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A REVIEW OF THE HISTORICAL DEVELOPMENT OF THE CETACEA

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ABSTRACT

A mysticeti sign of skull structure of the Eocene Archaeoceti has been found (supraoccipital bone extended and pulled forward). This sign is even more pronounced in the Late Paleogenic Archaeoceti (*Mirocetus*, *Aetiocetus*, *Ferecetotherium*). Gradual transition of archaeocetic characters to ones of Mysticeti can be followed in the evolution of forelimbs and dentition. It seems that Archaeoceti are phylogenetically related with Mysticeti. Analysis of the distinctions of two main evolution branches of the Cetacea shows, that their ancestor forms were already different from each other by feeding habits and hence by the mode of living.

The Cetacea inception from the archaic terrestrial mammals is doubtless, however the group of old mammals which should be considered as their ancestors hasn't been established yet. Wide distribution of Archaeoceti in the Early Eocene (Tarlo L. 1964, Andrews C. 1920, Gubkin N. 1950) and a highly developed adaptations to aquatic life of these early forms points to their old origin. Transition to the water environment of terrestrial ancestors of the Cetaceans probably has taken place in the Late Cretaceous period.

As it is known among the Therians Pantotheres is the most similar to the main group of animals that gave rise to new forms of the mammals. Cheek teeth structure of these early mammals seems to represent a basis for teeth development of the Marsupialia and real Placentalia. The analysis of the more archaic Cetaceans dentition provides no reasons for considering them close to Pantotheria. The early Archaeoceti (Protocetidae) possess all the basic elements of the upper cheek teeth typical for the Placentalia (protocon, metacon, paracon, which is advanced as the main cusp and parastil), though these elements are reduced, while paracon and metacon of the same teeth of Pantotheres are not divided yet and form an indivisible amficon. Protocetidae have an already reduced post-Pantotheres cheek teeth structure. According to the data of the mammals dentition development history, the teeth structure complication (appearance of the new elements) characteristic of Placentalia doesn't occur in the water environment, while on the contrary this structure is simplified. This gives a reason to suppose that the ancestral forms of Archaeoceti should have all the elements, i.e. protocon, a divided amficon and paracon, which their descendantans-Protocetidae possess in reduced form. The amficon division to meta- and paracon is characteristic of the old Insectivores (Late Cretaceous). Though the inception of Archaeoceti, possessing the highly developed lambdoidal and sagittal crests of skull from the Insectivores characterized by poor development or absence of these features is doubtful, since it is difficult to suppose that the aquatic forms may have structures, promoting reinforcement of muscles related with cutting and chewing, i.e. processes loosing their sense in water medium.

A number of features of the skull, teeth and second neck vertebrae connects Archaeoceti with Creodonta. But this similarity is convergentical (Antony R. 1926, Kellogg R. 1936, Simpson G. 1945). It is necessary to add that at the individualization of Creodonta Archaeoceti represented probably a group of animals well enough adapted to aquatic life.

According to the Van Valen's suggestion (Van Valen, 1966) the Archaeoceti ancestors could be only the representatives of Hyaenodontidae and Mesonychidae. He thinks that the Mesonychidae have more similarity with Archaeoceti. According to this author the separation of the Cetacea from the Mesonychidae should take place in the Middle or Upper Paleocene. Some typical features of the Mesonychidae dentition makes doubtful their immediate relation with Archaeoceti. The biggest tooth in the Archaeoceti dentition is P^3, evidently corresponding to the carnivorous tooth of the terrestrial mammals (Kellogg R. 1936). The carnivorous tooth doesn't develop in Mesonychidae and their P^3 doesn't differ from the other teeth. It is to be noted that the Mesonychidae

possess a praeglenoid process which is absent in Archaeoceti. It is natural to assume that Archaeoceti, subjected while their evolution only to the reduction of predaceous features inherited absence of the praeglenoid process immediately from the ancestral forms and didn't acquire it while their adaptation to aquatic life. Further, Mesonychidae might appear only in the Middle Paleocene and reached the acme in the Early and Middle Eocene ; and Archaeoceti are already so well adapted to the sea environment, that they are able of a considerable ecogenetical expansion. The time interval from the Middle Paleocene to the Late Eocene is too small for such a deep change in the structure of terrestrial mammals as the Archaeoceti experienced. It is difficult to suppose such a high rate of changes for the earliest stages of Cetacea evolution, especially as according to the data of the history of the groups of other marine mammals only period of amphibious mode of life in the ecogenesis of the Cetaceans ancestors was longer than all the Paleocene. That's why we consider, that the Archaeoceti though being connected with insectivore-carnivore stock of mammals, don't come from this stock, but from some oldest general trunk, which gave life both to the Insectivores and Condilarthra and to the Cetacea ancestors.

At the early stage of the history the Cetacea ancestors might inhabit the fresh water basins. The following stage of their development was already connected with coastal and shallow parts of the sea and only after they acquired a number of considerable adaptation to the open sea life, the Cetacea entered the ocean space. An example of such an ecogenesis provides the history of Delphinidae (Mchedlidze, 1964) ; some characters of life of modern Gray Whales can be used to prove this hypothesis.

In the Early and Middle Eocene period the area of distribution of Archaeoceti might be limited mainly by Thetis basin and by the Northern Indian Ocean connected with it. In the Late Eocene prochoresis rates of these animals considerably increased. Towards the end of the Eocene Archaeocetes already were widespread in adjacent Atlantic waters. At the beginning of Oligocene their distribution area was reduced to the Thetis limits. The latest representatives of these animals are mainly known from the South and North East regions of this basin (Kellogg R. 1936, Lydekker R. 1892, Mchedlidze G. 1970, Rjabinin A. 1938, Fedorovski, 1911).

The Late Paleogene group of Archaeoceti is represented by the relatively nannoid and in the certain measure aberrant forms. It is interesting that most of them are characterized by combination of the Archaeoceti and the Mysticeti characters. For example structure and situation of the maxillaries, their correlation with the supraorbital process of frontals, situation of the nasal passage, number of cheek teeth; general features of the forelimbs of *Mirocetus rjabinini* (Mchedlidze G. 1970) is certainly similar to the Archaeoceti, from which it at the same time differs by the basic characters of the skull. The known representatives of archeocetes don't have preorbital notches which are well expressed in *Mirocetus* like in Balaenopteridae. Temporal region of the skull of Protocetidae, Dorudontidae and Basilosauridae is considerably narrowed and elongated, while the *Mirocetus* have it wide and short. The differentiated teeth system and teeth structure of *Mirocetus* is similar to Archaeoceti. Situation of main elements of the skull and structure of its basal part also points to its similarity with Archaeoceti. *Mirocetus* differ from Archaeoceti by supraoccipital shield which has a triangular form, is slipped forward and provided with high crests, short and widened temporal bones, shortened temporal fossas, massive zygomatic processes and by a certain slope of the lateral walls of the brain case.

It is evident that the skull of *Mirocetus* differs from the skull of other Archaeoceti by the particular features which characterize Mysticeti. The scapula of *Mirocetus* which by its general outlines seems similar to the same bone of Archaeoceti however differs from latter by the Mysticetian features appearance (rudimentar crest, displaced to the cranial end of the bone and short pr. acromion).

The main characters of dentition of *Aetiocetus* (Emlong D. 1966) from the Upper Oligocene of the USA are of great importance for the understanding of Cetaceans phylogenetic history. M^1 of *Aetiocetus* differs from the same tooth of typical Archaeoceti (Protocetidae, Dorudontidae, Basilosaurida) by the structure of the root and the crown. M^1 of *Aetiocetus* is already one-rooted, the limits between the accessory cusps of crown are relatively effaced and the crown becomes conical. Considerable development of nasal bones, front situation of nasal passage, absence of preorbital notches, presence of parietal bones with well expressed cres at the vertex point to their resemblance with Archaeoceti. At the same time wide and massive supraorbital processes of frontals, shortened temporal fossas and especially occipital shield prove the resemblance of this form with Mysticeti. The general tendency of the dentition development, i.e. tendency to the homodontization of a system as a whole also points to this resemblance.

Among the Late Oligocene Archaeoceti *Fereceto-therium kelloggi* (Mchedlidze, 1970) from the Caucasus is the most evolved toward Mysticeti type. It is a whale of an average size (not exceeding 6-7 m in length) with low skull and short, transversally elongated cranial part. The zigomatic process of squamosal is short and widened, the supraoccipital is sloped forward and has nearly triangular form. The mandible (plate I) has horizontal low edge and gradually rising upper edge. The teeth number in one rampus of the mandible is increased to

30. All teeth are conical with small crown and one root. (plate II). The teeth can be considered as heterodont only according to their sizes (middle teeth are bigger than others). The teeth roots slight part is plunged into the jaw. This bone of *Ferecetotherium* is similar to that of Archaeoceti by a number of features : horizontal low edge, gradual rise of upper edge, presence of teeth at the ascending ramus and the general outlines, but it differs from the typical Archaeocetes jaw by the simplification of structure –the tendency to the low and upper edges parallel situation, the condyle of mandible shift to the jaw upper angle, homodontization, the crown strong reduction and the root slight plunging into the jaw. The knowledge of the structure pecularities of these representatives leads to the conclusion that the number of distinctive characters of the skeleton of these forms points to a considerable rearrangement of the skeleton morphology, directed toward the Mysticeti.

MYSTICETI

In the Mysticeti phylogenetic history two ways of skull evolution are marked—one probably corresponds to the adaptive type by V. O. Kovalevsky, another to the inadaptive. The forms following the first way had a strong growth and a forward overthrust occipital elements of the skull preceeding the rostral elements interdigitation or these two processes took place simultaneously, but still with some occipital bone movement predominated (Balaenidae, Balaenopteridae and such fossils as *Cetotheriopsis*, *Parietobalaena*, *Siphonocetus*). The second line, which followed Cetotherium and modern Gray Whale was characterized by the strong interdigitation of rostral elements and slight forward movement of occipital elements. What advantages could provide such a strong development of the occipital region to forms which we consider as adaptive in comparison with those, which had some lag in the occipital shield forward movement ? To answer this question we shall have to recourse to the modern Mysticeti. It is obvious that the Balaenidae having the biggest head (the skull length makes I/3 of the animals general length) and maximally increased mouth, have the occipital bone considerably developed and strongly moved forward, as to the neck vertebrae they are joint together and form one bone. The Balaenopteriidae, characterized by a considerably increased mouth and by a big, though in some measure smaller head, than the Balaenidae (the head length makes I/4 or slightly less of animals general length), have the occipital bone strongly developed and moved to the facial region ; as to the neck vertebrae they are mostly movable, but sometimes the two or three of them are joint. The Eshrichtiidae, characterized by a slightly increased mouth (the rostrum is hardly prominent and the mouth is very narrow) and by a relatively short head (I/5 part of the animals general length), have the less developed occipital bone and the neck vertebrae always even in the old forms are movable. The first animals under consideration feed exclusively by plankton food and they feed passively. The second feed by planktonic Crustacea as well as by fish, somtimes making for that jerklike movements. Their feeding has in certain measure active character. At last, the third feed by the bentonic organisms and for this they scoop by their massive jaws the slit mass from the shoal. They feed also by algae (Tomilin A. 1965). They are certainly the actively feeding forms. The Gray Whales are the most archaic among all the modern Mysticeti and that gives reason to compare them to the Plesiocetus. We suppose that in the process of the phylogenetical development of Mysticeti the increasing of the head size and correspondingly of the mouth size correlates with feeding mode (the great quantity of water with plankton food is filtered). It undoubtedly demanded strengthening of the skull bond with skeleton. On this connection the occipital shield increased, moved forward, forming vast surface to the musculature, which bonded the skull with the thorax and balanced the construction of the skull having a great increased rostrum and provided a relative deplacement caudally basal elements of the skull. So was developing the possibility of doublesided (oral-aboral) mouth growth. To the further strengthening of skull-thorax bone at the high evolution stage the neck vertebrae became concrescent to the indivizable bloc, forming a solid base for the bonding muscles insertion. Evolution of Mysticeti skull followed the way of adaptation to plankton feeding, which possessed the greatest quantity of calories and was easy to get it. Therefore we can suppose, that characters of the skull (increasing of the occipital shield and correlatively connected with it increasing of mouth volume), providing the feeding improve gave to forms developing by adaptive way advantages in comparison with those, which followed inadaptive way.

ODONTOCETI

Knowledge on fossil Cetacea from the Oligocene of the Caucasus accumulated during last years permits to bring the beginning of Delphinidae history to a much older epoch than it has been assumed till now. Study of osteologic characters of the Late Paleogene dolphins, *Oligodelphis* (plate IV, V, VI) has shown that according to the telescoping and to the development of the skull main adaptive abilities the Oligocene dolphins stand high in evolutionary level. Probably the Delphinidae type of skull was formed already in the Late Oligocene.

In the phylogenetic history of Odontoceti the maxillaries caudal movement began early. This earliest stages are observed in the Eocene forms (Agorophiidae). The maxillaries of these animals partly cover the frontals.

Maxillaries of the Oligocene Odontoceti, for example *Patriocetus* (Abel 0. 1913), are more advanced caudally, but they still cover slightly the temporal fossas. The maxillaries of the Upper Oligocene *Eosqualodon* (Rothausen K. 1968) are moved more backwards to the frontal bones, they even contact with the supraoccipital bone. The contact line between supraoccipital and maxillaries in the skull of Miocene *Squalodon* makes longer ; the maxillaries cover more the temporal fossas. This causes a gradual decrease of the frontal bones area on the dorsal surface of the skull and the frontals are preserved as small bones only in the central region of vertex. The further changes of skull characteristic of the general line of the development of Odontoceti are not known in the history of Squalodontidae.

Among the Acrodelphidae a number of forms are distinguishable reflecting separate stages of telescoping, but they still don't give any idea about the relatively late stages of changes of the Odontoceti skull. The relatively late changes in the Delphinidae skull which should occur in the Pliocene were connected with the motor apparatus improvement, with the formation of ability to dive to great depths and with the considerable increase of the brain case.

Fossil Delphinidae as well as the mostly evolved Squalodontidae have the maxillaries always closely adjoined with the supraoccipital crest and their frontals are naked only in the central part of the vertex, and together with the nasal bones they form angular square with horizontal dorsal surface. As to the modern Delphinidae their frontal bones always participate in the vertex structure, forming a line between the supraoccipital and maxillar bones. This line is characteristic not only of young but of the adult forms. Only in rare cases some highly specialised forms (*Orcinus*, *Monodon*) have the maxillaries expanded maximally over the frontals completely covering them.

There is every reason to suppose that the intensive increase of the frontal lobes of the hemispheres in modern Delphinidae, which is connected with development of the motor system, was followed by the expansion of the frontal parts of the brain case, which became more and more protuberant frontally. This caused gradual increase of skull height in its frontal region and flexuring of the maxillaries. Simultaneously occurred the thinning of brain case bones. As a result of considerable increase of the brain case volume and "extension of walls" the frontals reappeared as a line on the skull dorsal surface. The fact that the moder dolphins have on the vertex a relatively wide line of frontal bones should be considered as a secondary feature, which is conditioned by progressive development of the brain.

At the early stages of the adaptation to aquatic life, facial region of the skull of ancestral forms was considerably elongated. Further the changes occurred mainly in the skull cranial region. The temporal bones were gradually excluded from the dorsal surface and took a lateral position. As a result of this occurred the contact between the frontals and supraoccipital bone (first stage of telescoping). Simultaneously the maxillaries overlapping the frontal bones. Caudal movement of the maxillaries ended by their contact with the supraoccipital crest (second stage of telescoping), the frontals became nearly all covered and remained only as a small bones beyond the nasals. Further because of the progressive development of the brain case the frontal bones reappeared at the vertex as the lines. For strengthening the contact between facial and cranial regions transversal expansion of the frontals and maxillaries has taken place and these bones covered the temporal fossas. The maxillaries of highly specialized forms are advanced more backwards and connected again with the supraoccipital crest.

In the Oligocene forms (*Oligodelphis*) dentition is homodont. Certain differentiation, is preserved only in the root structure, and even not all the representatives of this group have them. The Miocene forms in more cases have their teeth quite similar in the roots as well as in the crowns structure (*Kentriodon*, *Imerodelphis*).

The Oligocene forms retained some archaic features which consist in the keellike cutting edge ; while teeth of dolphins from the Miocene deposits have the cutting edges sleek and the crowns mostly circular in sections. The different case is observed among the Acrodelphidae. The Oligocene and Miocene representatives of this family have a heterodont system. It is possible that in the historical development of Odontoceti at the beginning the teeth number increase should take place, at this stage the dentition became polydont, but it preserved the ancestral heterodont character. This stage of evolution of the Odontoceti dentition correlates with the Squalodontidae and Acrodelphidae dental systems, while the Delphinidae preserved this archaic feature only in the roots of the Oligocene forms. There is no doubt that the last Pliocene Acrodelphidae, though they show a tendency to teeth reduction (the ability sign of the latest stages of Odontoceti evolution) are the more archaic (according to the structure of a single teeth and to the system as a whole) than the Upper Oligocene Delphinidae. This fact should once more point to the relatively early separation of the Delphinidae from the main Odontoceti development trunk.

The shortening of the humerus, which is connected with the gradual improvement of the steering function of the forelimb, the shortening of the vertebrae and the development of skull asymmetry had a great importance in the phylogenetic history of Delphinidae and they certainly contributed to the increase of swimming speed. The phylogenetic changes of these osteologic characters so as the general changes of mode of life had an influence

on the phylogenetic changes of the brain (Mchedlidze G. 1964, 1970). The locomotion apparatus improvement and complication in Delphinidae occurred simultaneously with the successive increase of brain size and it's phylogenetical complication. We think that the high level of development of modern dolphin's brain is interrelated not only with maximal development of the ears, but also with their permanent motoric activity.

The Squalodontidae were also widely spread in the Upper Oligocene and Early Miocene times. Among the Oligocene Squalodontidae particular attentions hould be paid to the *Sulakocetus dagestanicus* (Plate V) and *Kelloggia barbarus* (Plate VIII, IX), found in the Upper Oligocene of Caucasus. The first is a small squalodon, characterised by quite a number of archaic features (the maxillaries contact with the supraoccipital bone in a very small region, maxillaries hardly widened transversally and cover the temporal fossas ; intermaxillaries have blunt caudal edges, which reach only the level of the nasals front edge, nasals are relatively big, the supraoccipital bone is nearly plane. The second form has wide, long and massive rostrum, strong molars, which are equal to premolars, the strong and short forelimbs and a special bone-shield formed by sternum, ribs and intercostal plates.

As to the *Patriocetus* which is believed by Rothausen (1968)to Squalodontidae we consider that the low level of maxillaries expansion (the maxillaries don't cover the temporal fossas and are separated from the supraoccipital bone by the temporals) may prove *Patriocetus* affinity with Agorophiidae. Similar forms as *Patriocetus* according to the structure of the cheek teeth (the crowns arer educed, the roots are advanced over the jaw edge) already weren't able to contribute to origin of Squalodontidae which has massive crowns and deeply plunged roots. Probably such an archaic form of Odontoceti as *Patriocetus*, presented a considerable deviation from the Squalodontidae branch of originally specialized Odontoceti. According to degree of skull telescoping Squalodontidae is at a high level of evolution. All representatives of this family have the frontal bones covered by maxillaries and connected with supraoccipital. In the Squalodontidae evolution we can note three successive stages of development of the supraoccipital and maxillary bones connection. The very primitive stage is represented in *Sulakocetus*, the more developed—in Eosqualodon, and the most developed in Squalodon.

Among the Squalodontidae there are forms, which differ both by the maxillaries and mandibles teeth number, and by the teeth general number. Squalodontidae is characterized by the common tendency of the teeth number increase (*Prosqualodon, Phoberodon, Squalodon, Neosqualodon*).

The teeth of Squalodontidae are arranged on the jaws with wide diastemas (they are closed only in the incisive region) and cheek teeth preserve a laterally compressed crown, able to fulfill the cutting. However the appearance of polydonty (the teeth number is always more than 44) already points to the predominance of catching and barrier function over the actively digestive function.

The polydonty isn't ancestral but it represents a character acquired by the different branches of Odontoceti at different stages of their phylogenetic history. The Eocene Odonticeti (Agorophiidae) didn't possess this quality of dentition. They have a heterodont apparatus consisting of the teeth number similar to primitive Eutheria. The Evolution of the Squalodontidae dentition seemed to stop at the polydont-heterodont stage, while the other groups (Delphinidae, Acrodelphidae, Ziphiidae, Physeteridae) acquired during the evolution the polydont-homodont apparatus which by the majority of groups at latest stages of their history had considerably reduced.

The history of Whales shows that the development of homodont-polydont apparatus of Odontoceti, as well as of the ancestral forms of Mysticeti, was preceded by the polydont-heterodont system of dentition, which in its main features may be similar with the Squalodontidae one.

ON PHYLOGENETIC RELATIONS OF CETACEA

The question of phylogenetic connections of Archaeoceti with living whales causes a disagreement between the researchers. Some of them (Abel O. 1913, Spasski P. 1954, Pomer A. 1966) consider such a connection with Mysticeti as quite possible. Others (Van Valen L. 1966, 1968) think that Archaeoceti have affinity as with Mysticeti so with Odontoceti. And finally, a number of authors (Kellogg R, 1928, 1936, Iablokov, A. 1964) consider Archaeoceti as a quite isolated group which has nothing in common with the typical Cetacea. R. Kellogg points out that morphologically the archaeocetes seem to stand relatively near to the typical Mysticeti and Odontoceti but it is more probable that the archaeocetes are collateral derivatives of the same stock from which Mysticeti and Odontoceti sprang.

On the other hand after the comparison of *Cetotherium* from Derbent environs with the *Microzeuglodon* aff. *caucasicum* lyd. Spasski made the conclusion, that these forms have very much in common. The author considers that the origin of Gen. *Cetotherium* from "*Microzeuglodon*" (*Mirocetus*) is quite possible (Spasski, 1954, pg. 224). As it is known, O. Abel considered Patriocetus as a connecting line between the old Cetacea and Mysticeti. R. Kellogg and D. Miller were against this opinion. And K. Rothausen (1969) proved that the correlation with Mysticeti was erroneous. In connection with the Archaeoceti and Mysticeti phylo-

genetic affinity, special attention should be paid to some considerable changes of the skull which are observed in the early Cetaceans history.

According to R. Kellogg (1928, pp. 36-41) not a single archaeocetes has a tendency to the skull telescoping. However the detailed investigation of Archaeoceti permits to observe the forward movement of the occipital shield, i.e. a Mysticeti sign. If we retrace the corresponding changes of *Protocetus*, *Dorudon*, *Zygorhiza*, *Basilosaurus*, *Prozeuglodon*, *Mirocetus*, *Aetiocetus* and *Ferecetotherium* we can see the following sequence : a gutter-like supraoccipitale of Protocetus is strongly turned backward (the line lowered from the acrocranion vertically is situated beyond the back edges of the occipital condyles (Fraas E. 1934, fig. 1). The acrocranion of *Dorudon* and *Zygorhiza* is moved forward (the line is situated in front of condyles, the occipital shield becomes vertical and the lambdoidal crest receives a semicircular form. *Basilosaurus* and *Prozeuglodon* have the acrocranion moved more forward, (the line lowered vertically from the acrocranion passes before the zygomatic archs back angle). The lambdoidal crest is relatively elongated and sharpened and the occipital shield is also sloped forward. *Mirocetus* already has the nearly horizontal occipital shield, and its front angle is situated at the zygomatic archs middle level (Rjabinin A. 1938). As to *Aetiocetus*, its occipital shield is moved forward beyond the back edges of the temporal fossas. The occipital shield of *Ferecetotherium* is much elongated forward and to all appearance has triangular form. Though an above mentioned range isn't phylogenetic, the skull changes discovered in it certainly point to the tendency of the occipital bone to move forward to the frontal region of the skull.

The forward movement and expansion of the occipital shield is even more pronounced in the Late Oligocene Archaeoceti (*Mirocetus*, *Aetiocetus*, *Ferecetotherium*). Intensification of this process leads to the Mysticeti type of the skull. We consider that the gradual intensification of the skull telescoping process which observed in the history of Archaeoceti and Mysticeti is a common sign of phylogenetically connected groups.

Gradual transition of Archaeoceti characters to the Mysticeti can be followed in the evolution of forelimb and dentition (Plate III). Protocetidae has tritubercular-sekodont cheek teeth, which possess all main elements of molars of primitive Placentalia. The most developed forms (Dorudontidae) have only the rest of postero-internal cusp at their P^3 and P^4. In Basilosauridae this cusp is slightly expressed—retained only on DP^3 and DP^4. The teeth of the latest forms (*Mirocetus*, *Aetiocetus*) are greatly simplified and the roots protuberance over the jaw edge is followed by reduction of the teeth crowns. Though *Aetiocetus* has still the teeth ordinary number (II), its cheek teeth are already singlerooted and small additional cusps on the crown became blunt and circular and crowns posses the reduction. The mandible of *Ferecetotherium* is typical for Archaeoceti by its outline but it already has homodont dentition with many conical teeth.

It's doubtful that the dentition of *Ferecetotherium* (divided along all the jaw and slightly plunged in the jaws) could participate only in catching of food. Their principal function was probably keeping and delay. Gradual slacking of main function and then the loss of the active role of teeth in digestion, as well as the change of food resulted in the complete reduction of dentition.

In the Oligocene time together with late archaeocetes such as *Mirocetus*, *Aetiocetus* and *Ferecetotherium* existed *Cetotheriopsis* and *Mauicetus* (Mysticeti). This fact certainly points to the origin of Mysticeti from the earliest Late Eocene or Early Oligocene Archaeoceti. A slightly changed representative of this animals might be *Ferecetotherium*, which lived till the Upper Oligocene.

The question of the phylogenetic relation between the Mysticeti and Odontoceti is the most difficult pages of the Cetacean history.

At the end of the last century the supposition was made about diphyletic origin of whales. Further this hypothesis was subjected to criticism and Cetacea were considered as the monophyletic group. At the XV International Zool. Congress in London the Soviet scientists suggest again the theory on the diphyletic development of Cetacea. Paleobiological investigation of whalest show that Archaeoceti might by phylogenetically related with Mysticeti. These groups according to our opinion represent one common line of development, which we oppose to the Odontoceti development direction.

To find out the Mysticeti and Odontoceti phylogenetic interconnections a critical consideration of their resemblance and difference character is necessary. Each character, which is taken for this comparison ground should be checked up by the information of its phylogenetic development. The following conclusion is made here : similarity of Mysticeti and Odontoceti which is found out according to a number of characters is not always sufficient for considering them as the representatives of the same order, i.e. not every similarity proves the common origin. Convergent development of several similar features of these groups can be established by means of detailed morphological analysis and paleontological researches. For example spongy structure of bones, which is considered as a common feature of all Cetacea histologically turned up to be quite different in Mysticeti and Odontoceti (Iablokov A. 1972). Odontoceti and Mysticeti have the similar outline of forelimbs. However even superficial analysis of morphology shows a considerable difference

between them as in the development of separate elements in number of bones and their joint character.

On the other hand, some difference between Odontoceti and Mysticeti, which exist on the modern stage of their development, completely disappeared at an early stage of their phylogenetic history. One of the main characters of modern Odontoceti, distinguishing it from Mysticeti, which possesses twin nasal passages, is single nasal passage. But according to Slepthov M. (1955), unpaired nasal passages formed only at the late stages of embrionic development ; as to the early stages (till the one month and half age) they preserve twin passage, which gives reason for objecting to supposition about the deep difference in the Odontoceti and Mysticeti nasal passage structure.

As to the such a considerable feature of modern Odontoceti as their skull asymmetry it is necessary to mention, that the Upper Miocene and probably even the Early Pliocene dolphins (*Kentriodon*, *Iniopsis*, *Cyrtodelphis*, *Anacharsis*), had a symmetrical skull, i.e. they didn't differ from Mysticeti by this feature.

Further, such a comparison : homodont dentition of Odontoceti in the contrary of Mysticeti filter apparatus. It is found out, that Upper Oligocene representatives of both the groups possess a similar, i.e. homodont and polydont dentition, that is proved by the data of paleontology and embriology. There is no doubt, that such correlations are not able to illustrate the deep difference and the congeneric relations between the groups.

We consider, that one of the most striking differences between Mysticeti and Odontoceti whales, not only between their modern representatives, but between the fossils too manifest itself in their own distinctive type of change of skull morphology. This process in Odontoceti is determined by the increase of caudal movement and development of rostral elements. Maxillaries and praemaxillaries gradually cover the skull bones situated towards them, and often touch the supraoccipital bone. We don't observe the same process among Mysticeti. Caudal expansion of the rostral elements of the skull is limited in Mysticeti. Maxillaries and praemaxilaries form relatively narrow and short processes on the dorsal surface of the skull, in the main, these bones stretch under the supraorbital processes of frontals. On the other hand as distinct from Odontoceti in phylogenesis of Mysticeti we observe the intensive increase of size and the gradually growing movement of the occipital shield, which in some forms reaches the proximal edges of maxillaries. To the same category of features may belong signs, pointing to the relatively old origin of the group. From this point of view the special attention should be paid to the fact that, general features of the skull of modern Odontoceti (Delphinidae for example), excluding the asymmetry, were formed already in the Oligocene. So the basic process of the skull reconstruction was already accomplished by the end of Paleogene.

If in the Eocene *Archaeodelphis* a relatively small maxillaries only partly cover the praeorbital process of frontals, in Upper Oligocene *Oligodelphis* (Plate V) the same bones greatly increase and are covering completely not only these processes but the temporal fossas as well and come in contact with supraoccipital region. As to the Oligocene Mysticeti—*Mauicetus* it is similar with supposed terrestrial ancestors, since its skull temporal region is elongated and nasal passage is shifted slightly caudally. So, from the point of view of the improvement in skull structure of this form, the development level is quite low. Probably the general features of the skull characteristic of each group of modern Cetacea in Mysticeti were formed geologically more later than in Odontoceti. This should point to a relatively old age of Odontoceti.

Between these two main directions of Cetaceans development (Archaeoceti-Mysticeti on the one hand and Odontoceti on the other) is established an important difference in development of the sagittal crest and the teeth range situation on the jaws. It is obvious, that the modern Odontoceti as well as all the Post- Eocene Odontoceti, haven't any sagittal crest, since their parietal bones are already forced out of vertex structure. But it is found out that this crest isn't characteristic of later Odontoceti-forms with vertex possessing well developed parietals. At the same time a teeth row of all Odontoceti terminated on upper and lower jaw far in front of praeorbital notches. Representatives of Archaeoceti-Mysticeti line have well developed sagittal crest, which gradually becomes reduced and disappears finally only in modern Mysticeti. In fossils this crest is well preserved (*Mauicetus*, *Imerocetus*). As to the teeth, the row of upper molars invades deep under the frontal bone and the posterior lower molars are always situated on the ascending part of the mandible. We should note the first of all that this difference greatly increases at the early stages of phylogenesis (it more regards the crests development). It is known, that in general a deep difference between the descendant is connected with transition of ancestral forms to sharply different environments, or with different food specialization. In our opinion such difference as mentioned above cannot be connected with these forms distribution in the different environments, since both groups (Odontoceti as well as Archaeoceti-Mysticeti) were developing in one and the same environment.

It is doubtful whether this difference can be connected with different food specializations of the groups. It is obvious that the Archaeoceti-Mysticeti line transition to plankton food took place only at the Paleogene stage of phylogenesis. At the preceding stages neither Archaeoceti nor Odontoceti have any important difference in their food specialization, both the groups

possess a similar, i.e. homodont and polydont dentition, while difference in development of crest and in teeth row situation is already typical for these groups.

It seems from the analysis of the distinctions of two main evolutionary branches of the Cetacea that their ancestor forms were already different from each other by feeding habit and hence by the mode of living.

REFERENCES

Abel, O. 1913. Die Vorfahren der Bartenwale. *Denkschriften der K. Akad. der Wissenschaften.* Bd. Xc. Wien.

Andrews, C. 1920. A description of new species of zeuglodont and leathery turtle from the Eocene of South- Nigeria. *Proc. Zool. Soc. London.*

Antony, R. 1926. Les affinites des Cetaces. *Ann. Inst. Oceanogr. de Monaco Paris.* N.s.v.3, N 2.

Emlong, D. 1966. A new archaic Cetacean from the Oligocene of North-West Oregon, *Bull. Mus. Nat. Hist.* Univers. Oregon. **3** (3) : 1-51.

G. Fedorovski, A. 1911-1912. Nahodka iskopaemoga kitoobajnogo v jmeevskom yejde Harkovekoi gub. *Tr. ob-va iepit. prirodi pri Xarkovskom Universitete* T XIV.

Fraas, E. 1914. Neue Zeuglodonten aus den unteren Mitteleocan vom Mokattam bie Cairo. *Denksch. der K. Akad. der Wissen., math-nat. klass.* 90 *b.*

Gubkin, N. M. 1950. Geologicheskie issledovanij v cevero-vostochnoi chasty Apsheronskogo poluostrova *Isbr. trudi, T.* 1 *Isdatelstnan SSSR.*

Lablokov, A. V. 1964. Konvergenchug ili parallelijm v rajbitic kitoobrajnih. *Paleont. journal No.* 1 *I An SSSR.*

Iablokov, V. A. Belkovich. i. dr. 1972 kite u delfini *I. nauka. M.*

Kellogg, R. 1928. The history of Whales, their adaptation to life in the water. *Quart. Rev. Biol.* **III.** (3).

Kellogg. R. 1936. A review of the Archaeoceti. *Carnegie Inst. of Washington.*

Lydekker, R. 1892. On Zeuglodont and other Cetacean remain from the Tertiary of the Caucasus. *Proc. of the Zool. Society of London.* N I.

Mchedlidze, G. A. 1964. Iskopaemie kitoobraznie karkaza. *Isd. "Mechniereba" an USSR Tbilisi.*

Mchedlidze, G. A. 1970. Nekotorie obshie chen istorii kitoobraznih *Isd "Mechiereba" An USSR Tbilisi.*

Rjabinin, A. H. 1938. *Microzeugladon aff Caucasicum Lyd* iz verhnemaikopanih- otloschii kabrstana *Problemi Plaontologii T IV Isd Maskowskogo gosuniversitetia.*

Rothausen, K. 1968. Die systematische stellung der europaische Squalodontidae (Odontoceti, Mamm.) *Palaont. Z.* 42, *I/2 Stuttgart.*

Slepthov, M. M. 1955. Osobennosti rajbitij kitoobraznih na rannih ambrionalnih etadiah. *Trudi jn-ta okeanologii T* 18 Isd An SSSR M.

Spasski, P. 1954. Nahodua Kostee verhutretichnih mlekopitawshih v okrestnostjh Derbenta. *Tr. murz. Zavdli, v* 3 *An A2 SSSR.*

Tarlo, L. 1964. A primitive Whale from the London Clay of the Isle of Sheppy. *Proc. Geol. Assoc. London.*

Tomilin, A.G. 1957. Zvezi SSSR i pnlerashih stran (Kitoobraznie) *Izdutelstvo An SSSR M.*

Van Valen, L. 1966. Deltatheridia, a new order of Mammals. *Bull. of Amer. Mus. of Nat. Hist.* **132.** Ar. I.

Van Valen, L. 1968. Monophyly or diphyly in the origin of Whales. *Evolution.* **22.** (1).

EXPLANATION OF PLATES

Plate I

Ferecetotherium kelloggi Mchedlidze Right and left lateral view of mandible

Plate II

Ferecetotherium kelloggi Mchedlidze Isolated teeth

Plate III

Ferecetotherium kelloggi Mchedlidze Skeleton of left forelimb

Plate IV

Oligodelphis azerbajdzanicus Mchedl. et Aslan. Incomplete skeleton

Plate V—VI

Oligodelphis azerbajdzanicus Mchedl. et Aslan.Dorsal and ventral view of skull

Plate VII

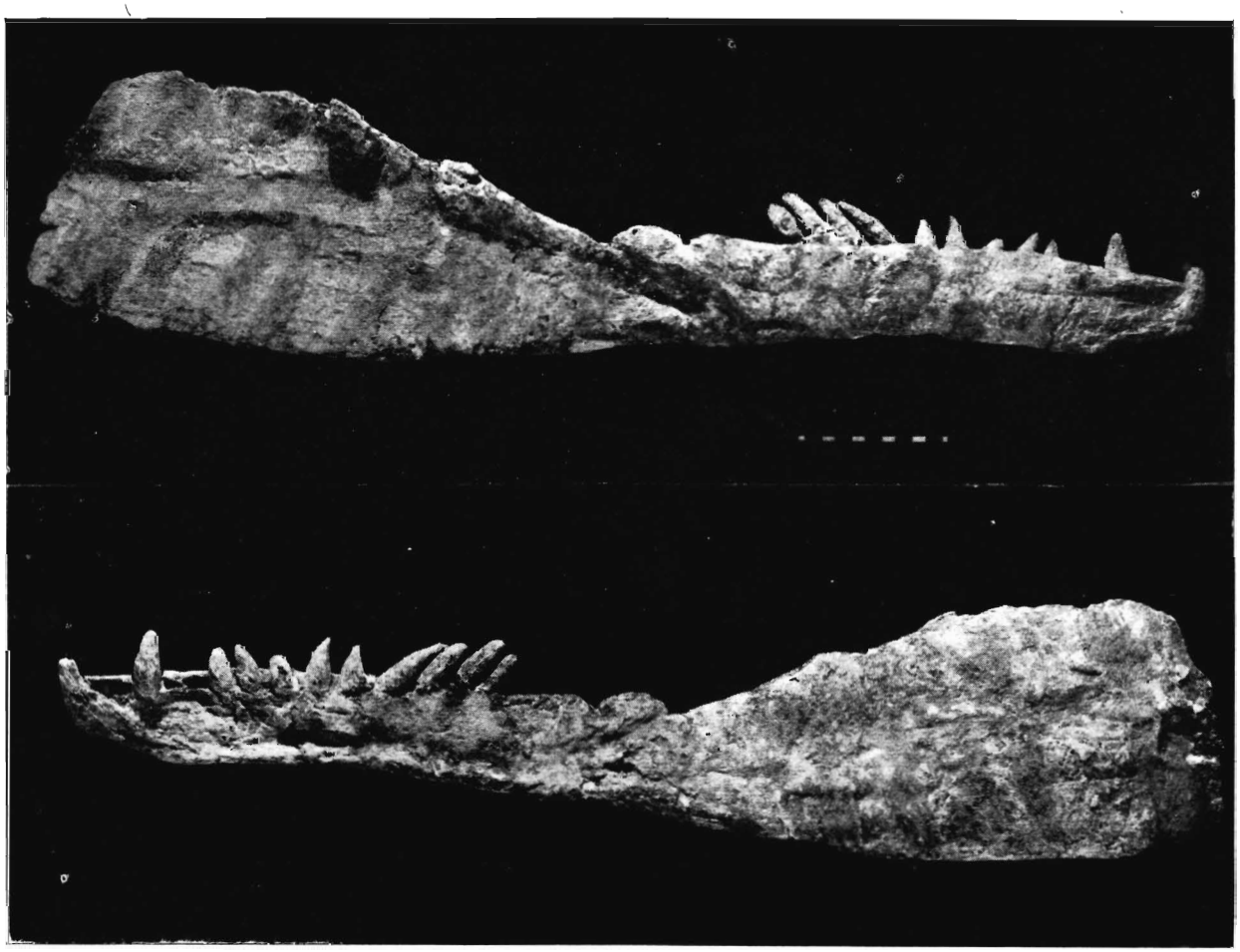
Sulakocetus dagestanicus Mchedlidze Dorsalview of skull

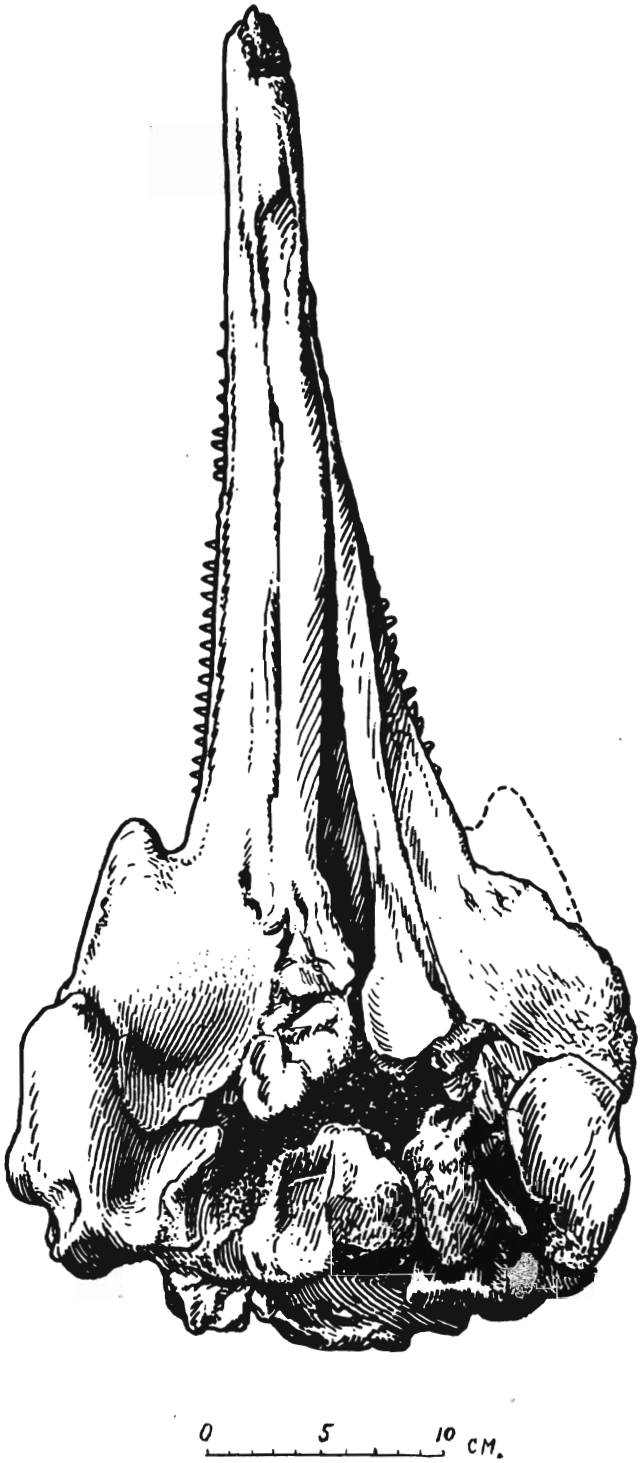
Plate VIII

Kelloggia barbarus (Mchedl. et Aslan.) Dorsal and ventral view of skull

Plate IX

Kelloggia barbarus (Mchedl. et Asian.) Left and right view of mandible

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