G. Andrews, 1920), and also the data of N. M. Gubkin (1950) on the finding of remains of zeuglodon in the Koun beds of Azerbaijan.

53/ In Lower Eocene time the archaeocetes already were rather specialized animals adapted to the marine environment, which along with other data indicates their extremely ancient origin. If we add

to this that in the beginning of Middle and possibly Lower Eocene time the archaeocetes already were characterized by such essential features of the skeleton structure (spine and limbs), then it is difficult to admit the possibility that they formed in the course of a relatively brief geologic interval (for instance, from Paleocene to Lower Eocene). Evidently the transition of the terrestrial ancestors of the cetaceans to the aquatic medium could not have been accomplished later than in Late Cretaceous time.

At the present stage of knowledge of the paleobiological history of the cetaceans, the problem of the origin of the archaeocetes cannot be solved with certainty. Therefore the considerations expressed hereinafter concerning the origin of the cetaceans in general and of the archaeocetes in particular will be only conjectural in character.

The origin of new groups of animals is preceded in most cases by a progressive development of the forms ancestral to them. This or that group of organisms, attaining a high degree of evolution and subjected to widespread adaptive radiation, gradually becomes accustomed to very different types of biotopes, frequently giving rise to completely different forms.

Among the Mesozoic mammals there were the multituberculates, rather highly organized and well adapted to their conditions of existence, which constituted one of the most flourishing groups of ancient mammals over a very long time beginning from the Triassic and almost to the end of the Cretaceous. However, the presence of a whole series of primitive features in them, to some extent resembling the Monotremata, and also the considerable antiquity of the group as a whole has led investigators to the opinion that the multituberculates were oviparous animals (A. S. Romer, 1939). This constitutes grounds for eliminating them from among the ancestors of the cetaceans.

As is known, among the members of the subclass Theria the pantotheres stood closest to that fundamental group of animals from /54/ whom newer forms of mammals were derived. The structure of the molars of these early mammals seems to have been material for the development of the teeth of the marsupials and the true placentals.

Therefore we deem it expedient to compare some features of the structure of the dentition of the oldest archaeocetes with those of the pantotheriids.

It is customary to take *Protocetus*, characterized by tritubercular secodont molars, as the connecting link between the archaeocetes and their ancestors. Almost all the basic elements of the molars of the placentals are represented on the molars of this animal: distinctly reduced protocone, metacone, parastyle, and paracone standing out as the main tubercle, (R. Kellogg, 1936; C. Dechaseaux, 1961, p. 845). The molars of the pantotheriids also consist of a protocone, parastyle, and an amphicone not yet separated into metacone and paracone (A. Romer, 1939, p. 230). Thus, in the protocete the amphicone, the single cone inherited by the pantotheres from the reptiles, is already separated into a meta- and a paracone, in this respect having the structure typical of the placentals. Thus an already reduced structure of the post-pantothere complication of the molars is represented in the protocete.

Judging from the data on the history of evolution of the dentition in general, the complication of tooth structure (manifestation of new elements) inherent in typical placentals does not take place in the aquatic environment; on the contrary, simplification takes place. Therefore it is natural to think that the ancestral forms of the archaeocetes must have had all those elements, namely a protocone already separated into amphicone and parastyle, whose reduction is noted in their descendants the protocetids. In particular, we should mark the presence of a separated amphicone in the protocetids. Separation of the amphicone into meta- and paracone is not noted among the pantotheriids. We observe the beginning of this process only in the primitive insectivores, the deltatheriids (Late Cretaceous), in which the paracone and metacone already are found almost in the center of the tooth but are separated from one another in the top part.

It must be assumed that in the Lower Eocene and particularly in the Paleocene forms of the archaeocetes, all tooth elements represented in the protocete were developed in unreduced form--/55/ corresponding as it were to the immediately post-deltatheriid stage of evolution of the molars. However, can it therefore be claimed that the insectivores gave rise to the ancient cetaceans? In our opinion, no.

In this connection we should turn attention to the character of evolution of some particulars of the skull in the protocetids on the one hand and in the insectivores on the other. The skull of the earliest representatives of the archaeocetes bears marks of a distinctly carnivorous character, the gradual disappearance of which is easily traced in these animals throughout the duration of their existence. Thus, for instance, there is a considerable shortening and constriction of the temporal fossae, the surfaces for the *m. masseter* and *m. temporale* are reduced, the occipital and sagittal crests, well developed in the oldest archaeocetes, disappear. All these features of skull structure must have been well developed in the ancestors, that is, in the land forms, and evidently they gradually became reduced only after the animals' transition to the aquatic environment.

On the other hand, skull crests (both sagittal and occipital) are absent or very weakly expressed in the insectivores (CA. Romer, 1939), whereas they are rather well developed in the Eocene archaeocetes.

We believe that the origin of the archaeocetes, with their strong skull crests, from the insectivores, characterized by weak development or absence of these formations, is extremely doubtful. For in aquatic forms it is not possible to achieve the evolution of formations which cause strengthening of the muscles related to the cutting and chewing of food, that is, with processes which gradually lost their significance in the course of evolution in an aquatic environment.

As is known, all those features of the skull which bear the character of carnivorous animals are well developed in the creodonts. The particulars of the dentition of the early cetaceans--secodont teeth, tritubercular molars and last premolar--and also the presence of a long second cervical vertebra, indicate a definite similarity of the archaeocetes to the creodonts. This similarity is of convergent character, according to R. Antony (1926) and R. Kellogg (1936). Moreover, if we take into account the fact that there is no reliable evidence for the existence of creodonts in the Cretaceous epoch and that /56/ in all probability they originated at the very end of the Cretaceous or beginning of the Paleocene, then we have to reject the hypothesis that the archaeocetes originated from the creodonts, for by the time the

creodonts had individualized the early archaeocetes apparently already formed a group of animals satisfactorily adapted to the aquatic environment.

In the opinion of Van Valen (1966) the ancestors of the archaeocetes could have been members of just two families of ancient mammals, the Mesonychidae and the Hyaenodontidae. However, comparing the particulars of structure of the dentition and a number of bones of the skeleton of these animals with those of the archaeocetes, he found greater similarity to the latter in the mesonychids, for both these groups (Archaeoceti, Mesonychidae) have features in common which are different from the hyaenodontids. Splitting off of the cetaceans from the mesonychids took place, according to Van Valen, in the Middle or Upper Paleocene (ibid, p. 90-93).

There is no doubt that the hyaenodontids being members of Eocene-Oligocene groups of mammals (Gromova, V. I., 1952, p. 52; Van Valen, 1966, p. 111), could not be the ancestors of the archaeocetes.

The Paleocene Mesonychidae, referred by Van Valen to the Condylarthra along with the Arctocyonidae (ibid, p. 103), do as a matter of fact show a number of features similar to the early cetaceans (see ibid, p. 90-93). However, the existence of differences in the evolution of several particulars of the dentition and skull, which in our opinion are essential, and also the unique fundamental features of the historical evolution already manifested at the very early stage of evolution of each of the groups in question, compels us to doubt a direct relationship between the mesonychids and the early cetaceans as postulated by Van Valen.

Thus, for instance, the largest and best developed tooth in the dentition of the archaeocetes (*Protocetus*) is P³ which, as R. Kellogg (1936, p. 276) rightly remarks, corresponds to a carnassial tooth. But in the mesonychids, as is known, the carnassial pair of teeth is not generally formed and P³ is no different in size from the rest of the cheek teeth (Gromova, V.I., 1952; Piveteau, 1961, p. 655).

Although the upper molars of the mesonychids retain the original tritubercular type of structure, the paracone and metacone, /57/ already separated in the Cretaceous placentals, nevertheless are united

at the base and separated only at the top (Gromova, 1952, p. 69). It is difficult to see how animals which had acquired a distinct tendency toward union of the para- and metacone could give rise to forms having separated cones. Let us know, moreover, that in the mesonychids there is always a well developed protocone, which is strongly reduced or completely absent in the archaeocetes (Van Valen, 1966, p. 91). Nevertheless Van Valen perceives some kinship of the archaeocetes with *Dissacus*, namely the fact that in it the protocone is not so strongly elongated lingually as in the rest of the mesonychids.

Here it should also be noted that a preglenoid process, absent in the archaeocetes, is always present in the mesonychids (including *Dissacus*), but is almost completely reduced in forms of the creodonts as well adapted to a carnivorous regime as the hyaenodontids. Evidently the absence of this process, which enabled some fixation of the mandible in its sidewise and forward-backward movements, in the hyaenodontids is probably best explained by the great predominance of vertical movements of the jaws. Therefore the correlative relationship of the reduction of the preglenoid process to the evolution of the carnivore features of the dentition in these animals is understood (in the course of the historical development of the hyaenodonts the protocone disappears, the paracone and metacone are completely united, the posterior cutting edges are enlarged, and the pair of carnivore teeth is formed, while in the mesonychids, which retain this process, the primitive structure of the upper molars is retained without a tendency toward development of the pair of carnassial teeth.

It is natural to assume that in the archaeocetes, which underwent only a reduction of the carnivore features in the course of evolution, the absence of the preglenoid process is a feature directly inherited from the ancestral forms and not a detail acquired in the course of adaptation to life in an aquatic environment., (see p. 55). It is noteworthy that this process is lacking in *Eoconodon*, which is regarded as the ancestor of the mesonychids (Van Valen, 1966, p. 92). Consequently, if the Mesonychidae are considered to be the ancestors of the archaeocetes, we are then obliged to accept that the process of evolution of a number of features (development of the preglenoid process and of elements

of the cheek teeth) was reversible, which is extremely /58/ unlikely. In addition, such as assumption is contradicted by the overall course of evolution of the cetaceans as a whole.

As is known, the mesonychids are manifested only in the Middle Paleocene and reached their peak in the Early and Middle Eocene, while the archaeocetes were already so well adapted to the marine environment in Early Eocene time that they had undergone rather considerable ecological expansion" (see p. 52). The interval from Middle Paleocene to Lower Eocene is far too small, it seems to us, for such profound changes in the structure of land animals as are observed in the cetaceans to have been accomplished in that time (reduction of hindlimbs, abrupt change in structure of fore limbs, conversion of tail into the main propeller of a fast-swimming aquatic animal, reorganization of the skull, etc., with which there undoubtedly were related extremely essential changes in the biology and physiology of the organism). It is difficult to accept such a high tempo of the aforesaid changes even for the earliest stages of evolution of the cetaceans, the more so as, judging from the data on the history of the evolution of other groups of marine mammals, the period of amphibian form of life during the ecogenesis of the ancestors of the cetaceans should alone have taken a longer time than the whole Paleocene.

Therefore we are inclined anew to keep to the hypothesis of R. Kellogg, according to which the archaeocetes, which to a known extent are related to the carnivore-insectivore branch of the mammals, were split off not from that branch but rather from same older and more general trunk which gave rise both to the insectivores and to the carnivores and cetaceans.

The lack of forms transitional from land mammals to the archaeocetes led R. Kellogg to the opinion that in the early stage of evolution the ancestors of the archaeocetes possibly were linked to freshwater streams (the waters of rivers and lakes) whose deposits, and consequently any fossil occurrences related to them, are very rarely preserved.

However, fossil localities related to lake deposits are not so rare for the Mesozoic and in particular for the Cretaceous. (N. A. Efremov, 1950, p. 65). Nevertheless no forms similar to the archaeocetes have been found in any of the /59/ known vertebrate localities of lacustrine origin.

On the other hand, there is as yet not a single locality of cretaceous or even Early Cenozoic vertebrates, with the exception of the Laramie (Upper Cretaceous of the U. S.A.), which is related to fluvial sediments.

The failure of the ancestors of the archaeocetes to be buried perhaps can be explained by the fact that the remains of these animals fell into formations which were not involved in major sedimentation processes.

Fluvial deposits may be entirely such, the more so as the ancestors of these animals probably were originally linked to rivers.

As we conceive it, in the beginning the individual ancestors of the cetaceans obtained their food along the banks of rivers and then, gradually adapting to feeding on aquatic organisms, moved completely into the aquatic environment. Naturally this process was accompanied by profound changes in the external and internal structure and also in the behavior of the forms infiltrating the new environment.

In this connection, the example of the modern insectivore *Potamogale* (the otter shrew) is noteworthy. This animal is about 60 cm long, lives in Africa on river banks, eats fish, and mainly clings between stones, from whence it watches for its prey. It swims rapidly, but not by using its limbs which are devoid of webs between the toes, but by movements of its thick, long, and laterally flattened tail; the body is long, the limbs relatively short, and in contrast to all other insectivores it has no clavicle in the [shoulder] girdle, of the fore limbs. Valves of a special kind cover the nostrils when it swims (A. E. Brehm, 1941, p. 126). Thus we see that this animal has a number of those features inherent to the cetaceans in a more developed form.

In our view, the terrestrial ancestors of the cetaceans could have resembled the *Potamogale* somewhat in body structure and lived a somewhat similar kind of life.

According to the suggestion of G. Simpson (1941, p. 214), certain "crucial moments" in the history of evolution of the archaeocetes must have been related to the open ocean spaces and not to the

shallow /60/ water or littoral parts of the seas where, as that author notes, most of the Miocene cetaceans lived. He thinks that this circumstance is the cause of the absence of post-freshwater transitional forms in burials.

In our opinion it is difficult to agree with such an explanation of the absence of forms transitional to the archaeocetes. First, it is not clear why the "crucial moments" in the early stages of evolution should have been related to the open ocean and not to the offshore parts of the seas. In our view it is more logical to assume that after the transition from a freshwater to a marine environment, the early cetaceans still would have stayed in the shallow water offshore parts of the seas for a fairly long time. The paleobiological history of the dolphins, whose Tertiary representatives undoubtedly were more closely tied to the offshore parts of the seas than the modern (G. A. Mchedlidze, 1964), can serve as an example of this sequence of ecogenesis. The form of life of the most primitive of the modern toothless whales, the gray whales, also supports this contention: they, the most primitive with respect to the structure of the skull, mandibles, pelvis, and humerus, are tied to the shallow-water parts of seas, unlike all the other modern toothless whales (A. G. Tomilin, 1957).

Secondly, even if we accept that the earliest archaeocetes lived in the open oceans, their remains would be expected in offshore formations all the same, for regardless of where the animals died, the carcass of a mammal for the most part is carried by waves or currents into the coastal belt, where it is subject to burial. Therefore in our opinion, the lack of information on the earliest members of the archaeocetes should be attributed to the incompleteness of the geologic record and of our knowledge.

On the basis of the fact that the remains of the most primitive members of the archaeocetes (*Protocetus*, *Pappocetus*, *Eocetus*) have been found in Africa, C. Andrews (1920) suggested the possibility that they arose off the shores of that continent. Of course that possibility is not ruled out, but to prove that Africa was the source of the cetaceans in general is at least risky, the more so as /61/ the presence of a member of the archaeocetes, *Anglocetus*, has recently been established in the Lower Eocene of England (L. Tarlo, 1964). However, if some information on the distribution of the cetaceans

in the Eocene is taken into account, and also the particulars of the paleogeographic changes of the northern part of the African landmass over the stretch of time from the Cretaceous to the Lower Eocene--that is, in the period when the first aquatic forms of mammals are supposed to have been manifested--then Andrews' hypothesis possibly becomes convincing.

Judging from the data available at present, the area of distribution of the Early Eocene archaeocetes was localized mainly in the Tethys region. Vast accumulations of the remains of these animals are preserved in the south coastal belt of this basin, on the present territory of Egypt, whereas only individual finds of Eocene fossil cetaceans are known from other places. While this may be due to exceptionally favorable conditions of burial on the territory of Egypt, it still does not rule out the fact that the center of evolution of the ancient Eocene archaeocetes was located in the waters of the Tethys adjacent to the African landmass.

The transgression of the sea onto the northern part of Africa, lasting from the Early Maastrichtian to the Lower Eocene, brought about a considerable shift of the shoreline to the south (Rushdi Said, 1965), after which there ensued repeated retreat of the sea as a result of which the shoreline shifted to the level of the Fayum in the Middle and Upper Eocene. As it advanced from the north, the sea apparently gradually penetrated all the continental water bodies in the territory which might have been inhabited by the forms ancestral to the cetaceans, and thus promoted the expansion of those of them which adapted to the changing conditions of existence.

Such circumstances as the finding of remains of the most primitive members of the early cetaceans in Africa, the probable localization of the main center of evolution of the archaeocetes (at least in Middle Eocene time) in the waters of the Tethys adjacent to Africa, and also the paleogeographic changes occurring there from the end of the Cretaceous to the lower Eocene which caused the expansion of the ancestors of the cetaceans, in our view support Andrew's hypothesis /62/ that the transition of the terrestrial ancestors of the cetaceans to an aquatic form of life was accomplished on the territory of Africa.

The process of adaptation of the ancestral cetaceans to the new (aquatic) environment went by way of profound morphological and physiological changes of the organism. The shape of the body changed, approaching the torpedo-like shape typical of marine vertebrates. The limbs changed correspondingly: the front were converted to the streamlined shape of fins, the back were gradually reduced. Contrary to the opinion of some investigators (V. I. Gromova and B.A. Trofimov, 1962) it seems to us that in the course of evolution the spine of the cetaceans did not lose but acquired considerable flexibility. As is known, in land forms the originally flexible spine of marine forms became adapted almost exclusively to front-and-back movements of the legs so that other movements were hampered or even not possible, and in connection with this the spine lost flexibility. The connection between the individual vertebrae was strengthened as a result of the development of special articular processes, the zygapophyses. The strength of the skeleton as a whole was also conditioned by a great number of sternal ribs.

In the course of adaptation to the aquatic environment, the limbs lost their main role in forward motion (the front ones fulfilled only a steering function and the back ones were completely reduced), the spine again acquired considerable flexibility, the zygapophyses and pelvic girdle were reduced, the number of sternal ribs was reduced, etc. With respect to the flexibility of the spine, the long-bodied members of the Zeuglodontids stand at a higher level of evolution than all the other representatives of the Archaeocetes. The changes in the structure of the spinal column which took place in the history of these animals certainly promoted an increase in flexibility of their trunk. The morphological particulars of the thorax (short sternum, flexible thoracic section of the spine, decrease in number of sternal ribs) also indicate greater flexibility of the front part of the trunk than in the others, which possibly was related to adaptation of these animals to diving (C. Dechaseaux, 1961; J. Gidley, 1913). Elongation of the caudal section (to 21 vertebrae), whose vertebrae in contrast to the others had great metapophyses and relatively broadened lateral surfaces of the body, leaving /63/ a large surface for attachment of the caudal muscles, evidently indicates the power of the tail and strengthening of its propulsive function. Judging from the

skeleton structure, for instance of the basilosaurs, their locomotion evidently could be accomplished by serpentine movements of the body and vertical movements of the tail.

As for the short-bodied forms, they evidently had a less flexible trunk. The vertebrae of these forms had wide and high spinous processes, well developed lateral processes and non-elongated body, and large and interconnected zygapophyses. Nevertheless the zygapophyses in the posterior part of the sacral section of the spine already were somewhat smaller, giving relative flexibility to this part of the spine. It can be assumed that locomotion of the short-bodied forms was accomplished by vertical movements of the relatively powerful tail, similar to the large representatives of the modern cetaceans. We must not lose sight of the fact that in the zeuglodontids the elbow joint nevertheless still functioned. Possibly the front limbs of these animals still played some part in the forward movement of the body (in addition to a steering function). In the course of the phylogenetic history of the archaeocetes a gradual simplification of the dentition is traced. The front teeth are converted into grasping teeth and the back teeth are laterally flattened, acquiring a serrated anterior and posterior cutting edge. In the early forms the premolars and molars are three-rooted; in later forms these teeth become two-rooted. Ultimately the evolution tends toward simplification, to homonomy of structure of the dentition, which is fully understandable from the point of view of adaptation to feeding in the water.

As systems, the morphological changes of the skeleton only partially reflect the considerable progress attained in the course of animal evolution. Naturally, the skeleton of an animal, which is the main object of investigation of paleontologists, cannot completely reflect all the changes taking place in an organism; but this gap can be filled to a certain extent by the data of paleoneurology.

The brain of the Eocene zeuglodontids, judging from R. Kellogg (1936), was elongated in length and triangular in shape. The hemispheres of the cerebrum were weakly developed. Gradually tapering anteriorly, /64/ they passed into a well developed olfactory part of the brain. The olfactory stalks were very long, ending in strongly inflated olfactory bulbs. The cerebellum, in comparison to other parts of the brain, was relatively large and markedly expanded in width. The width of the cerebellum was

somewhat greater than the width of the hemispheres of the cerebrum, which possibly was due to the intensive development of its floccular parts. The medial portion of the cerebellum was also well developed, evidently indicating the presence of a large corpus. Such a structure of the cerebellum, in our view, must have depended on the unique character of locomotion of these animals. As has already been mentioned, the locomotion of the zeuglodontids evidently was accomplished by movements of the trunk and tail, with which the intensive development of the flocculi of the cerebellum certainly was related.

In our opinion the enlargement of the floccular parts of the cerebellum, already typical of the Middle Eocene archaeocetes, was a secondarily acquired feature related to the regression of the ancestral cetaceans to the means of locomotion used earlier. As is known, the morphological precursors of the flocculi, the auriculae, had already arisen in the Cyclostomata and were well developed in all aquatic vertebrates in which undulatory motions of the trunk and tail played the leading role in locomotion. With loss of these motions in the land mammals, the flocculi were strongly reduced, but upon intensification of the role of the paired extremities in their motor system, the corpus of their cerebellum was intensively developed. In the cetaceans, whose locomotion surely was accomplished by movements of the trunk and tail, flocculi again developed and reached tremendous size. The intensive development of the medial part of the cerebellum in the zeuglodonts, obviously corresponding to the corpus of the cerebellum, apparently is a feature inherited from the terrestrial ancestors, related to locomotion on legs. Probably the presence of fore limbs with movable elbow joint in the zeuglodonts is a function of the evolution of the corpus of their cerebellum.

Studying a series of endocranial casts of representatives of the archaeocetes, R. Dart (1923) established that the reduction of the sense of smell in the ancient cetaceans went on parallel to the development of the trigeminal /65/ and auditory apparatus, which provided more complete adaptation of these animals to the environment they inhabited.

As a result of a number of these morphological changes which took place at various stages of phylogenetic development, the members of the archaeocetes acquired more and more substantial

advantages compared to their ancestors. In the Middle Eocene these animals comprised a group of mammals which were fairly well adapted to life in the sea, and by that time had already undergone very widespread ecological changes.

Whereas in Middle Eocene time the area of distribution of the early cetaceans was limited mainly to the Tethys region, in Upper Eocene time the archaeocetes were widely dispersed in the warm and moderately warm waters of the Atlantic and Indian Oceans.

In the Upper Eocene the archaeocetes were widely distributed inhabitants of the waters of the Atlantic Ocean adjacent to the southeastern part of North America. Discoveries there of numerous remains of various representatives of the suborder are evidence of that (O. Abel, 1913; G. Simpson, 1945; R. Kellogg, 1928, 1936; J. Huller, 1849; N. Gilley, 1913; and others). At the same time some representatives of the zeuglodontids, for example *Microzeuglodon harwoodi* Sanger (E. Sanger, 1881), reached the south shores of Australia. In the Upper Eocene the zeuglodontids also inhabited the waters washing the shores of the ancient Brittanian landmass (H. Seeley, 1876).

Whereas the end of Eocene time evidently was a period of very intensive development and "wide dispersal of the early cetaceans, from the Oligocene the area of their distribution began to shrink gradually, being restricted approximately to the Tethys region. The last representatives of these animals were inhabitants of the greater part of the northern and northeastern parts of that basin. Remains of Oligocene archaeocetes are known so far only from the Ukraine --*Platyosphys* (A. S. Fedorovskiy, 1911-1912), the Caucasus --*Mirocetus* (= *M. aff. caucasicum*) (A. N. Ryabinin, 1938), and Austria -- *Patriocetus* and *Agriocetus* (O. Abel, 1913). The Lower Miocene forms --*Phococetus* from the Burdigalian of France and *Kekenodon* from the Burdigalian of New Zealand (C. Dechaseaux, 1961) -- evidently were the last of the archaeocetes.

The fact that the Late Paleogene-Neogene /66/ group of archaeocetes, localized mainly in the Tethys basin, was represented by relatively undersized and to some extent aberrant forms like *Patriocetus*, *Agriocetus*, *Phococetus*, *Mirocetus*, *Microzeuglodon*, and *Ferecetherium*, is worthy of

certain interest. It is noteworthy that among these forms there fall those characterized by a unique combination of features of the archaeocetes and of the toothless whales, which are united in the family Patriocetidae Abel (A. S. Romer, 1966).

ON THE POSSIBLE RELATIONSHIPS BETWEEN THE EARLY AND THE TOOTHLESS CETACEANS

An investigation of the paleobiological history of the early cetaceans shows that these animals occupy an intermediate position between the ancient mammals and the typical cetaceans. Nevertheless the problem of the genetic relationship of the archaeocetes to the typical cetaceans is one of those questions which has provoked very great differences of opinion among investigators. Some (O. Abel, 1913; P. I. Spasskiy, 1954; A. S. Romer, 1966), fully accept the possibility of a relationship with the toothless whales. Others (Van Valen, 1966, 1968) accept the possibility of a genetic relationship of the archaeocetes with both the toothless and the toothed cetaceans. And finally, a number of investigators (R. Kellogg, 1928, 1936; G. Hinler, 1923; A. N. Yablokov, 1964; and others) object to such assumptions and regard the archaeocetes as a completely separate group which has nothing in common with the typical cetaceans.

Thus, for example, R. Kellogg thinks that although morphologically the archaeocetes are similar to typical cetaceans, nevertheless this does not make it correct to consider their representatives to be the ancestors of any group of the modern cetaceans. All the same, however, he thinks that the archaeocetes constitute a collateral line of the branch from which, the true whales are descended (R. Kellogg, 1936). G. Miller (1923) maintains that the representatives of the zeuglodonts known so far cannot be the direct ancestors of the modern cetaceans, and may represent a transition from the skull inherent in the zeuglodons to the skull of the Odontoceti rather than to the skull of the Mysticeti. Let us note that this latter conclusion of Miller's seems to us to be /67/ unconvincing, as it is not supported by the particulars of skull structure of the toothed cetaceans.

In embarking upon an examination of the opposite point of view on the origin of the toothless cetaceans, we will begin with consideration of an interesting comparison.

A comparison of the Sarmatian cetothere from the vicinity of Derbent with *Mirocetus* (= *M. aff. caucasicum* Lyd.) led P. N. Spasskiy to the conclusion that these forms stand very close to one another. In the skull of both animals, writes Spasskiy (1954, p. 224), the brain case is smaller in length than in width (a typical feature of modern cetaceans), the supraoccipital bones are similar in shape (although in the cetotheres they extend somewhat farther forward). The parietal bones are found on the dorsal surface, forming the short parietal part of the skull. The squamosal bone and its zygomatic process are of the same shape and approximately of the same length in both forms. There is a similarity both to land animals and to the cetotheres in the rest of the details of structure of the skeleton of the species described by A. N. Ryabinin, according to Spasskiy. That author believes it fully possible that the genus *Cetotherium* originated from "*Microzeuglodon*," which suggests that the *microzeuglodon* turned into the cetothere in the time interval from Upper Oligocene to Upper Sarmatian (P. N. Spasskiy, 1954, p. 224).

Actually, the similarity in structure of the skull of the cetothere and the "*microzeuglodon*" is so great that at first glance their direct genetic relationship might seem obvious. However, let us remember that *Cetotherium* is known only from the Sarmatian, and other members of the group of cetotheres which are rather similar to this genus already existed in the Upper and even in the Middle Oligocene (genus *Cetotheriopsis*), that is, almost contemporaneously with the "*microzeuglodon*" (*Mirocetus*).

As is known, O. Abel thought the connecting link between the ancient cetaceans and the toothless whales was the *Patriocetus* described by him (*Patriocetus ehrlichi* Van Beneden, see Fig. 10), /68/ which according to the data of that author is characterized by the presence of a number of features in common with the toothless cetaceans (O. Abel, 1913, p. 168). R. Kellogg objects to this idea. He states that in the patriocete, restored by Abel the premaxilla bones are extended forward [backward?] to the parietal bones, occupying the central part of the roof of the skull, while the maxillae are contiguous

with the anterior edges of area of the maxilla which is present in members of the Mysticeti is completely lacking in the skull

of *Patriocetus*. Finally, according to R. Kellogg, the patriocete could not be the link connecting the archaeocetes with the toothless whales because it is no older than some of its presumed descendants among the toothless whales. G. Miller (1923) holds the same opinion as Kellogg.

While accepting in its general lines O. Abel's hypothesis concerning a possible genetic connection between the archaeocetes and the toothless cetaceans, we nonetheless find it necessary to add, following R. Kellogg, some remarks about Abel's reconstruction of the skull of *Patriocetus*. But before turning to a discussion of our reasons, we believe it desirable to give here some information from the history of evolution of the skull of the cetaceans.

The main feature of the skull of modern cetaceans, as is known, is its flatness, brought about by interdigitation of the facial and overriding of the occipital elements /69/ and also by the manifestation of a substantial broadening of the brain case related to this.

This process occurs differently in the different groups of cetaceans. In the toothed cetaceans (see Fig. 11, 12) the overriding of the facial elements is more intensive than of the occipital: the maxillae and premaxillae override the caudally situated elements and, overlapping them, come in contact with the supraoccipital region.

70/ In the toothless cetaceans, in addition to relatively slight interdigitation of the rostral elements, there is rather intensive overriding of the occipitals by the supraoccipital bone. The supraoccipital bone in some forms (the rorquals) is in contact with the maxillae and nasal bones (see Fig. 13), in others (the right and gray whales) the frontal bones emerge between them (see Fig. 14, 15).

The maxillae in the modern toothless whales lie mainly below the frontals; on the dorsal surface they form relatively narrow frontal nasal processes which, together with the markedly constricted premaxillae, either overlap the frontals only in the mid-sagittal part of the skull (rorquals) or abut against the anterior edges of the frontal bones (right and gray whales and all fossil toothless whales). The

premaxillae, carrying along the fronto-nasal processes of the maxillae, do not enter, or very slightly enter (only in some modern members of the Balaenopteridae) behind the nasal bones and never show a tendency to broaden.

Premaxillae which are strongly thrust caudally and moreover are widened in the prenasal part are typical of the toothed cetaceans, in which these bones, accompanied along almost their whole length by, strongly diverging maxillae, approach and sometimes even touch the supraoccipital. As for the parietal bones, in all modern cetaceans and also in most fossil toothed whales they are displaced from the composition of the roof /71/ of the skull. In the archaeocetes and fossil toothless whales (for instance, in the cetotheriids, see Fig. 16) the parietals are present in the composition of the roof of the skull. Apparently the displacement of the parietal bones from the roof of the skull in the toothless cetaceans is related to the intensity of overriding of the occipital shield. In forms characterized by strongly overriding shield (modern toothless whales) the parietal bones are always absent, and in those distinguished by a relatively slightly overriding shield (for example the cetotheriids), there are parietals.

In the toothed cetaceans the displacement of the parietals is probably caused by the intensive expansion of the maxillae. Evidently the premaxilla bones are thrust more or less substantially caudally only where the maxillae, strongly expanded and overriding the cranial part, overlap the elements situated caudally from them and do not lie under the frontal bones as in *Patriocetus*.

Taking into account this information on the phylogenetic development of the cetacean skull, we find that in *Patriocetus*, in which as in all toothless cetaceans (both modern and /72/ fossil) the maxillae do not override the frontals but lie below them, the premaxillae should not have been thrust strongly caudally. In our opinion, the posterior edge of the premaxilla bones in *Patriocetus*, as in all cetaceans characterized by similar structure of the maxilla (all the toothless), should be found at the level of or slightly behind the nasal bones. It is fully apparent that here the structure of the corresponding part of the skull of the patriocete has not been deciphered with sufficient accuracy, which for a while will probably constitute grounds for objecting to the suggestion offered by Abel.

The presence of large parietal bones in the make-up of the roof of the skull in the patriocete, with relatively strong overriding of the occipital shield inherent in this form (anterior edge of the shield reaches the posterior edge of the temporal fossae) is likewise open to some doubt. As for the very fact that the presence of parietal bones on the dorsal surface of the skull, that ought not be inconsistent with its affinity with the toothless whales, in whose fossil representatives parietals are still retained on the dorsal surface of the skull in connection with incomplete overriding of the occipital shield, as in the patriocete.

As has already been mentioned, according to Kellogg the absence of the maxillary process in the orbital arch in *Patriocetus* is inconsistent with a tendency toward its rapprochement with the toothless cetaceans. Probably, precisely that structure can be explained by affinity with the archaeocetes, characterized by a structure of the orbital part of the skull similar to the patriocete. The processes of the maxillary bones enter the orbital /73/ part of the skull in almost all modern toothless cetaceans and also in their fossil representatives (for instance, the cetotheriids). Evidently this is a typical mysticete feature and perhaps is developed as a function of the lengthening of the rostral part of the skull and the concomitant need to strengthen union of the rostrum with the cranial part (there is a widening of the basal parts of the maxillae which in later forms, moreover, go in under the frontal bones considerably farther than in the early ones).

Here it is relevant, in our view, to give a brief description of a representative of the archaeocetes which is unique and interesting in many respects, which was discovered by us in the Upper Maikop formations of Azerbaijan (vicinity of the village of Perekishkyul). Investigation of this fossil cetacean has given us valuable clues to the relatively late stage in the history of the archaeocetes (U. Oligocene - L. Miocene) (G. A. Mchedlidze, 1968).

A number of characteristic features of the skeleton of this form resemble members of the family Patriocetidae Abel, 1913, but a unique combination of features of the archaeocetes and of the toothless

cetaceans peculiar to it alone apparently provide grounds for separating it in the independent genus *Ferecetotherium*.

Family PATRIOCETIDAE Abel, 1913

Genus *Ferecetotherium*, gen. nov.

Type of genus, *Ferecetotherium kelloggi* sp. nov.

Diagnosis of the genus: A medium-sized representative of the archaeocetes (not more than 5-6 m), with non-elongated vertebrae. Skull relatively low, with short and considerably transversely tended cranial part. /73/ Squamosal and parietal bones participate in the formation of the roof of the skull. Zygomatic process of squamosal bone short and wide. Supraoccipital bone slanted forward and nearly triangular in shape. Mandible with almost horizontal and gradually ascending upper edges. Proximal half of mandible thin and high. Number of teeth increased to 30. All teeth of mandible cone-like, with small dome-shaped crown. Heterodont nature of dentition manifested in the different sizes of the teeth in different sections of the jaw. Teeth with only a small part of the root sunk in the jaw. Limb bones elongated; hand five-fingered; hyperphalangia slightly manifested (not more than 4 phalanges in each finger). Humerus with long diaphysis somewhat constricted in the middle, deltoid tuberosity relatively short and situated near the proximal end of the bone. Head of humerus slanted slightly outward. Tubercles and *sulcus bicipitalis* well expressed. Distal end of the bone angular and transversely broadened.

Description: Mandible long (Plate II, Fig. 1). Its lower edge is almost horizontal, the upper gradually rises caudally. Jaw low in the front half, markedly convex from the inner surface and somewhat flattened from the outer. From the middle of the length of the jaw there begins a gradual increase in height and a flattening of the bone. The proximal half is thin and strongly convex outward. The toothed part of the jaw occupies more than 2/3 of its total length. Teeth situated both in the horizontal front half of the jaw and on a large stretch of the ascending ramus. The tooth row in the front

third of the length runs almost along the outer edge of the bone and in the middle and posterior parts along its upper edge.

The anterior terminal edge of the jaw is bounded by the first incisor; ventrally it passes over into a diagonal edge with somewhat rough surface which forms an obtuse angle with the horizontal ventral edge of the jaw. The length of this segment is $1/2$ the length of the jaw. Apparently there was no symphyseal concretion.

The high location of the head of the articular process on this jaw is noteworthy. The junction surface 75° of the condyloid process here is not quite at the very top edge--that is, in the top posterior angle of the bone--but in any case is very close to it (on the specimen in our collection the process is much damaged). The coronoid process apparently was weakly developed and in connection with the cranial shift of the articular process, the edge of the bone below it probably had a nearly arcuate outline. The angular process is not preserved.

Teeth of the mandible: There are about 30 teeth on the mandible. All the teeth are cone-shaped and have one root (see Plate II, Fig. 1, and Plate IV). Unlike all the rest of the teeth, the first tooth (apparently I_1) is set deep in the jaw, is relatively lower, and forms the anterior edge of the jaw. The next two teeth in the jaw are not preserved but the corresponding shallow and wide alveolae are quite different. The fourth tooth (apparently C) is distinguished from the teeth in front of it by its height, large size, and marked inward curvature. Due to the strong plastering-over of the material, it is difficult to distinguish crown from root on the basis of the surface finish of the teeth; however, judging from the strongly inflated lower part, with parallel edges, and the abruptly constricted upper part, it can be concluded that the crown here occupied at least half the whole visible height of the tooth, a fact which sharply differentiates it from the rest of the teeth in which the crown has the appearance of a small dome. Evidently the cutting part proper of this jaw took up a very small segment, representing only $1/10$ of the whole tooth row. The 7 teeth situated behind the canine tooth are characterized by the same structure. In contrast to the canine and the teeth of the posterior section of the jaw, these teeth are

relatively low and are set somewhat deeper in the jaw than the back ones. All the teeth examined above are situated almost on the outer edge of the jaw; the rest are shifted toward the upper edge. The teeth in the middle section of the jaw differ sharply in height from the teeth in front of them: the height of the visible part of the tooth there is twice as great as that of the front teeth (except C). Strongly protruding from the alveolae, these teeth are wholly situated on the upper edge of the jaw. In contrast to the front teeth, which are characterized by a broad basal part, the teeth of the middle section have a relatively narrow base and are cylindrical in the greater part of their height. Only in the upper fourth of their height are these teeth gradually tapered and slightly recurved lingually. In the back part of the tooth row only four teeth are preserved in the jaw; the rest are represented in isolated form. The teeth of the back section are thinner compared to the middle teeth, but the height is the same in these as in the others.

Thus the jaw of *Ferecetotherium*, similar to the archaeocetes in several features of structure (horizontal lower edge of the bone, gradual rise of the upper edge, presence of teeth on the ascending ramus, and overall shape), at the same time differs from that of the early cetaceans in the essential simplification of the structure (tendency toward parallel arrangement of upper and lower edges, shift of condyloid processes to the upper corner of the wide part of the jaw, homodontization of the dentition, strong reduction of the crown and very slight embedment of the root in the jaw), which certainly is related to the loss of active participation of the teeth in the feeding process and, probably, to the acquisition by the latest forms of the archaeocetes of structural features inherent in the toothless cetaceans. The same can be said in connection with the structure of the fore limbs.

As in the Eocene representatives of the archaeocetes (R. Kellogg, 1936, p. 62), the limbs of *Ferecetotherium* are characterized by a five-fingered hand and long arm and forearm bones (see Plate I, Fig. 1). However, in contrast to earlier forms (*Basilosaurus*), in which the humerus was almost one and a half times longer than the forearm (see Fig. 7), the Upper Oligocene *Ferecetotherium* has arm and forearm bones of the same length. Features similar to the archaeocetes also are the slight inclination of the almost terminally situated head of the humerus, the presence of relatively well developed greater and

lesser tubercles with clearly manifested *sulcus bicipitalis* and large deltoid tuberosity, and also the presence of a large olecranon. On the other hand, the clearly manifested angularity of the distal ends of the limb bones, the shift of the deltoid tuberosity to the proximal part of the humerus, the straightening of the anterior and posterior edges of the humerus in the greater part of the length of its diaphysis, and also the increase in the number of /77/ phalanges on the second and third fingers (the terminal phalanges of these fingers are not preserved, but articular surfaces are well developed on the distal ends of the third phalanges of the second and third fingers) distinguish this animal from typical representatives of the archaeocetes, at the same indicating a change of structure of the skeleton of the forelimbs of the archaeocete in the direction of that the toothless cetaceans (see Plate I, Fig. 5).

The combination of features of the archaeocetes and of the toothless cetaceans peculiar to this form is also observed on other bones of the skeleton which have been preserved (see Plate III).

In our opinion it is also pertinent here to touch upon "*Microzeuglodon*" (*M. aff. caucasicum* Lyd.) from the Oligocene of Azerbaijan, which we have separated into a special genus of archaeocetes (*Mirocetus*). This animal, like other members of the family Patriocetidae Abel, occupies a morphologically intermediate position between the toothless cetaceans and the archaeocetes.

On the basis of the presence of the differentiated dentition, as well as on the basis of the nature of the tooth structure, *Mirocetus* is similar to the archaeocetes. The arrangement of the fundamental elements of the skull (structure of the squamosal bones, presence of a large zygomatic process, participation of the parietal bones in the formation of the crown of the skull, large supraorbital processes of the frontal bones not overlapped by the maxillae, absence of maxillae in the orbital arch, etc.), and also the structure of the basal part of the skull (basioccipital bone strongly broadened posteriorly, thick transversely elongated exoccipitals, etc.) also indicate its similarity to the archaeocetes, from which it is distinguished, however, by the triangular shape and by the forward tilted, considerably overriding supraoccipital shield which moreover is provided with high crests, and also by the change in structure of some skull bones in connection with the overriding of the cranial part: shortening of the parietal region

[the parietals comprise a narrow triangular bone at the top of the skull, with a posteriorly extended crest which evidently is the vestige of a sagittal crest (A. N. Ryabinin, 1938, p. 147)], shortening of the temporal fossae, massiveness of the zygomatic processes, some sloping of the side walls of the [brain]case, etc.). As is obvious from the above-mentioned features, the skull of *Mirocetus* /78/ differs from the skull of representatives of the archaeocetes in those features which characterize the toothless cetaceans.

However, changes in skull structure in this animal evidently are related not only to overriding of the occipital part but also to interdigitation of the rostral elements. The anterior edge of the nasal bones, which occur at the level of M¹, are strongly displaced caudally in contrast to the archaeocetes--to the level of the preorbital grooves (see A. N. Ryabinin, 1938, Plate I, Fig. 6). The premaxillae in all probability do not run far beyond the short nasal bones and evidently are pinched out together with the maxillaries between the processes of the frontal bones. According to the data of A. N. Ryabinin (1938, p. 147), the supraorbital processes of the frontal bones in this animal were shortened along the medial line and broadened at the orbital ends, resembling the relationship inherent in the toothless whales. The posterior margins of the nasal, premaxilla, and maxillary bones evidently were situated approximately on a line, as the maxillae here do not overlap but underlie the frontals.

In structure of the ribs and vertebrae *Mirocetus* is similar to the archaeocetes or, more Exactly, to the dorudontids. As for the scapula, according to the data of A. N. Ryabinin (1938, p. 164) it differed from the scapula of the archaeocetes by the absence of a crest. However, close acquaintance with the material shows that there is a crest on the scapula of this animal, but in contrast to typical archaeocetes, which are characterized by a strongly developed crest, it is rudimentary and displaced toward the cranial edge of the scapula as in the cetotheres. In the opinion of the author cited, the small size of the spinous process is characteristic of the fossil toothless whales, particularly the cetotheres.

Consequently, the scapula of the mirocete, resembling the same bone in the archaeocetes in its general lines, differs from the latter in the manifestation of mysticete features. On the basis of the overall

shape of the humerus and the structure of its head and (tubercles, the mirocete is like /79/ the archaeocetes, differing from them mainly in a slight angularity of the distal end of the bone.

Familiarity with the particulars of skull structure of these members of the Family Patriocetidae Abel leads to the conclusion that in these forms a number of distinguishing features of the skull indicate essential reorganization of the morphology, tending toward the acquisition of features characterizing the skulls of the toothless whales. In this connection some essential changes of the occipital part of the skull, traced in the history of the early cetaceans, merit particular attention.

According to the data of R. Kellogg (1928, p. 36-41) a tendency toward flattening of the skull (overriding of the occipital and facial elements of the skull is implied) is not found in any of the representatives of the archaeocetes. However, contrary to the opinion of that scientist, thorough familiarity with the particulars of skull structure of a number of representatives of the archaeocetes permits the tracing of a process of gradual anterior movement of the occipital shield in them.

If corresponding changes can be followed in the series *Protocetus*, *Dorudon*, *Zygorhiza*, *Basilosaurus*, *Prozeuglodon*, *Mirocetus*, *Patriocetus*, *Aetiocetus*, *Ferecetherium*, then we can note the following sequence: the almost trough-like supraoccipital bone in *Protocetus* is strongly recurved caudally [a straight line dropped vertically from the acrocranium runs considerably behind the posterior edges of the occipital condyles of the skull in this animal (E. Fraas, 1914, Plate I, Fig. 1)]; in *Dorudon* and *Zygorhiza* the acrocranium /80/ is thrust markedly forward [a straight line dropped vertically from the acrocranium here runs in front of the condyles, the occipital shield becomes vertical, and from above the lambdoidal crest assumes the shape of a semicircle (Fig. 8 and 17)]; in *Basilosaurus* (Fig. 2,3) and *Prozeuglodon isis* (E. Stromer, 1908, Plates VI-VII) the acrocranium is thrust forward still more strongly—a straight line dropped from the acrocranium in these runs in front of the posterior angles of the zygomatic arches. The lambdoid crest is relatively elongated and tapered, the occipital shield evidently is also relatively tilted forward. *Mirocetus* (Fig. 18) already has a distinctly overriding, almost horizontal occipital shield, the anterior angle of which is situated at the level of the middle of the zygomatic arch

(A. N. Ryabinin, 1938). As is known, an occipital bone still more strongly thrust forward and spreading is characteristic of *Patriocetus* (O. Abel, 1913). In it the anterior angle of the occipital shield is at the level of the posterior edges of the temporal fossae. and the shape of the shield is nearly rectangular (see Fig. 10). But the occipital shield in *Aetiocetus* (Emlong, 1966), triangular in shape, is thrust considerably forward beyond the level of the posterior edges of the temporal fossae. As has already been mentioned, only fragmentary remains of the occipital part of the skull of *Ferecetootherium* have been preserved, but they too indicate, convincingly enough, the presence in /81/ this animal of an occipital shield which was strongly elongated anteriorly and apparently triangular in shape (see Plate III, Fig. 4).

Although the series given above is not phylogenetic, the changes in it in the structure of the occipital part of the skull of the archaeocetes with time (from Middle Eocene to Upper Oligocene) certainly indicate that in the history of these animals the occipital bone tended to override the facial part of the skull. As is clear from the morphological series examined, overriding of the supraoccipital shield is particularly clearly manifested in the latest (upper Oligocene) representatives of the archaeocetes, that is, in representatives of the family Patriocetidae.

If the process of overriding of the occipital part of the skull, which in the latest forms is gradually intensified and leads to the formation of a skull of the type of the toothless cetaceans, is observed already in the Eocene archaeocetes, and if the main process of reorganization of the skull of the ancestors of the cetaceans was flattening, then in our view the gradual and systematic intensification of this process which is observed in the history of the archaeocetes and toothless cetaceans should be regarded as a general feature of the evolution of groups genetically related to one another.

The evolution of the dentition in this chain of forms also is consistent with this assumption. Thus, in the representative of the archaeocetes which stands closest to the terrestrial ancestors, *Protocetus*, the dentition is of tritubercular secodont type, with all the essential elements of the molars of primitive placentals (see p. 54). In more advanced forms (members of the family Dorudontidae) only vestiges of the posterointernal cone are preserved on P³ and P⁴, and the teeth are flattened like a saw.

Already this cone is very rarely manifested on the teeth of the Basilosauridae (only on P⁴). In the latest -- *Patriocetus* and *Mirocetus* --the tooth structure strongly simplified, and in addition to an intensification of the projection of the roots of the teeth above the edges of the jaw, there begins a reduction of their crowns. Although *Aetiocetus* also retains the normal number of teeth (11), its cheek teeth already have one root, the teeth are blunt and rounded on the crowns, and the crowns as a whole bear signs of reduction. *Ferecetherium*, which has the mandible shape typical of the archaeocetes, /82/ already has homodont dentition with numerous cone-shaped teeth barely held in the jaw. On the whole, in the course of evolution of the archaeocetes the incisors and front cheek teeth become larger, the premolars become higher, and the molars become smaller. The teeth of late archaeocetes acquire a lamellar shape and a crown with several accessory denticles on the cutting edges arranged in one plane. In the early forms (protocetids) the molars and premolars are characterized by a rudimentary internal part of the crown and a reduced but always present posterointernal cone (in them the cutting edges do not have accessory denticles).

The molars of the earliest archaeocetes (*Protocetus*) resembled terrestrial forms in the degree to which they were embedded in the jaw--they were set deeply in the jaw. Of the main elements, only the posterointernal cone is present in the late forms (moreover, rarely), the teeth project strongly above the edge of the jaw, and the relative height of the crown gradually diminishes. In the group of the patriocetids the crown is already present in the form of a dome, covering a root which projects high above the edge of the jaw. In *Ferecetherium*, the most highly evolved in the direction of the toothless whales, the teeth are already homodont, conical, and only slightly embedded in the jaw.

Separated along the whole jaw, to some extent turned outward, and not firmly set in the jaw, the teeth of *Patriocetus*, *Mirocetus*, *Aetiocetus*, and in particular of *Ferecetherium* could hardly have been involved in the cutting of food. Their main purpose probably was catching prey.

The gradual weakening of the main function must inevitably have led to loss of teeth in the later archaeocetes, thus giving rise to groups of forms similar to the toothless cetaceans.

It is noteworthy that those very forms which underwent a reduction of the dentition are also characterized by a mysticete aspect of the skull and limb structure.

ON THE ORIGIN OF THE HOMODONT DENTITION IN THE LATE PALEOGENE

ARCHAEOCETES

The presence of homodont dentition in the Upper Oligocene *Ferecetoherium*, which has features of the toothless whales, suggests the possible derivation of the cone-like single-rooted teeth of this animal from the two-rooted and multi-coned cheek teeth of the Eocene archaeocetes which, as is known, had a heterodont dentition. This process of evolution appears to us to be the following: the tritubercular secodont molars of the earliest archaeocetes (*Protocetus*) took on a strongly flattened serrated form with numerous denticles in the later stages of the phylogenetic evolution of the group (Dorudontidae, Basilosauridae). Finally, in *Ferecetoherium* there already is manifested a homodont dentition with an increased number of conical teeth in a closed row.

In this connection it is not without interest to give some data here on the embryonic development of the dentition of some representatives of the toothless whales.

After Geoffrey Saint-Hilaire (1807) discovered the rudiments of teeth in the mandible of the embryo of the Greenland whale (*Balaena mysticetus* L.) in the beginning of the last century, a number of investigations have been made on the embryogenesis of the dentition of the cetaceans. The most interesting were the results of W. Kükenthal (1893). According to that author's data, in the early stages of embryogenesis of the whalebone whales there are two-rooted teeth with numerous cusps in the back part of the tooth row. With further growth of the embryos, individual single-rooted teeth are manifested and their number is considerably increased. Investigating about 30 embryos of *Balaenoptera rostrata* L., W. Kükenthal came to the conclusion that in the course of ontogenesis the molars, initially few but with a great number of cusps, divide into a number of individual conical teeth corresponding to the total

number of cusps (at the 123-cm stage of development, there are 53 individual teeth in each side of the upper jaw of the embryo of the finback whale).

On the other hand, studying the particulars of the embryonic development of the tooth rudiments and surrounding jaw structures of /84/ *Balaenoptera physalus* L., Karlsen Kill [sic] (1962) showed that the first traces of tooth rudiments in these animals are manifested in the very early stages of embryogenesis (2-cm length), but the number of tooth rudiments varies in different individuals and also is different in both halves of the jaw in one animal. In the 82-cm stage, resorption of dentine begins, extending to the cutting part of the jaw. No separation of the rudiments is observed, whereas their widespread fusion is accomplished in all parts of both rami of the jaw at extremely early stages of development. In an embryo 330 cm in length, no traces of tooth rudiments are observed according to the data of that author.

Having considered these differences of opinion on the ontogenesis of the dentition of the whalebone whales, we now turn to an analysis of data on the phylogenetic history of the archaeocetes.

Describing the dentition of *Patriocetus*, O. Abel noted that I 3, C 1, Pm 4, and M 3 (thus, all 11 teeth), the total number of whose cusps is 53, are present in each side of the maxilla of this animal. In overall aspect the dentition here is in a stage of reduction, as the crowns of the teeth are strongly diminished and the roots are very weakly joined to the jaw (the roots are set in the jaw only by their tips). Comparing these data with the data of W. Kükenthal on the embryogenesis of the dentition of the whalebone whales and accepting the hypothesis of separation of multi-coned teeth into individual conical teeth, O. Abel (1913, p. 187) came to the conclusion that the jaw of the patriocete, with 11 teeth and 53 cusps, is the parent of the jaw of the toothless whales.

The circumstance that the total number of cusps of the already reduced teeth of *Patriocetus* (53) exactly coincides with the number of single-cone teeth of the 123-cm embryo of the Greenland whale was the basis for this conclusion to begin with. As for the process of separation itself, according to Abel

that should have occurred in the following way: teeth were divided off perhaps one by one from the front and back of a seven-cusped molar, and this went on until no one central tooth was left.

Agreeing in principle with the assumption of a genetic relationship of forms like *Patriocetus* to the toothless cetaceans, /85/ we nevertheless find it necessary to express a few remarks concerning the process of origination of a multitude of conical teeth.

If the origination of the single-root, single-cone teeth actually occurred by division of multi-cone serrated teeth and moreover in the aforesaid sequence, then in our opinion the following should have been observed: the number of denticles should always have been constant; the denticles should have been situated symmetrically on the cutting edges; a phylogenetic process of gradual intensification of the subdivision of the crowns into separate teeth (the grooves between the denticles should have been deepened and lowered nearly to the root) should be traced at least in part, and the crown as a whole should not have been reduced.

The data on the phylogenesis show a completely opposite picture, namely: the number of accessory denticles on the molars is not constant (see p. 37), the crowns are asymmetrical and for the most part denticles are developed only on the posterior cutting edge (particularly in the later forms); there is a distinct reduction of the denticles (which become smaller and blunter) and of the crowns as a whole, and also an obliteration of the boundary between the denticles. It is interesting to note that on some isolated back teeth of the ferecetothere we found traces of coalescence of two pointed halves of the crown into one cone, and also fusion of the two forks of a considerably caudally recurved root.

However, it remains incontrovertible that the ferecetothere, the member of the archaeocetes which stands closest to the toothless whales chronologically and in the particulars of skeleton structure, has a homodont dentition with a greater number of teeth than in the ancestors.

Taking into account all that has been said above, we find it possible to depart from the idea of the origin of single-cone, single-root teeth by division of multi-coned, as it is supported neither by the

evidence from phylogenesis of the dentition of the archaeocetes nor by an attempt to reconcile that evidence with the results of embryological investigations.

It seems more natural to us to explain the origin of the numerous conical teeth by joint cutting /86/ of different generations of teeth. This is not so difficult to imagine, the more so as polyphyodontism evidently was natural to the mammals (L. L. Natadze, p. 77).

Data on the paleobiological history of the groups in question have shown that in addition to continuous changes in skull structure, in the course of phylogenesis the archaeocetes also underwent a gradual simplification of the dentition, leading to loss of active participation of the dentition in digestion and then to its complete reduction.

ON A STUDY OF THE PALEOBIOLOGICAL HISTORY OF THE TOOTHLESS CETACEANS

(On the history of the genus *Cetotherium*)

In this section of the work, devoted to the toothless cetaceans, main attention will be paid to the exposition of a number of general traits of the paleontological history of the genus *Cetotherium*, which differs from other genera of the family Cetotheriidae in the nature of its distribution and in the particulars of evolution of some parts of the skeleton. We will also attempt here to expound the fundamental trends of the phylogenetic changes in skull structure in the toothless cetaceans in general.

The area of distribution of members of the genus *Cetotherium*, according to presently available data (G. Simpson, 1941; C. Dechaseaux, 1961; G. Mchedlidze, 1967), is limited mainly to the waters of the Ponto-Caspian basin. A single member of this genus has been found outside the territory of that basin, "*Cetotheriopsis*" *furlongi* Kellogg from California, concerning whose affinity with this genus the author himself had, doubts, (R. Kellogg, 1928, p. 188). However, the Tortonian *Cephalotropis coronatus* (E. Case, 1904), the Anversian *Mesocetus longirostris* (P. Beneden, 1886), and others similar to *Cetotherium* also inhabited other regions of the vast Miocene basin.

The genus *Cetotherium* was already established by Brandt in 1843 and described by him in the following fashion: “Sharp-pointed nasal part of the skull twice as long as brain case. /87/ Vertebral arches more or less thickened. Spinous processes of posterior dorsal, lumbar, and caudal vertebrae flattened. Lumbar and caudal vertebrae have very low, sometimes almost slit-like medullary canal. Sternum simple. Posterior ribs moderately broadened. Humerus shorter than forearm. Ulna has olecranon. Lumbar vertebrae shorter and wider than in *Pachyacanthus*.”⁴

As is evident from this diagnosis, the description of the genus *Cetotherium* was drawn up by the author mainly on the basis of features of the postcranial skeleton and the particulars of the skull were neglected, probably because of the inadequacy of the corresponding material. Because of this the genus *Cetotherium* was at first considered to be in the composition of the family Balaenopteridae. Only much later were the cetotheres separated into the special independent family Cetotheriidae (Cabrera, 1926).

The most detailed description of the cetotheriids (fam. Cetotheriidae) was given in 1931 by R. Kellogg. According to Kellogg the parietal bone in these animals lies wholly behind the level of the ends of the nasal bones and ascending processes of the maxillae and premaxillae. The occipital shield does not extend forward beyond the level of the orbit or of the anterior ends of the articular parts of the squamosal bones. The frontal bone is widely exposed in the interorbital space, the widened lateral (articular) part of the squamosal bone is relatively small and its lower surface is slightly concave. The supraorbital processes of the frontal bones are gradually tipped sideways and forward from the level of the dorsal surface of the interorbital region, the parietals meet or almost meet at the top of the brain case between the occipital shield and the frontal bones. The nasal bones are small and their whole dorsal surface is much less than half the supraorbital part of the frontal bones, the rostrum extends farther in

⁴ Brandt included three subgenera in the composition of the genus *Cetotherium*: *Eucetotherium*, *Plesiocetopsis*, and *Cetotheriophanes*.

width than in depth. The mandibles are thin and considerably convex to the sides (Kellogg, 1931, p. 305).

Judging from this description, inclusion of the suborders *Plesiocetopsis* and *Cetotheriophanes* in the composition not just of the genus *Cetotherium* but even of the family Cetotheriidae, as P. I. Spasskiy rightly remarks, /88/ does not seem fully justified (Spasskiy, 1954).

Plesiocetus and *Cetotheriopsis* are characterized by a strongly forward-thrust supraoccipital shield. Therefore the parietal bones in these animals do not meet, but remain at the sides of the skull. The supraorbital process of the frontal bones is strongly broadened in them. All this is evidence in favor of referring the whales in question rather to the balaenopterids (fam. Balaenopteridae).

The diagnosis of the genus *Cetotherium* given by Brandt was supplemented somewhat by P. I. Spasskiy on the basis of a study of an almost complete skeleton of a form resembling *Ct. mayeri* Brandt, from the Sarmatian formations of the vicinity of Derbent.

However, despite the sufficient abundance of material, the diagnosis in this case also was made without taking into account the particulars of the skull. We give the diagnosis of the genus *Cetotherium* according to Spasskiy (1954, p. 224):

"Skull not shorter than 1/4 the whole skeleton. Condyles of the mandibles consist of two rounded unequal parts separated by a small fossa. Coronoid process in the form of a small protuberance of the upper edge of the jaw. Cervical vertebrae shortened but free. First six ribs two-headed, others attached only to the transverse processes. First pair of ribs broad, flat, particularly in the distal part; middle ribs, beginning from the 7th from the top, thin, rounded, convex in middle on inner and outer sides, tapered on the ends. Scapula with slightly convex dorsal edge, well developed acromial and coracoid processes. Sternum simple. Humerus shorter than forearm. Ulna with acromion."

We do not think it appropriate to give a description here of the individual members of the genus in question, but it probably would be of interest to give at least a brief description of the osteological

features of members of *Cetotherium* and to try to compile a more complete and more accurate diagnosis of this genus on the basis of the latest data.

Members of the genus *Cetotherium* were animals of medium size. The length of their body evidently varied within 5-6 meters. The length of the skull comprised about 1/5 the length /89/ of the whole skeleton. The rostral part of the skull was considerably longer than the cranial (see Fig. 16). The brain case was strongly extended transversely, the fossae temporalia were relatively constricted, the supraorbital crests of the frontal bones were markedly curved. The nasal bones did not extend forward farther than the anterior edges of the supraorbital crests of the frontal bones. The zygomatic arches for the most part were directed forward and had an unusually elongated articular surface. The triangular supraoccipital bone, which formed the so-called supraoccipital shield, was wider than long; its lateral crests protruded less than in Middle Miocene forms. The apex of the triangle did not reach the level of the posterior edges of the orbits in them, sometimes barely reached the anterior edges of the articular surfaces for the lower jaws. The supraoccipital shield frequently bore a well expressed medial crest extending backward from the anterior angle of the shield; the mandibles were long and relatively fragile; with convex external and flattened internal surfaces. Traces of tooth compartments are often preserved.

The particulars which distinguish the cetotheres from other Miocene members of the cetotheriids are the presence of a sharply defined temporal crest, which according to Kellogg seems to presage the abrupt flattening of the basal part of the supraorbital processes of the frontal bones observed in the balaenopterids, and the meeting of the parietal bones, which form the interorbital region on the top of the skull. This presence of a relatively well expressed interorbital part composed of the parietal bones certainly indicates a relatively slight change in the skull construction of the cetotheres, which distinguishes them from other genera of the cetotheriids and in particular from the balaenopterids and the other modern toothless whales.

The cetotheres, in our opinion, are a typical Upper Miocene genus which, as has already been mentioned, mainly inhabited the Ponto-Caspian basin. Remains of its: representatives are found in great

numbers in the Middle and Upper Sarmatian formations of the belt once covered by Paratethys waters. The presence of cetotheres (genus *Cetotherium*) has been noted in Rumania, Moldavia, western Ukraine, the North Caucasus, Azerbaijan, and on the Mangyshlak.

90/ The sum total of a number of very typical features of the skeleton in the majority of forms investigated from this belt definitely indicates the independence of the genus *Cetotherium*. Some limitation of the area of distribution of members of this genus suggests that was formed in the Paratethys seas. Probably this may explain its extreme individualization among the cetotheriids in general and the Late Miocene forms in particular.

In this connection, some as yet sparse data on the Middle Miocene cetotheres living in the same belt of the Paratethys merit attention. We have in mind information on the genus *Imerocetus*, described from the Karagan of western Georgia (G. Mchedlidze, 1964, p. 58-68).

Of course it is difficult to speak with confidence on the genetic relationship of the Middle Miocene *Imerocetus* and the Upper Miocene *Cetotherium*, but forms similar to the Middle Miocene *Imerocetus* could quite easily have given rise to the genus *Cetotherium*.

As the Middle Miocene representatives of the cetotheriids have not been well studied, we believe it desirable to dwell more thoroughly on the description of the genus *Imerocetus*.

The cranial part of the skull of *Imerocetus*, in contrast to that part of the skull of the Upper Miocene cetotheres, is narrow and long, somewhat like that of the archaeocetes. The supraoccipital shield is triangular in shape but without a medial ridge and oval indentations. The surface of the shield is considerably slanted caudally, which probably indicates a relatively slight overriding of this bone on the facial part of the skull. The lateral crests, in contrast to the Upper Miocene cetotheres, are very high and flattened from the sides, taking on the aspect of wing-like blades. The exoccipital processes are short and slightly curved laterally. Near the posterior edge at the level of the posterolateral angles of the occipital shield, the skull is considerably constricted, which also distinguishes it from the Upper Miocene whales. This feature evidently indicates the slight transverse broadening of the braincase which

is typical of representatives of the early cetaceans. The anterior angle of the occipital shield in *Imerocetus* is sharp-pointed and extends only to the middle of the temporal fossae. The occipital condyles are slightly convex. Indeed they are little different in shape from those of the Upper Miocene cetotheres, but their unique arrangement clearly calls attention to itself. The lower half of these condyles is broad and so down-curved that it appears in part on the lower surface of the skull, constituting part of its base. This feature probably is also related to a slight forward shift of the occipital elements of the skull. The nasal bones, which in most Upper Miocene cetotheriids begin approximately at the level of the exit of the second pair of nerves of the encephalon, occupy a considerably more anterior position in this form (the distance between the base of the nasal bones and the exit of the abovementioned nerve is equal to the height from the upper edge of the occipital foramen to the top of the skull). The side wall of the brain case is high and elongated. It is formed by the parietal, squamosal, and pterygoid bones. Of these the parietal comprises the greatest part; it is elongated and extends to the level of the middle of the supraorbital process of the frontal bone. The parietal bones are wholly situated behind the nasal bones and converge along a line 45 mm long. The squamosal bone, is forced back toward the lower edge and is present in the form of a narrow band, due to strong widening of the parietal. The suture between these bones is parallel to the lateral crest of the shield, while in members of the cetotheriids so far known it is usually situated perpendicular to the lateral crest of the occipital shield and forms a bend in the lower part. The triangular pterygoid bone, which in the species described occupies a lateral position, is wedged between the parietal and squamosal bones near the back edge of the foramen for the second pair of nerves of the encephalon. The pterygoid and parietal bones bound the foramen of the above mentioned nerve on the posterior side. The distance between the anterior angle of the occipital shield and the base of the nasal bones is considerably lengthened; it is approximately equal to the height of the skull at the anterior angle of the occipital shield.

As is evident from this description, the elements of the posterior and posterolateral part of the skull (zygomatic process, exoccipital bones, and also the occipital condyles) in the Middle Miocene

representative of the cetotheriids are situated caudalo-ventrally, /92/ while in the Upper Miocene representatives they occupy a more or less dorsal position. These features of *Imerocetus* evidently are related to the slight overriding of the occipital elements on the facial part of the skull. Upon more intensive overriding of these elements, observed precisely in the Upper Miocene cetotheriids (genus *Cetotherium*), there evidently occurs a gradual shift of these bones upward and forward from below.

Consequently, the overriding of the occipital elements and interdigitation of the rostral in the Middle Miocene cetotheres of the Ponto-Caspian basin is at a considerably lower level than in the Upper Miocene cetotheres.

However, attention should be paid to the fact that the overriding the occipital elements is better expressed in the Upper Miocene members of the cetotheriids which lived outside of the territory of the occipital elements is better expressed; more accurately, the occipital elements in them are thrust forward considerably more than in their contemporaries living in the Ponto-Caspian basin.

Whereas in members of the genus *Cetotherium* the anterior angle of the occipital shield does not reach the posterior angles of the orbit, in members of such Upper Miocene (Upper Sarmatian) genera as *Idiocetus*, *Mesocetus* (see Fig. 19, 20), and others the top of the shield projects considerably farther forward, beyond the level of the posterior angles of the orbit. Thus a certain lag in the evolution of the occipital part of the skull is characteristic of the inhabitants of the Ponto-Caspian basin. On the other hand, interdigitation of the facial elements plays a large part in the reorganization of their skull construction, namely a pinching out of the inter-rostral elements of the skull as a result of which the anterior edges of the supraorbital processes of the frontal bones in the cetothere acquire an arcuate form (see Fig. 16). It can be thought that this acceleration of the rate of reorganization of the skull due to strong interdigitation slowed up the further evolution of the skull of the cetotheres to some extent.

It should be noted that whereas the representatives of the Upper Miocene genera of the cetotheriids differ considerably from the species of the aboriginal genus of the Ponto-Caspian, *Cetotherium*, the Middle Miocene inhabitants of that same basin show considerable /92/ resemblance to

the members of some genera living outside the basin in question. For example, the Middle Miocene imerocete apparently is in many respects to the Californian plesiocete from the Middle Miocene (Kellogg, 1936, p. 332).

As a result of strong interdigitation of the rostral elements there took place a considerable shift of the nasal opening toward the top of the skull, thus promoting the approach of the external nasal opening to the choanae and facilitation of breathing. An increase in the volume of the oral cavity was also related to the interdigitation of the rostral elements, in response to the unique method of feeding of these animals--straining a large amount of water for planktonic food.

We have the impression that over the stretch of time from the Oligocene to the beginning of the Upper Miocene, members of the cetotheriids both in the Mediterranean and in other basins were characterized by a number of fundamental features of skull structure in common. However, after the formation of the Paratethys toward the beginning of the Neogene, one branch of the cetotheriids which continued to live in the unusual setting of semi-closed basins must have proceeded along a special path of evolution leading to the origination of the subsequently widely distributed genus *Cetotherium*.

Evidently there was no corresponding anatomical basis for the strongly interdigitized rostral elements and lengthening of the rostral part in the cetothere skull: the cranial part was insufficiently developed (slight development of the occipital shield, probably related to insufficient strength of its skull construction).

In the cetotheriids living in other basins, and also in the balaenopterids and balenids, modification of the structure of the cranial part of the skull either preceded interdigitation or in any case both these processes went on in parallel, and consequently the groundwork for reorganization of the facial part of the skull was already laid in them. This sequence in the evolution of the skull evidently guaranteed the relatively long existence of some genera of the cetotheriids which lived in the open seas, and the domination of such cetaceans as the balaenopterids and balenids in the present marine fauna.

94/ Thus, a study of the genus *Cetotherium* first of all draws attention to the aforesaid singularity of the skull, which sharply differentiates this genus from the other genera of the family of cetotheriids.

Differences also exist between the Middle Miocene genera of the Ponto-Caspian basin and the Upper Miocene cetotheres in the structure of other parts of the skeleton, for example the limb bones. The limbs of the cetotheriid forms found by us in the Chokraksii formations of the North Caucasus are characterized by relatively very long and massive humeri. Such humeri are inherent in the Maragan and Kongs members of the cetotheriids from western Georgia (genus *Imerocetus*). However, in the Sarmatian cetotheres (genus *Cetotherium*) the humeri are already strongly shortened and in most cases narrowed in the middle of the diaphysis (see Mchedlidze, 1964, Plates XIII, XVI).

It is noteworthy that among the modern toothless cetaceans the gray whales (Eschrichtiidae), the most archaic in structure of the skull, pelvis, and mandibles and most conservative in way of life, have the longest humeri (Tomilin, A.G., 1957).

The shortening of the length of the humeri observed by us in the history of the cetotheriids evidently was related to the perfection of the steering apparatus as the manner of swimming became more complicated (Mchedlidze, 1964).

Gradual adaptation of the cetaceans to life in the aquatic environment and the concomitant changes in skeleton structure as a rule found their reflection in the evolution of their encephalon. Investigations of endocranial casts of the Middle and Upper Miocene cetotheriids studied by us, and also an analysis of the specialized literature (C. Dechaseaux, 1961; A. Breathnach, 1960) convince us of that.

There are very few data on the central nervous system of the Miocene cetotheriids in the literature. Only one badly damaged endocranial cast of any cetotheres has been described (Dechaseaux, 1961, p. 885). This lack is filled to some extent by the data of our investigations.

95/ The brain of the Karagan whale (see Plate V) was markedly elongated and had a triangular-oval shape. Its posterior part was relatively narrow and slightly broadened transversely. The hemispheres of the cerebrum were almost devoid of curvature in the region of the cerebellum. The frontal portions

were small, slightly convex and strongly constricted in an anterior direction. They passed relatively gradually into an elongated olfactory portion, represented on the endocranium in the form of a finger-like protuberance. contrary to the opinion of Edinger (T. Edinger, 1955), who considered that the anterior elongation of the *Cetotherium* brain mold studied by him was a cavity in the cast corresponding to the olfactory stalks twisted into a vascular plexus, we are convinced that this formation, like an analogous excrescence on our specimen (see Plate V), is the case of a cavity in the skull capsule which was wholly-occupied by the relatively well developed olfactory portions of the brain and the olfactory stalks issuing from them. Certain comparisons of the endocranial cast of *Imerocetus* with the brain of the modern balaenopterids leads us to that conclusion.

As for the brain of members of the Upper Sarmatian cetotheres of the Ponto-Caspian basin (genus *Cetotherium*), it should be noted that their brain was somewhat broadened transversely in the region of the temporal portion, whose width considerably exceeded the length (see Plate VI). The frontal portions, in contrast to the Middle Miocene *Imerocetus*, were markedly enlarged, broadened in the anterior part and relatively downcurved. Their convex surfaces were turned forward, and the longitudinal axes of these belts were situated parallel to one another, while in Middle Miocene forms (*Imerocetus*) these same surfaces were turned to the side and their axes converged anteriorly. The olfactory portions in the Sarmatian cetothere were greatly diminished and, as a result of the already beginning curvature of the hemispheres, were shifted considerably ventrally but still remained on the anterior edge of the brain.

We suggest that in the Miocene forms the frontal portions and the parts of the brain adjacent to them were not overlapped by substantial accessory formations which could have caused a difference between the anterior portions of the brain and the corresponding parts /96/ of the endocranial cast. In our opinion the presence of the impression of the central artery of the solid meninx on the endocranial cast should indicate that. This artery would not have left a trace on the internal wall of the skull if any

substantial accessory formations such as are usually situated between the solid meninx and the bony brain case had been present.

Comparing the particulars of the structure of the brain of the Middle Miocene and Upper Miocene cetotheres we come to the conclusion that the rates of phylogenetic changes in the cerebrum of the cetotheriids were relatively high in the epoch corresponding to the segment of time from the Karaga to the Middle Sarmatian inclusive. On the basis of the latest investigations of cetothere remains, particularly of its skull, we supplement and refine the diagnosis.

Family CETOTHERIIDAE Cabrera, 1929

Genus *Cetotherium* Brandt, 1842

Diagnosis: Medium-sized cetotheres. Skull comprises 1/4 of the total length of the animal. Supraorbital processes of the frontal bones considerably curved, almost arcuate; anteriorly they are slightly covered by the posterior sections of the maxillae. The elements of the facial part are strongly interdigitized. The posterior ends of the premaxilla and maxillary bones reach almost to the level of the posterior edges of the supraorbital processes. Supraoccipital shield slightly overriding: its anterior angle reaches the posterior edges of the supraorbital processes. Sometimes it is observed to advance still farther forward, but in such cases the parietal bones form the interorbital space between the shield and the terminations of the facial elements. Protemporal crest sharply defined. Zygomatic processes with elongated glenoidal surface, directed forward rather than to the side. Condyles of mandibles consist of two rounded unequal parts separated by a shallow notch. Coronoid processes small. First six ribs with head and tubercle. Humerus shorter than forearm. Ulna with well developed olecranon' hand four-fingered. Brain almost spherical, rhinencephalon strongly reduced.

ON THE TRENDS OF EVOLUTION OF THE SKULL OF THE TOOTHLESS CETACEANS

The first representatives of the cetotheriids are known from the Upper Oligocene formations of Austria (Vicinity of Linz), whence Meyer in 1849 and then Brandt in 1873 described the remains of *Cetotheriopsis lintianus* Brdt., characterized by a high and narrow, triangular supraoccipital bone directed forward. The elongated zygomatic process does not extend farther forward in this form than the level of the anterior angle of the supraoccipital shield. This finding merits particular attention, as it shows that flattening of the skull had already been completed toward the end of Oligocene time and thus the foundation was laid for further profound changes in skull construction. Data on the Oligocene cetaceans indicates that the overriding of the supraoccipital bone on the facial part of the skull was also well expressed in forms which had not yet lost the dentition.

Another member of this same genus *Cetotheriopsis*, *Ct. moreni* Lyd., was found in the Lower Miocene formations of Patagonia (R. Lydekker, 1894). At first it was referred to the genus *Cetotherium*, but on the basis of the absence in this animal of an anterior temporal crest, the presence of a flattened skull, and an occipital shield extending beyond the level of the posterior edges of the supraorbital processes, strongly widened maxillae and long nasal bones situated completely in front of the preorbital angles, it was later provisionally referred to *Cetotheriopsis* (R. Kellogg, 1928).

A relatively strong shift of the occipital elements and very slight interdigitation of the rostrals are characteristic of this form.

The Lower Miocene "*Plesiocetus*" *dyticus* Cab. (Cabrera, 1926) from Patagonia represents a still more advanced type of overriding of the occipital shield, but the mesorostral elements and long nasal bones in this form are slightly interdigitized with the cranial part of the skull (Kellogg, 1928). Evidently the overriding of the supraoccipital shield preceded interdigitation in this form also.

98/ On the basis of the character of the change in skull construction, the following three types can be distinguished among the members of the cetotheriids known at present: the first is characterized by a certain limited interdigitation of the rostral elements and more intensive overriding of the occipital elements (*Cetotheriopsis*, *Parietobalaena*, *Siphonocetus*) (see Fig. 19); in the second the occipital

elements are substantially overriding, almost to the same extent as in the first group, but the mesorostral elements are very well interdigitized (*Metopocetus*, *Mesocetus*, Fig. 20); and finally, a weaker /99/ overriding of the occipital shield and stronger interdigitation of the rostral part of the skull (see Fig. 16) than in groups I and II are characteristic of the third *Cetotherium*).

In the modern toothless cetaceans the skull structure has the following character in the general lines: occipital shield strongly overriding and so enlarged that the parietal bones are completely displaced from the composition of the dorsal surface of the skull. Joining of the facial part to the cranial is accomplished by moderate (in the balenids, see Fig. 21) or intensive (in the balaenopterids, see Fig. 22) interdigitation of the rostral elements and also by considerable expansion of the processes of the maxillae along the ventral surface of the skull. In contrast to the fossil forms, in these the rostral elements do not deflect the interorbital region upon interdigitation, but frequently overlap it (balaenopterids). Thus, whereas in the fossil representatives of the toothless cetaceans the anterior edge of the supraorbital processes of the frontal bones are situated at an angle to the median sagittal line of the skull or are arcuately convex (as in the cetothere), in modern whales in addition to interdigitation) the maxillae curve around the lateral parts of the skull as if for supplementary strengthening of the union with the cranial part and their supraorbital processes are slanted caudally.

Rather primitive and to some extent similar in skull structure to the fossil toothless whales are the gray whales, *Eschrichtius* (see Fig. 23). Their mesorostral elements /100/ are strongly interdigitized but the nasal bones are not shortened and the occipital shield does not extend to the posterior edge of the supraorbital processes. The suture between the maxilla and the supraorbital processes of the frontal bones is almost horizontal, as in some fossil forms.

From what has been said above it follows that in the phylogenetic history of the toothless cetaceans, two paths of evolution of the skull are noted: one possibly corresponds, perhaps, to V. O. Kovalev's adaptive type, and the other to the inadapative.

The first path: strong enlargement and overriding of the occipital elements either preceded interdigitation of the rostral elements, or these two processes went on almost simultaneously, but never the less with the overriding of the occipital bones somewhat predominant (balaenopterids, balenids, and also a number of fossil groups). This path led to the flourishing of the balaenopterids and balenids in the modern fauna and possibly to the long existence of *Cetotheriopsis*, *Parietobalaena*, and *Plesiocetopsis* compared to the cetotheres (adaptive evolution).

The second path, which the cetotheres and modern gray whales followed: strong interdigitation of the rostral elements went on with slight overriding of the occipital elements (inadaptive evolution).

According to presently available data, members of the genus *Cetotherium*, which underwent inadptive evolution, did not survive the end of the Miocene (they disappeared from the geologic record at the very end of the Sarmatian stage).

101/ Indeed, there are indications of the occurrence of members of the genus *Cetotherium* in the Pliocene of the Ponto-Caspian, but in the opinion of V. V. Bogachev (1939) these fossil remains of toothless cetaceans here always occur in secondary emplacement--probably redeposited from the Sarmatian.

However, as our review has shown, some forms have also lived to our times which, judging from their skull structure, evolved like the cetotheres by the inadptive route (the gray whales). Their survival, in our opinion, is explained by, adaptation to benthonic food and their being tied to the shallow-water parts of seas where they were not subjected to competition from the other cetaceans.

As has already been mentioned (see p. 93); the formation of the genus *Cetotherium* was related to the formation of special hydrological and bionomic conditions in the Ponto-Caspian basin toward the end of the Miocene. /102/ Members of this genus, living in a semi-closed basin, evidently evolved considerably faster than the other cetotheriids distributed in the open seas. However, as has been explained, in the course of this accelerated evolution of the cetothere skull, the overriding of the occipital elements lagged greatly behind the interdigitation of the rostral elements, which evidently

created some disharmony of structure—a disparity in the evolution of the cranial and facial parts of the skull.

Almost all the toothless whales living to our times and dominating the present marine fauna (except the gray whales) evolved by a different route: in them the overriding of the occipital elements preceded interdigitation.

Strong development and overriding of the supraoccipital bone evidently strengthened the cranial part proper of the skull and at the same time balanced the construction of the skull, which was characterized by a long and relatively heavy rostral part. In addition it provided intensive development of the musculature which connected the skull to the body and took part in the motion and support of the head. Finally, in connection, with the relative caudal displacement of the basal elements of the skull, it allowed the possibility for enlargement of the oral cavity not only in an oral but also in an aboral direction.

What advantages could such skull structure give to the forms which we consider to be adaptive, over those in which some lag in the overriding of the occipital shield is observed?

In order to answer this question, we must turn to some indications on the skeleton structure and particulars of the biology of the modern representatives of the toothless cetaceans.

In the modern balenids, as is known, the cervical vertebrae almost always are fused into a single block. The vertebrae are united not only by their bodies but also by their spinous and lateral processes (their cervical vertebrae are free only at an extremely early stage of development). Here it should be mentioned that the balenids feed exclusively on planktonic food (crustaceans), and fish are never found in their ration; not only their /103/ inability to swim fast but also the spoon-shaped structure of the opened-in front mandible are related to this.

The balaenopterids feed on both plankton and fish. In feeding, these animals move sideways with open mouth, and some of their members even turn almost belly-up on the axis of the body CA. G.

Tomilin, 1957). On the one hand such a jerk does not let fish escape, and on the other it accelerates closing of the mouth. Their cervical vertebrae are separate (in rare cases the first 2-3 are fused).

In the gray whales the cervical vertebrae are separate. As a whole the cervical section of the spine is longer than in the others, comprising 2% of the total length of the body. The cervical vertebrae are separate even in very old individuals. They feed on bottom [-dwelling] amphipods. And the uniquely constructed mandibles (coronoid processes are lacking and the mandibular rami are massive), moreover, afford the possibility of plowing the soft bottom (Tomilin, 1957, p. 354).

As for the fossil toothless whales, the cetotheres, their cervical vertebrae likewise are not conerescent. However, their mandible is not massive; the condyles of the mandible are separated, the upper part is rounded and wide, the lower part is twice as narrow as the upper (there is a small fossa between them). The coronoid process in the cetotheres is low but long, in the form of a convex rounded protuberance of the upper surface of the jaw. Some atrophy of the condyloid and coronoid processes and their roundedness evidently are related to the adaptation to feeding on small animals and the corresponding weakening of the chewing musculature.

Thus, in the forms of the Balaenidae, which have a large head (the length of the skull in the balenids is 1/3 the total length of the animal) and maximally enlarged oral cavity, the occipital bone is strongly enlarged and thrust considerably forward, and the cervical vertebrae form one bone. In the balaenopterids (Balaenopteridae), which are characterized by a substantially enlarged oral cavity and a large head, though smaller than in the balenids (the length of the head is 1/4, or a bit less, than the length of the animal), the occipital bone is strongly developed and overrides the facial part; the cervical vertebrae also are mainly free, but sometimes there already is observed /104/ fusion of the first two or three vertebrae. In the forms of the Eschrichtiidae, which are characterized by less enlarged oral cavity (rostrum slightly convex but oral cavity very narrow) and relatively short head (1/5 the length of the animal; A. G. Tomilin, 1957, p. 333), the occipital bone is relatively slightly developed and the cervical vertebrae are always free, even in old individuals.

The first of the animals examined above feed exclusively on planktonic food (crustaceans) and their method of feeding is passive. The second feed both on planktonic crustaceans and on fish, sometimes making fishlike movements. Their feeding bears a somewhat active character. Finally, the third feed on benthonic organisms, scooping up a muddy mass in shallow waters with their massive and keel-like (underneath) mandibles. Frequently they also feed on algae (A. G. Tomilin, 1957, p. 147). This undoubtedly is an actively feeding form. The actively feeding gray whales, as is known, are the most archaic of all the modern toothless whales in skeleton structure (skull, limbs, and pelvis), on the basis of which they are sometimes compared with the fossil genus *Plesiocetus* (Tomilin, 1957, p. 343).

Consequently, in the course of evolution of the toothless cetaceans the size of the head increased relative to the total length of the animal with the need to improve the possibilities for feeding, and the oral cavity increased correspondingly in response to the nature of their feeding (straining a vast amount of water for planktonic food). This certainly required strengthening of the union of the skull with the postcranial skeleton. In connection with this the occipital shield became much larger and was thrust forward, creating a large surface for the musculature connecting the skull to the body and also balancing the construction of the skull itself, with its much enlarged and elongated rostrum. Thus the possibility developed for two-way (oral-aboral) enlargement of the oral cavity. For greater strengthening of the union of the head with the body, the cervical section of the spine fused into a single block at a certain high level of evolution, creating a strong base of attachment for the connecting muscles. Evidently the evolution /105/ of the skull of the toothless cetaceans proceeded via an adaptation to feeding on planktonic organisms, which were the most calorific, most plentiful, and moreover most easily obtained food in a marine setting. From this it follows that the features of skull structure (enlargement of the occipital shield and correlative enlargement of the volume of the oral cavity) which facilitated feeding gave the forms which evolved in an adaptive way a considerable advantage over those representatives which followed the inadapative route.

The cetotheriids (and possibly other toothless cetaceans too), already evolved since Oligocene time and probably localized mainly in the belt of distribution of Tethys waters, underwent a vigorous flowering and widespread ecological expansion from the beginning of the Neogene. In the Miocene they already inhabited vast aquatic ranges along the shores of New Zealand, North America, and also South America and very different regions of the Paratethys, which was forming at that time. A rapid decline of the group apparently began toward the end of the Miocene, and in the Lower Pliocene, according to presently available data (G. Simpson, 1945), members of only two genera of this genus-rich family survived. The remains of cetotheriids have not been found in formations younger than the Lower Pliocene.

In our view, the cause of the extinction of the cetotheriids as a whole should be sought in competition from representatives of the true toothless cetaceans, which already were intensively developed at the end of the Miocene. Certainly the inadapative evolution of their skull must also have been an important condition of the disappearance of the cetotheres.

FIGURE CAPTIONS

[Figures are not reproduced here. Figure captions were extracted from the original translation and compiled here. Please see the original for images.]

Fig. 1. *Mauicetus lophocephalus* Marples. Schematic drawing of the skull (after Kellogg)

Fig. 2. *Basilosaurus cetoides* (Owen). Skull from above (after Kellogg).

Fig. 3. *Prozeuglodon isis* (Andrews). Skull from above (after Stromer).

Fig. 4. *Basilosaurus cetoides* (Owen). Skull from the side (after Kellogg).

Fig. 5. *Basilosaurus cetoides* (Owen). Mandible (after Kellogg).

Fig. 6. *Basilosaurus cetoides* (Owen). Second cervical vertebra (after Kellogg).

Fig. 7. *Basilosaurus cetoides* (Owen). Skeleton of fore limb (after Kellogg).

Fig. 8. *Zygorhiza kochii* (Reichenbach). Skull possible to assume the existence of from above (after Kellogg).

Fig. 9. *Zygorhiza kochii* (Reichenbach). Skull with mandible (after Kellogg).

Fig. 10 *Patriocetus ehrlichi* Van Beneden. Skull from above (after Abel).

Fig. 11 (left). *Squalodon calvertensis* Kellogg. Skull (after Kellogg)

Fig. 12 (right). Modern dolphin, *Delphinus sinensis* Osbeck. Skull (after Flower).

Fig. 13 (left). *Balaenoptera borealis* L. Skull (after Kellogg).

Fig. 14 (center). *Balaena mysticetus* L. Part of skull (after Kellogg).

Fig. 15 (right). *Eschrichtius gibbosus* Erchl. Skull (after Andrews).

Fig. 16. *Cetotherium rathkii* Brandt. Skull (after Brandt).

Fig. 17. *Dorudon serratus* Gibbes. Skull (after Kellogg).

Fig. 18. *Mirocetus riabinini* Mchedlidze. Schematic drawing of the skull.

Fig. 19. Schematic drawing of the skull of cetotheres of type I: a. *Cetotheriopsis* b. *Siphonocetus* c. *Parietobalaena*.

Fig. 20. Schematic drawing of skulls of cetotheres of type II: a. *Metopocetus* b. *Mesocetus*.

Fig. 21 (left). *Balaena*. Schematic drawing of the skull.

Fig. 22 (center). *Balaenoptera*. Schematic drawing of the skull.

Fig. 23 (right). *Eschrichtius*. Schematic drawing of the skull.

PLATE I.

Ferecetotherium kelloggi Mchedlidze

1. Skeleton of the left fore limb. 1/4 nat. size.
2. Lateral bodies of the first cervical vertebra. 1/4 nat. size.
3. Second cervical vertebra. 1/4 nat. size.
4. Fragment of thoracic bone. 1/4 nat. size.

5. Humerus of the Sarmatian whale *Cetotherium maicopicum* Spass.

PLATE II

Ferecetotherium kelloggi Mchedlidze.

Left ramus of mandible. 1/4 nat. size.

Fragment of right ramus of mandible. 1/4 nat. size.

Fragment of maxilla. 1/4 nat. size.

PLATE III

Ferecetotherium kelloggi Mchedlidze.

1. Fragment of maxilla with nasal bones. 1/4 nat. size. 2, 3. Fragments of supraorbital crests of frontal bones. 1/4 nat. size.

4. Fragment of supraoccipital shield. 1/4 nat. size.

5, 6. Fragments of posterolateral parts of the skull. 1/4 nat. size. 7, 8. Perioticum* 1/2 nat. size.

*Labeled "Bullae tympanicum" in the publication; corrected on the errata slip inserted into the book. --

Translator.

PLATE IV

Ferecetotherium kelloggi Mchedlidze. Isolated teeth of mandible. 1/3 nat. size.

PLATE V.

Endocranial cast of the Middle Miocene whale *Imerocetus karaganicus* Mch.

Endocranial cast of the olfactory part of the Middle Miocene whale *Imerocetus* sp.

PLATE VI.

Endocranial cast of the Upper Miocene whale *Ct. maicopicum* Spass.

Endocranial cast of the Upper Miocene whale *Ct. mayeri* Brdt. I

BIBLIOGRAPHY

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