FOSSIL CETACEA OF THE CAUCASUS

G A MCHEDLIDZE

This book by Guram Andreevich Mchedlidze, a young scientist of the Institute of Paleobiology and Kandidat of Geological and Mineralogical Sciences, reviews in detail, for the first time, the fossil cetaceans of the Caucasus. It is based on rich collections from the author's own excavations, supplemented by those preserved in the museums at Tbilisi, Baku, Krasnodar, Armavir, Stavropol' and other towns. A study of this material helped the author to explain the composition of the Tertiary cetacean fauna of the Caucasus (two new genera and a new species were identified, and the taxonomic status of many other forms described earlier was established more accurately). He was able to establish the ecological and phylogenetic importance of many of their features and also reconstructed the living conditions of these animals. The author has shown the close dependence of structural changes in fossil cetaceans on environmental changes and, in this light, has examined some important evolutionary trends of the development of cetaceans in general. Finally, this book contains valuable data on the stratigraphic importance of fossil cetaceans.

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January 1988

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G.A. Mchedlidze

Scientific Editor
Frank C. Whitmore, Jr.

Smithsonian Institution Libraries
and
National Science Foundation
Washington, D.C.
1988

TT 81-52177

Iskopaemye Kitoobraznye Kavkaza

Akademiya Nauk Gruzinskoi SSR
Institut Paleobiologii
Metsniereba Publishers
Tbilisi, 1964

Translated from the Russian
Translator: P.M. Rao
General Editor: Dr. V.S. Kothekar

Library of Congress Cataloging-in-Publication Data

Mchedlidze, G.A. (Guram Andreevich)
Fossil Cetacea of the Caucasus.

Translation of: Iskopaemye Kitoobraznye Kavkaza.
Bibliography: p.
Supt. of Docs. no.: SI 1.2:F79
1. Cetacea, Fossil. 2. Paleontology—Caucasus.
I. Whitmore, Frank C. II. Title.
QE882.C5M33813 1988 569' 5 88-600135

Translated and published for the Smithsonian Institution Libraries, pursuant to an agreement with the National Science Foundation, Washington, D.C., by Amerind Publishing Co. Pvt. Ltd., 66 Janpath, New Delhi 110001

Printed at Prem Printing Press, Lucknow, India

UDC 569.5 (47.92) + [016.3]

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During the time from the Oligocene through the Pliocene Epochs (about 37 million to two million years ago) whales evolved from archaic forms to animals that we would recognize as modern. The study of this evolution, and of the past geographical distribution of whales, depends on specimens from a few very rich areas, supplemented by scattered finds from many other places. The major producing regions are in Belgium, the east and west coasts of the United States, and Peru. As this book demonstrates, the Caucasus must be added to the list of areas crucial to our understanding of the evolution and paleogeography of the Cetacea.

The Cetacea described here come from the Paratethys, a northern arm of the east-west trending, world-circling sea of which the Mediterranean is a remnant. This is an important geographic point in our plotting of the distribution of whales in the past, and of the relationships between the whales of the different areas.

G.A. Mchedlidze is the foremost student of the fossil whales of the Caucasus. His work, presented here, will allow the English-reading student to compare the whales of the Caucasus with those described in the West; to evaluate their stratigraphic position; and to benefit from the author's ideas on whale evolution.

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Introduction

5 The paleobiological history of Tertiary Cetacea has not yet been thoroughly understood. The osteology of the fossil as well as present-day forms has not been adequately studied, as a result of which identification of the paleontological material becomes considerably difficult. While a study of some limb bones or teeth is adequate for establishing the taxonomic position of representatives of various mammalian orders, the precise determination of the taxonomic relations of cetaceans requires in most cases a study of the skull.

Our inadequate knowledge of these animals, in my view, is largely due to the fact that the phylogenetic relations between toothed and toothless cetaceans have not been understood at all so far.

The inadequacy of past studies of fossil cetaceans is explained primarily by the relative scarcity of their finds and also, evidently, by the fact that the earlier investigators did not assign any stratigraphic importance to them. Possibly this is the reason for the inadequate study of the osteology of cetaceans, since a detailed understanding of the skeleton, especially of limb bones and the dental apparatus, of many groups of present-day vertebrates owes a lot to paleontology.

The exceptional importance of the study of fossil cetaceans for working out the theoretical aspects of biology as well as geology, and especially for reconstructing the ecological conditions of ancient basins, has now become clear.

Paleontological material on cetaceans, which represent a group of mammals with secondary adaptations, clearly reveals salient features of the adaptation of land animals to an aquatic mode of life. This enables us to trace and verify some general principles of vertebrate
6 evolution. Later, a study of the fossil remains of cetaceans could clearly throw light on the facies of their host rocks, thus facilitating reconstructions of the conditions of a given ancient basin with which the precise stratigraphy of corresponding formations is associated. For example, at present, there is no doubt that a thorough investigation of fossil cetaceans, of which individual representatives are encountered almost throughout the Maikop section of the Apsheron

peninsula formations, could be used for a stratigraphic delineation of this massive suite.

Recent investigations have shown that for the reconstruction of the salt water regime of ancient basins, the results of spectroscopic studies and chemical analysis of the bones of fossil cetaceans for fluorine, phosphorus and trace elements are very important. The trace elements in the bone remains of cetaceans and fish reflect the presence of dissolved chemical compounds in the salts of the basins' water, which respond to the changes of the acid-alkali regime and could serve as indicators.

My problem was to establish the faunal composition of the fossil cetaceans of the Caucasus, provide a geological description of the major sites, reconstruct the conditions under which the cetacean remains were fossilized in the territory under study and, along with an explanation of the functional importance of the skeletal features, investigate some aspects of their biology and evolution.

I express my sincere gratitude to L.Sh. Davitashvili, L.K. Gabuniya, L.V. Muskhelishvili, L.S. Maisuradze, and also to the personnel of the regional museum at Armavir who extended great help in the course of the work.

Chapter I

Review of Literature on the Fossil Cetaceans of the Caucasus

7 Verneuil (1838) was the first to record information on the fossil remains of cetaceans found in the Caucasian territory: he reported on the vertebra of a small whale from the Sarmatian formations of the Taman peninsula.

The results of studies of more valuable material covering this group of mammals are contained in the work of Brandt (1873–1874), who described a new member of Delphinapteridae, *Delphinapterus fockii* Brdt. from the Sarmatian formations in the vicinity of Stavropol'.

Among the early studies is also a report of Pallas (1883) about his find of a cetacean vertebra in the vicinity of Taman.

An interesting bone collection of fossil cetaceans was made by the Swedish scientist, Sjegren, in the Maikop formations around Perekishkyul village (Azerbaidzhan) from where Lydekker in 1892 described the fragment of a lower jaw, shoulder bone and incomplete vertebra of a new member of Zeuglodontidae *Zeuglodon caucasica*, later known as *Microzeuglodon caucasica* Lyd., and the skull of a typical dolphin, *Iniopsis*.

In 1899, in the Chokrak formations of Taman peninsula, Andrusov discovered the fossil remains of a dolphin, based on which Abel in 1905 established a new genus and species of dolphins, *Paleophocaena andrussowi* Abel. [According to Abel, features of a contemporary genus, *Phocaena*, are seen in this form, but Kirpichnikov's studies (1952) showed that Abel's dolphin resembled the present-day *Delphinus* more than *Phocaena*.]

8 In the Apsheron formations of Cheleken Island, dolphin remains were found for the first time in 1901–1902 by A.P. Ivanov (1908). Specimens were sent to Abel for study, but this valuable scientific material (complete skeletons) remained undescribed and were obviously lost.

In 1907–1908, in these same formations on Cheleken Island, V.V. Veber and K.P. Kalitskii (1911) discovered an immense quantity of disarticulated dolphin bones which, as identified by Ryabinin (1908), were of *D. delphis* L.

Information on the fossil cetaceans of the Caucasus is also contained in the work of Andrusov (1909–1912), devoted to a study of the fossil Bryozoan reefs of the Taman peninsula.

In 1916, A.P. Ivanov discovered the bones of a whalebone whale *Cetotherium priscum* Brdt. in the Upper Sarmatian formations of the Kutsai mountains (Stavropol' region).

The remains of Cetotheriidae were described by Bogachev in 1928 from the Sarmatian diatomite clays of the Apsheron peninsula (near Dzhoar village).

In 1933, M.V. Pavlova published a note on the skull fragments of an unidentified dolphin from the Sarmatian formations in the neighborhood of Stavropol'.

A nearly complete skeleton of a Sarmatian whale, *Cetotherium mayeri* Brdt., was described by A.N. Ryabinin (1934) from the Sarmatian formations near Kudako in the Kubano-Chernomorsk petroleum zone, discovered by A.N. Fedorov in 1927. A report about this find was published a little earlier by A. Anosov* (1927) in an article dealing with the fauna of the Upper Sarmatian formations of the Kubano-Chernomorsk zone.

In 1938, V.V. Bogachev described the remains of *D. delphis* L. from the Apsheron formations around Baku.

In 1938, Ryabinin published the findings of his study of a skeleton of a cetacean of the family Zeuglodontidae discovered by Weber in Kabristan in 1927.

In a review of the fossil cetaceans of the Caucasus, Bogachev (1939) reported on the skeletal remains of dolphins discovered in the Upper Sarmat of Eldar, but this material was evidently not studied any further. In this same article, the author also reported about his finds of bones of the dolphin *Champsodelphis* from the Karagan formations around Zestafon (Western Georgia).

9 The reports of P.I. Spasskii (1933, 1939, 1943 and 1951a) deal with a study of the Upper Sarmatian cetaceans found in the neighborhood of Derbent town; he also described the remains of these animals from around Maikop town (1951 and 1951b).

Based on a study of an incomplete skull of a Middle Sarmatian dolphin, in 1954 A.A. Kirpichnikov established a new genus and species of fossil delphinid, *Leptodelphis stavropolitanus* Kirpich.

In 1956, Bogachev published a description of an almost complete skeleton of the Sarmatian delphinid *Anacharsis orbus* found near Stavropol' in 1927.

In 1959, I established a new genus of fossil dolphins, *Imerodelphis,*

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*Not listed in bibliography—General Editor.

based on a study of a dolphin skeleton from the Lower Sarmatian formations around Kvaliti village (Zestafon zone) and described in 1960 as the remains of the genus *Champsodelphis* from the Sarmatian formations around Armavir.

In 1961, S.M. Aslanova published preliminary reports about her finds of Delphinidae in the Upper Maikop formations near Perekishkyul.

The above brief review shows that literature on Tertiary Cetacea of the southern USSR is extremely scanty, which was one of the reasons that prompted me to study the systematics of fossil cetaceans of the Caucasus.

Chapter II

Description of the Fossil Remains of Cetacea

ORDER CETACEA BRISSON, 1762

Suborder ARCHAEOCETI Flower, 1883
(=Zeuglodontia Gill, 1871)

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

Genus Microzeuglodon Stromer, 1903

Microzeuglodon caucasicum Lyd.

10 *Material.* A fragment of the right ramus of lower jaw with P_4, M_1, M_2 and M_3 (specimen No. 116-29, Georgia Museum, M.G. collection), a fragment of the right side of upper jaw with five greatly damaged molars (specimen No. 116-28, M.G. collection), left upper arm bone (specimen No. 116-15, M.G. collection), three sterna (specimens No. 116-47, No. 116-56 and No. 116-59, M.G. collection), eight lumbars (specimens No. 116-18, 116-13, 115-10, 116-74, 116-6, 116-24 and 116-63, M.G. collection) and one caudal vertebra.

Site. Vicinity of Perekishkyul village (western Apsheron peninsula, left bank of Sumgait River).

Geological age. Lower or Middle Oligocene.

Diagnosis of genus.[1] Small dimensions. Skull relatively short (length of lower jaw about 280–300 mm), trunk long (ratio of length to width of centrum of thoracic vertebrae 0.8–1; lumbar 1.4–1.5 and anterior caudal 1.5). All molars of lower jaw separated by diastemata increasing in length anteriorly. Teeth crowns triangular, leaf-like, flattened laterally, and cutting edge with a fixed number of serrations perhaps on all lower molars (five on each side, not reckoning the apex); moreover, on the buccal as well as on the lingual sides of the crown are pits corresponding to the boundary position between roots of teeth.

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[1] Diagnosis was drawn based on a review of Sjegren's material, taking into consideration the results of Lydekker's studies.

In the upper jaw, diastemata absent between teeth. Upper arm bone with greatly inclined medial head with a poorly developed deltoid ridge and fairly well-developed greater and lesser tubercles.

11 *Description and comparison.* Lower jaw (Plate I, Fig. 1). Represented by a fragment of right ramus (from the last molar to the anterior margin of P_4). Height of jaw at level of last molar more than dental segment M_3 to P_4. Lower margin of jaw at level of M_1 slightly deformed and flexed: upper margin all along the length of fragment steeply sloping anteriorly. From among the teeth, P_4 and M_1 wholly preserved; M_2 broken along the middle of crown; only a small portion of anterior half of crown of M_3 preserved. Teeth not deep set in jaw, roots rise above the alveolar rim of jaw, forming one-fourth of the entire exposed height of the tooth. Ryabinin's note (1938, p. 143) that the teeth of *Microzeuglodon* are deeply set in the jaw arises from his judgment of it from the drawing of an inadequately prepared specimen. All preserved teeth with two roots. Crowns of teeth compressed in lingual-buccal direction and nearly leaf-like. Cutting edge of teeth serrated. Five serrations present on each of the anterior and posterior edges, not reckoning the apices. Full number of serrations seen only on P_4 and M_1. On each side of M_2, three serrations were retained which fully correspond to the position of the first, second and third lower serrations of the preceding teeth. It could, therefore, be assumed that in an incompletely preserved M_2, the number of serrations should have been the same as in M_1 and P_4. Buccal surface of crown of all teeth has triangular collar with a finely serrated edge. At the middle of buccal as well as lingual surfaces, close to the teeth roots is a vertical sulcus representing an extension of the boundary between two roots. Molars of lower jaw separated by distinct diastemata increasing in the anterior direction; length of diastemata between M_3 and M_2, 3 mm; between M_2 and M_1, 4 mm; and between M_1 and P_4, 6.5 mm. The total length of lower jaw was obviously no more than 300 mm.

The fragment of right ramus of upper jaw with five greatly damaged molars belongs perhaps to this form (evidently P^3, P^4, M^1, M^2, and M^3; Plate I, Fig. 4). Maxilla characterized by greatly thickened alveolar margin. Its lateral surface noticeably bulged; the medial flattened. Only the roots of P^3 and P^4 and the anterior alveolar parts of crowns of M^1 and M^2 preserved. Maxillary teeth not separated by diastemata and, in relation to the alveolar region of the jaw, noticeably
12 inclined backward. All teeth preserved in the upper jaw have two roots and are not set particularly deep in the jaw, though deeper set than the corresponding teeth of lower jaw. Roots cone-shaped, anterior roots weakly curved; posterior straight. Root considerably longer than crown (Plate I, Fig. 5).

When describing the remains of *Microzeuglodon caucasicum* Lyd. s. *Z. caucasicum* Lyd. along with a fragment of the lower jaw, upper arm bone and caudal vertebra, Lydekker (1892) mentions the presence of a fragment of the upper jaw, but did not describe it. This would explain why in later works of other paleontologists like Stromer, Abel, Ryabinin and others, the characteristics of the upper teeth of *Microzeuglodon* were not described.

The above description shows that the maxillary and mandibular teeth of *Microzeuglodon* differ noticeably from each other in their structure and disposition in the jaws. The upper jaw teeth are somewhat shorter than the lower and are more deeply set in the alveoli, inclined backward and form a compact series. Such differences between the upper and lower jaw teeth do not, however, preclude placing the two specimens under consideration as belonging to the same animal. On comparing the upper and lower teeth of several other members of Zeuglodontidae, I noticed quite similar differences. For example, among *Z. osiris* Stromer, the height of the crown of the upper molars is considerably less than the lower, and the former more deeply set in the alveoli than the latter (Stromer, 1903, Plate IX; 1908, Plate IV). A similar relation between the upper and lower teeth is also noticed in *Z. isis* Beadnell, characterized additionally by a backward inclination and a prominent projection from the alveoli of the upper molars. I have unfortunately no information relating to the lower molars of such members of Zeuglodontidae as *Protocetus atavus* Fraas, *Microzeuglodon* aff. *caucasicum* Lyd. and *Zeuglodon wanklini* Seeley.

It should, however, be pointed out that the upper molars of Zeuglodontidae have relatively low crowns and, in some members, these teeth are deeply set in the alveoli (*Z. cetoides* Owen and *Protocetus atavus* Fraas). In others, they project prominently from the alveoli, (*Microzeuglodon* aff. *caucasicum*), forming at times a compact series (*Protocetus atavus*) and at other times an open series with small diastemata (*Z. cetoides* Owen. Zittel, 1894, p. 167; *M.* aff. *caucasicum* Lyd. Ryabinin, 1938, p. 146).

13 Thus, I have reason to assume that the upper molars of Zeuglodontidae have a relatively low crown compared with the lower (see Table 8). Insofar as the exposure of the root above the surface of the jaw is concerned, it evidently is an individual variability, being more evident on the lower than on the upper jaw of the animal.

The inclination of the upper molars relative to the alveolar margin could aslo perhaps be regarded as an age related feature.

Insofar as the size differences of upper and lower molars—to be more accurate, crown sizes—are concerned, these undoubtedly constitute a taxonomic feature.

The nature of the diastemata between the molars of Zeuglodontidae and their importance for the systematics of archaic cetaceans will be examined below.

Vertebrae. Lydekker described only an incomplete caudal vertebra of *Microzeuglodon* from the collection of Sjegren. In my opinion, the three thoracic and seven lumbar vertebrae preserved in Sjegren's collection belong to this same animal.

Thoracic vertebrae massive, articular surfaces enlarged and curved from sides of centrum. Lower vertebral surface smooth. Articular surfaces more broad than high. Posterior articular surface broader than anterior.

Lumbar as well as thoracic vertebrae represented mainly by centra. Characterized by considerably elongated centra, articular surfaces oval-round and a broad neural canal. On the ventral surface of centrum is a ridge shaped oblong bulge extending to the succeeding vertebrae of the same section, forming a pointed and slightly expanded ridge at the posterior end.

The vertebrae of *Microzeuglodon*, as a whole, are relatively small with an elongated centrum (ratio of length to width of vertebra 1–1.5).

Humerus (Plate I, Figs. 2 and 3) has been described in detail by Lydekker. I will, therefore, confine myself to its deformation and some features of histology.

14 The limb bones of cetaceans, unlike those of [land] mammals, do not

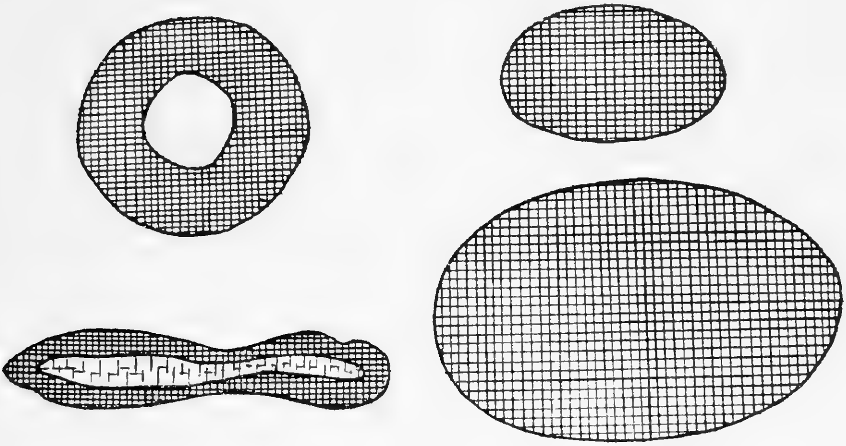

Fig. 1. Cross sections of humerus.

1. *Canis lupus* L. 2. *Microzeuglodon caucasicum* Lyd. 3. Mysticeti (*Cetotherium*). 4. Odentoceti (*Champsodelphis*).

have a tubular structure. Among these animals, the cavity, often filled with bone marrow in terrestrial forms, is filled with a homogeneous spongy mass of bone tissue (Fig. 1). As a result, the shaft of these bones in the fossil state rarely undergoes any significant deformation. The shaft of *Microzeuglodon*, unlike the shaft among the toothless and toothed cetaceans known to me, is highly flattened, uniformly compressed and bears a distinct depression all along the length. Such a deformation, in my opinion, could arise if the bone were hollow or the central portion of the cavity filled with the bone tissue were far less compact than the peripheral layer. As a matter of fact, a study of a cross section of the shaft in the specimen of *Microzeuglodon* showed the presence of two layers of bone tissue sharply differing from each other, a compact and relatively thick outer layer and a spongy, very loose, thin inner layer.

Taking into consideration the deformation of the shaft, which is unusual among cetaceans, and the differentiated structure of the bone tissue, I would assume the presence of a poorly developed medullary cavity in the humerus of *Microzeuglodon*. In my view, this feature of *Microzeuglodon* points to the antiquity of the histological structure of hollow bones in cetaceans, since the described structure of the humerus to some extent resembles in shape that of terrestrial ancestors undoubtedly possessing limbs with hollow bones. Evidently the archaic *Microzeuglodon* still retains this antique feature representing somewhat of a transition to the cetacean already possessing limb bones consisting of homogeneous compact bone tissue.

Microzeuglodon caucasicum Lyd. differs from other members of the Zeuglodontidae known to me by its small dimensions, greatly raised posterior teeth of the lower jaw, presence of diastemata between the lower molars as well as in the structural features of the molars (fixed number of additional serrations on both cutting edges of the teeth, slightly rounded form of crown, presence of a collar on the labial surface of the crown etc.).

By comparing *M.* aff. *caucasicum* Lyd., obtained from the vicinity of Dzhenga with *Microzeuglodon caucasicum* Lyd., A.N. Ryabinin detected considerable similarity in dentition between them. According to him, the existence of diastemata between the molars of the species described by him provides grounds for assuming utmost proximity and even identity with *M. caucasicum*, thus excluding the possibility of affinity with the family Zeuglodontidae, among whose members such diastemata are not noticed (Ryabinin, 1938, p. 152). To me, this conclusion of the author is not wholly justified for the following reasons.

Microzeuglodon has been described and separated based only on the structural features of the lower jaw (small dimensions and diastemata between molars). Moreover, diastemata between molars in *Microzeuglodon* are present only on the lower jaw, but are absent on the upper as can be seen from the description. Moreover, the lower jaw of *M.* aff. *caucasicum* Lyd. is not known and to judge the structure of mandibular teeth from the structure of maxillae is risky, to say the least. This is because among members of the Zeuglodontidae, there are forms with diastemata between molars on the upper, but without diastemata on the lower jaw (*Zeuglodon isis* Beadnell), and also forms with reverse arrangement of teeth (*M. caucasicum* Lyd.).

16 Finally, apart from *M.* aff. *caucasicum*, the wide-set molars of the upper jaw are seen in *Z. isis* Beadnell (Stromer, 1908, Plate VI, Fig. 9) and in *Z. cetoides* Owen (Zittel, 1894, p. 167, Fig. 131).

In my view, the above facts point out that the "*Microzeuglodon*" described by Ryabinin is closer in structure of the dental apparatus to *Z. isis* Beadnell than to *M. caucasicum.*

At this juncture, let us study the taxonomy of *M. caucasicum* Lyd.

It is well-known that *Microzeuglodon* was first described by Lydekker as a new species of the genus *Zeuglodon* (*Z. caucasicum*) and the main feature of this species, according to him, was its small size (Lydekker, 1892, p. 567). Later, Stromer separated the Caucasian Zeuglodon into a separate genus, *Microzeuglodon*, based on the presence of diastemata between the molars of the lower jaw (Stromer, 1903, p. 89). On this very basis, Abel recognized the possibility of the erection of a new family, Microzeuglodontidae, and included *M. harwoodi* Sanger from the Upper Oligocene of southern Australia in it, as distinct from the Caucasian forms (Abel, 1904, p. 220). The accuracy of identification of the Australian form is rather doubtful, since only one isolated molar of it is known.

While isolating the family Microzeuglodontidae, Abel evidently relied on the fact that the presence of diastemata between the molars of the lower jaw in *Microzeuglodon* should be regarded as an important taxonomic feature. This permitted identification of the family, since members of Zeuglodontidae (whose lower jaws have been studied) have compact rows of lower molars.

Having been acquainted with the characteristics of the tooth structure of the different members of the family Zeuglodontidae, I have come to the conclusion that Abel clearly overestimated the taxonomic importance of this feature, i.e. the presence of diastemata between the molars of the lower jaw. Firstly, it is not yet possible to judge the permanent nature of the location of molars within the entire family of Zeuglodontidae since the lower jaws of many of its members are not known (*Z. wanklyni* Seeley, *Z. rossicum* Brdt., *Z. zitteli* Stromer and
17 others). Moreover, the fact that in the upper jaw it varies even within

Table 1. Dimensions (in mm) of fragmentary maxilla and upper molars of ***Microzeuglodon caucasicum*** **Lyd.**

Length of fragmentary maxilla	73
Height of maxilla at P^4	23
Height of M^1 (restored)	8
Height of M^2 (restored)	8
Width of molars at base	12–13
Width of roots (anteroposterior)	12–12.5

Table 2. Dimensions (in mm) of the lower jaw fragment of ***Microzeuglodon caucasicum*** **Lyd.**

Length of fragment	100
Length of dentate segment from posterior of M_3 to anterior end of P_4	65
Height of jaw at M_3	75.5

Table 3. Dimensions (in mm) of lower teeth of ***Microzeuglodon caucasicum*** **Lyd.**

	P_4	M_1	M_2	M_3
Height of tooth from surface of jaw to apex	18	18	—	—
Height of crown	13	13	—	—
Length of crown of first pair of teeth	15	14.5	14.15	12
Length of crown at level of third tooth	12.75	12.5	—	—
Width of crown	5.5	5.75	5.5	5.5

the genus *Zeuglodon* points to the likely variability of this feature at least within the family (widely spaced upper molars in *Z. isis* Beadn. and closely spaced in *Z. osiris* Stromer).

All of this, in my view, does not support separation of *Microzeuglodon caucasicum* Lyd. into a different family. Therefore, I would still regard *Microzeuglodon* as genus of the family Zeuglodontidae along with the genus *Zeuglodon.*

20 Genus Zeuglodon Owen, 1874 (Basilosaurus Harlan, 1834)

Zeuglodon sp.

Material. One lumbar vertebra (specimen No. 11, IMB collection).

Description. Vertebra of large dimensions with centrum significantly elongated and expanded at the ends. Articular surfaces

Table 4. Dimensions (in mm) of lumbar vertebrae of *Microzeuglodon caucasicum* Lyd.

	No. 116-18	116-13	116-16	116-74	116-6	116-24	116-63
Length of centrum	45	45	51	54	57	58	65
Width of anterior articular surface	35	—	38	42	37	53	44
Width of posterior articular surface	—	41	40	47	38	51	51
Height of anterior articular surface	30	36	35	38	30	47	49
Height of posterior articular surface	35	36	38	40	33	42	37
Width of transverse process at base	—	31	—	34	39	38	35
Width of neural canal	18	18	14	16	—	12	13
Ratio of length to width=1.3 to 1.5							

Table 5. Dimensions (in mm) of caudal vertebra of *Microzeuglodon caucasicum* Lyd.

Length of centrum	70
Width of anterior articular surface	48
Width of posterior articular surface	45
Ratio of length to width=1.3	

Table 6. Dimensions (in mm) of thoracic vertebrae of *Microzeuglodon caucasicum* Lyd.

	No. 116–47	116–56	116–59
Length of centrum	37	37	40
Width of anterior articular surface	45	45	—
Width of posterior articular surface	50	37	43
Height of anterior articular surface	35	31	—
Height of posterior articular surface	42	—	—

19 **Table 7. Dimensions (in mm) of lower jaws of members of the family Zeuglodontidae**

	Z. osiris Stromer	*Z. zitteli* Stromer	*Z. isis* Beadnell	*M. caucasicum* Lyd.
Full length of lower jaw	580–710	600	990–1100	290 (restored)
Height of lower jaw at level of M_3	115–130	112–115	115–200	75.5

circular. The characteristic longitudinal crest on the centrum of lumbar vertebrae distinct. Neural canal considerably constructed. Judging from the preserved remains, transverse processes evidently broad. Length of centrum 100 mm, width of articular surface 74 mm and height 75–76 mm.

Suborder—Odontoceti Flower, 1867
Superfamily—DELPHINOIDEA Flower, 1864
Family—DELPHINIDAE Gray, 1821
Genus—*Imerodelphis* Mchedlidze
Type species—*Imerodelphis thabagarii* Mch.

Site. Zestafon region, Kvaliti village, left bank of Kwirila river.

Geological age. Lower Sarmat.

Material. Incomplete skull, vertebral column up to the third lumbar vertebra and fragments of ribs and limbs (specimen No. 1, IPB collection).

19

Table 8. Dimensions (in mm) of molars among members of family Zeuglodontidae

	Z. osiris Stromer			*Z. zitteli* Stromer			*Z. isis* Beadnell			*M. caucasicum* Lyd.		
	P_4	M_1	M_2	P_4	M_1	M^2	P^4	M_1	M_2	P_4	M_1	M_2
Length of tooth	34–39	24–35	20	42	23–24	18	55–65	31	31	15	14.5	14.5
Thickness of crown	16–18	—	12–13	—	—	—	27–28	—	14	5	6	6
Height of crown	30–40	—	20	—	—	—	32	—	20	13	13	—

19

Table 9. Comparison of vertebral dimensions (in mm) among members of family Zeuglodontidae

	Z. osiris Stromer	*Z. zitteli* Stromer	*Z. isis* Beadnell	*M. caucasicum* Lyd.	*M.* aff *caucasicum* Lyd.	*Protocetus atavus* Fraas
Lumbar vertebrae						
Length of centrum	52–60	52	305	45	86	40
Width of centrum	53–58	58	175	35	85	53
Height of centrum	53	49	165	30	73	38
Thoracic vertebrae						
Length of centrum	38–42	45	265	37–40	39–60	—
Width of centrum	61–69	54	165	45	56–73	—

Diagnosis of genus. Animal of small dimensions, length of centrum not more than 130–140 cm. Rostral part of skull longer than the cranial, maxillae wider than premaxillae, the latter flattened at base, bulged anteriorly and separated by a broad sulcus. Lower part of rostrum with a distinct ridge and sulcus. Posterior part of ridge with a crest and the anterior part, a central sulcus. Choanae large, quadrangular-oval; ridge of vomer broad and high; orbits set in the anterior half of the cranial part of skull; anterior margin of choanae and posterior margin of orbits fall on the same line. Teeth small with cone-shaped, very pointed and considerably curved crown; root bulging in middle, nearly straight and weakly pointed. There are three teeth to a centimeter length of jaw. Centrum elongated, transverse processes of lumbar vertebrae wing shaped.

Description and comparison. Skeleton embedded in a solid block of marly clay, considerably deformed (Plate II).

21 The right side of the vertebral column, the ventral side of the skull and the medial side of the left ramus of the lower jaw project on to the surface of the block.

Skull of average size. Rostral part longer than cranial. In spite of considerable flattening, the circular shape of the foramen magnum, as well as the left occipital condyle, could be distinguished. The articular surface of the latter bulges intensely in a dorsoventral direction and descends steeply toward the foramen magnum.

In the ear region of the skull, the lateral side of the left tympanic is well-preserved. It has a conical anterior and a posterior with slightly bulging ends. The high and fairly thick ridge of the vomer dividing the infranasal passage into rectangular-oval, relatively large choanae is easily noticeable.

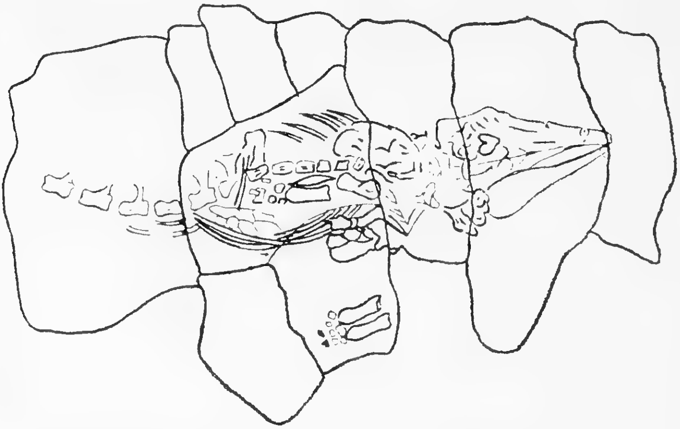

Fig. 2. *Imerodelphis thabagarii* Mch. Sketch of skeleton.

The anterior margin of the choana lies at the level of the posterior margin of the orbits. This points to a fairly considerable displacement of the posterior nasal openings, which in all probability is associated with the adaptation of the animal to respiration at the surface of the water.

The crest of the vomer is continued into a very short and thin plate, i.e. into a ridge of the palatine bone. Wings of the pterygoid are totally crushed because of which the highly deformed sulcus along the sides of the crest of the vomer is exposed.

The palatal plates of the maxillae are distinguished with difficulty. 22 From the level of the posteriormost upper tooth to the end of the part of the upper jaw seen in the specimen, the jaw is divided, on the ventral side, by a distinct sulcus. The part of the jaw to the right of the former bulges greatly and is broader than the left.* On the lower surface of the rostral part, there is a distinct ridge and lateral sulcus (a feature characteristic of *Delphinus*). On the right side of the jaw is a row of the remnants of ten teeth and on the left, two. The teeth are directed slightly forward and sideward.

A study of the dorsal part of the rostrum helps establish the following features. Premaxillae separated all along the length. Maxillae broader than premaxillae.

The left ramus of the lower jaw shows only the medial side. The upper margin of its raised posterior portion is horizontal. Later, bending sharply, it descends steeply toward the dentate portion. The curvature of the lower margin of the jaw is distinct. In modern dolphins, this flexure is borne in the midportion of the jaw bone.

With respect to the rostral and cranial parts of the skull, the dolphin described differs from the long-snouted *Anacharsis* (Bogachev, 1956) and *Cyrtodelphis* (Dal Piaz, 1903) as also from such short-snouted forms as *Leptodelphis* and *Sarmatodelphis* (Kirpichnikov, 1954). The skull and rostrum of *Imerodelphis* more closely resemble modern *D. delphis* and the Middle Miocene North American form *Kentriodon pernix* Kell. (Kellogg, 1927).

In form and size of choanae, the Zestafon dolphin is also close to the modern dolphin, but differs sharply, for example, from *Leptodelphis*, which has extremely small choanae. The form under description differs from *Leptodelphis* and *Kentriodon* also in the structure of the ventral surface of the rostrum, which in these genera does not bear the ridge bounded by a longitudinal sulcus. In *Sarmatodelphis*, on the ventral surface of the rostrum, there is a vallate ridge which is flattened posteriorly and disappears gradually, while in our forms, this

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*This is probably due to distortion after burial—Editor.

ridge with its longitudinal sulcus is distinctly seen even in the posterior part of the rostrum.

Imerodelphis differs from the fossil Delphinidae known to me in the considerable rearward shifting of the choanae and the relatively broad maxillae. The latter in the Zestafon dolphin are noticeably broader than the premaxillae, while in most of the fossil dolphins (*Leptodelphis*, *Sarmatodelphis* and *Delphinodon*), an inverse ratio of the dimensions of these bones is distinctly noticeable.

I have with me only three nearly complete teeth of *Imerodelphis* 23 from the midsection of the lower jaw. The teeth are small. The crown is slightly shorter than the root and is coated with smooth enamel. The root is almost straight, somewhat thicker than the crown and slightly pointed. In the upper half, the root has a thickening, but it narrows gradually downward and terminates in a slightly pointed tip.

The teeth of *Imerodelphis* differ from those of *Delphinus* in the root structure and in the much smaller size. Moreover, they have a far thicker enamel layer than the contemporary dolphin. In the tooth structure, the Zestafon dolphin differs sharply also from *Kentriodon pernix* Kell. (Kellogg, 1927), *Araeodelphis natator* Kell. (Kellogg, 1957), *Champsodelphis letochae* Brdt. (Brandt, 1873, Plate IV, Fig. 3), *Cyrtodelphis sulcatus* Ger. (Dal Piaz, 1903, Plate 31), etc. In this respect, it is closer to *Anacharsis orbus* Bog. (Bogachev, 1956). However, the teeth of the latter have a longer crown. The roots are rounded at the tip and are less broad than the crowns.

From the cervical region, only the atlas projects onto the surface of the block. It is in the form of a centrum and a lower arch. Its left half is better preserved with a pear-shaped articular surface. The ventral ends of the articular facets are very close together. The lower arch is thick. The lower tubercle is well-developed. The narrow, left transverse process is preserved and directed downward.

The second cervical vertebra is almost fully covered by the preceding one. Only its right transverse process and a part of the right articular surface project onto the surface. The third vertebra is evidently disk-shaped.

The first cervical vertebra of *Imerodelphis* differs from that of *Champsodelphis* cf. *fuchsii* Brdt. (Mchedlidze, 1960) in relatively small dimensions, very closely placed ventral ends of anterior articular surfaces, etc. However, there is also similarity between them as seen in the identical shape of the articular surfaces and in the presence of a thickened lower arch.

The atlas under description differs from the atlas of *Anacharsis orbus* Bog. in the form of much larger anterior articular surfaces and their more vertical disposition. It differs from the atlas of *Kentriodon pernix* Kell. (Kellogg, 1927, Plate 12. Figs. 3 and 4) and from the atlas of *Cyrtodelphis sulcatus* Ger. (Dal Piaz, 1903, Plate XVIII, Fig. 1a and 1c) in the structure of the lower arch and the anterior articular facets.

In the thoracic region, ten vertebrae are preserved. Only a few
24 of them have been relatively well-preserved. The first vertebra of this region has evidently been lost. The ventral part of the second and third are preserved. The height is more than the length. The anterior articular surface of the second vertebra has a triangular, heart-shaped form. The fourth thoracic is quite elongated (length of centrum almost equal to height), and the fifth is characterized by a considerably elongated centrum intensely constricted in the middle and with enlarged articular surfaces.

In all the vertebrae of the thoracic region, the bases of neural spines are greatly damaged. Judging from the reconstructed fragments of these spines, it could, nevertheless, be concluded that they were relatively high, broad and somewhat posteriorly inclined.

The sixth vertebra has a long centrum constricted in the middle and a heart-shaped anterior articular surface. The right base (of the neural spine), located at the anterior margin of the vertebra, is well-preserved.

Evidently, the shortening of the base of the spines commences with this vertebra and the bases of the spines posterior to this are increasingly separated from those anterior and posterior to them. The transverse process is placed almost at the dorsal margin of the centrum. The next vertebra is even more elongated; the separation of the bases of the transverse process and neural spine is distinctly seen, although the transverse process is still away from the upper margin, but not from the lateral surface of the centrum. The bases of the processes extend over a large part of the length of the body. The neural spine is long and lamellar and its base noticeably constricted. The posterior margin of the neural spine forms a sharp angle connecting it with the anterior articular process of the next vertebra.

The anterior half of the eighth vertebra is covered with bits of various bones and the terminal part of the neural spine is worn out. The centrum of the ninth vertebra is greatly elongated and broadened. The bases of processess are completely separated.

The base of the transverse process constitutes over one-half of the length of the centrum and is located in the dorsal part of the lateral surface of the vertebra. The base of the neural spine, however, is wholly located on the dorsal surface of the centrum. The articular surfaces of the vertebra are circular.

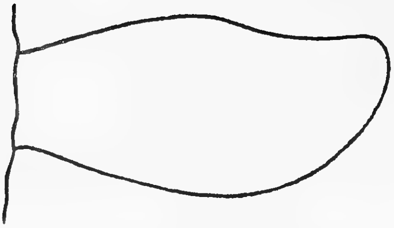

Fig. 3. *Imerodelphis thabagarii* Mch. Outline of transverse process of last thoracic vertebra.

The tenth vertebra appeared on the surface of the block as irregularly shaped pieces, but we could reconstruct the ventral surface of its left transverse process which was embedded in the rock. This process is of moderate length, slightly constricted at the base, but on the whole almost uniformly wide over its entire length. The anterior margin has an undulating form and the posterior, together with the tip (terminal), forms a smooth arch (Fig. 3). As a result of this, the shape of the process is lanceolate.

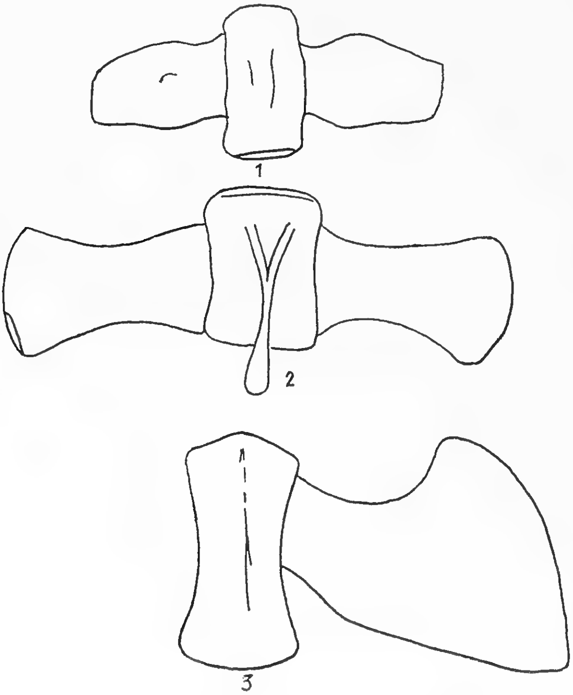

Fig. 4. Lumbar vertebrae of fossil dolphins.
1—*Anacharsis orbus* Bog. (after Bogachev), 2—*Kentriodon pernix* Kell. (after Kellogg), and 3—*Imerodelphis thabagarii* Mch.

25 Immediately behind the above described vertebra are the vertebrae of the lumbar region with very large sized centra, rounded articular surfaces and, what is more interesting, very prominent broad transverse processes.

26 The first lumbar vertebra is characterized by an elongated centrum constricted in the middle, and by expanded surfaces [of the ends of the centra? Ed.]. The bases of neural spine constitute more than half the length of the centrum and are located in the anteriormost section of the vertebra. The transverse processes are long, wing-like, narrow at their bases, with parallel margins, inclined to the vertebral axis at an angle of 45°; the posterior margin of the transverse process straightens into a line perpendicular to the centrum, the anterior margin curves medially and is intensely curved in the lateral part. Therefore, the process acquires a wing-like form (Fig. 4; Plate III, Fig. 3). The rest of the lumbar vertebrae are also characterized by similar features.

In the structure of thoracic and lumbar vertebrae, the Zestafon dolphin differs considerably from the other members of contemporary and fossil Delphinidae known to me. A special feature of this species is the characteristic shape of the transverse process, which I have described above in detail. An abrupt change in the shape of the transverse process from thoracic to the lumbar regions is noteworthy. The narrow, nearly lanceolate transverse processes of the thoracic vertebrae immediately change into wing-like, intensely broadened processes characteristic of lumbar vertebrae.

From the above material's description, it is clear that I have with me the complete cervical and thoracic regions of the vertebral column. Only three vertebrae of the lumbar region are preserved intact.

Considering that there are ten lumbar vertebrae and twelve or fifteen caudal, almost one-half of the vertebral column may have been lost.

Consequently, the formula of the vertebral column of our dolphin may be tentatively put down as: C–7, D–10, L–10 and Ca–15. Thus, the total length of the skeleton should be roughly 140–150 cm.

Scapula. Only fragments of the left scapula are present in the specimen. The blade is totally crushed. Head greatly flattened. The short and narrow coracoid process and the acromion process are fairly elongated and considerably broadened at the ends and are more or less fully preserved. Length of the coracoid process, 7.5 mm and of the acromion, 21.5 mm; width of the latter at the base, 8 mm and its terminal width, 16 mm.

Both the forelimbs are not fully preserved. The humerus, all carpals and the proximal end of the fifth metacarpal of the right side

are preserved; the incomplete humerus and radius, incomplete carpus
27 (intermedium), Ca (2+3) and Ca (4), two metacarpals and a few left phalanges are preserved.

The humerus is greatly damaged: more than one-half of the head and a part of the unpaired tubercle are missing. Judging from the preserved remains, this bone is relatively greatly elongated, comparatively narrow and greatly flattened. The line passing through the head and the unpaired tubercle forms a right angle with the line passing through the long axis of the distal end. Head is hemispherical.

The articular surfaces for the radius and ulna at the distal end of the bone are well-developed. The slightly deformed radius is set almost in the natural position with the humerus. At its proximal end is a large, well-preserved, deep, articular surface for articulation with the humerus and, on the medial margin, a triangular surface for articulation with the ulna.

Of the preserved carpals of the left limb, the intermedium is pentagonal; while Ca (2+3) and Ca (4) are quadrangular.

The forearm bones of the right limb are considerably flattened (Plate III, Fig. 2). The medial margins of the ulna and radius are concave, as a result of which a wide cleft is visible between them. The olecranon process is well-developed. The ends of both bones are considerably broadened.

The carpus of present-day, as also of several fossil dolphins (Vokken, 1946, Colbert, 1944 and Bogachev, 1956), normally consists of five bones of which three (radiale, intermedium and ulnare) form the proximal row and the remaining two Ca (4) and Ca (2+3), the distal. The carpus of my dolphin, however, has six bones (Plate III, Fig. 2). The distal as well as the proximal row consists of three bones. Among them, one is Ca (4) and the other two are possibly unfused, Ca (2) and Ca (3). It is well-known that the evolution of the limbs of Delphinidae proceeds toward a reduction in the number of carpals.
28 It is, therefore, natural to assume that the presence of a six-member carpus in *Imerodelphis* is an archaic feature. However, it should also be remembered (Vokken, 1946) that an increase or decrease in the number of carpal bones can be considered as an exception among contemporary dolphins.

The sternum is represented by a fragment resembling a part of the body (corpus) of the sternum of the present-day dolphin in shape.

In the block are also seen fragments of vertebral and sternal parts of ribs. The head and tubercle could be distinguished only in one of them. The ribs are extremely narrow, brittle and slightly broadened dorsally. Their width varies from 7 to 10 mm.

28 **Table 10. Main skull dimensions (in mm) of *Imerodelphis thabagarii* Mch.**

	Actual	Restored
Condylobasal length	232	275
Length of cranial part	100	
Length of alveolar segment of upper jaw	76	116
Maximum width of skull	130	
Width of rostrum at base (along the line of maxillary notch)	60	
Width of rostrum at last tooth	38	
Width of rostrum in the middle	27	
Width of rostrum at level of the 15th tooth (reckoning from the posterior margin)	20	
Total width of premaxillae at mid-portion of rostrum	20	
Width of condyle	55	
Height of condyle	35	
Distance between two premaxillae	5	
Width of left premaxilla	9	
Number of teeth per cm of jaw	3	
Suggested number of teeth on one ramus of upper jaw	39	

29 **Table 11. Main dimensions (in mm) of cervical vertebrae of *Imerodelphis thabagarii* Mch.**

	I cervical	II cervical	III cervical
Maximum height of left articular surface	31		
Maximum width of articular surface	18–19		
Total width of vertebra—distance between ends of transverse processes	68	64–68	
Distance between lower ends of anterior articular surfaces	16		
Length of centrum			5
Height of right articular surface		16	
Approximate width of right articular surface		10–12	
Height of vertebra (approximate)	42		13

31

Genus Iniopsis Lydekker, 1892

Iniopsis caucasica Lyd., 1892

Material. Incomplete skull (specimen No. 116-21, M.G. collection) and vertebrae (specimens No. 116-13 and 116-77, M.G. collection).

Site. Around Perekishkyul village.

Geological age. Lower Miocene.

Table 12. Dimensions (in mm) of thoracic vertebrae of *Imerodelphis thabagarii* Mch.

	II	III	IV	V	VI	VII	VIII	IX	X
Length of centrum	11	14	17	19	23	27.5	30	32	32
Height of anterior articular surface	15		16	17.5	17.5			19	
Width of anterior articular surface	17	18			16				
Height of posterior articular surface			19			18	17	19	
Width of posterior articular surface	18						14	19	
Height of neural spine from base				54	53.5	49			
Maximum width of neural spine						22			
Length of transverse process									45
Maximum width of transverse process									23

30 **Table 13. Dimensions (in mm) of lumbar vertebrae of** *Imerodelphis thabagarii* **Mch.**

	I	II	III
Length of centrum	35.5	38	40
Height of anterior articular surface	21	22	22.5
Width of anterior articular surface	20	20	
Height of posterior articular surface	20	21	
Height of posterior articular surface		20	
Width of transverse process at base	16	17	
Length of transverse process along anterior margin		32	
Length of transverse process along posterior margin	49.5	51	
Maximum width of transverse process		42	41

30 **Table 14. Dimensions (in mm) of limb bones of** *Imerodelphis thabagarii* **Mch.**

Length of humerus	48.5
Maximum width (at distal end)	24.5
Length of bone from distal end to the beginning of head	30
Area of head	20×20
Thickness of bone at midlength of shaft	12.5
Length of articulation with radius	15
Width of articulation with radius	10
Length of articulation with ulna	9
Width of articulation with ulna	8
Height of articulation with olecranon process	8
Length of radius	50
Width of radius at distal end	23
Thickness of radius at distal end	8
Length of ulna without olecranon process	50
Width of ulna at distal end	22
Thickness of ulna at distal end	8
Thickness of ulna at proximal end	9.5
Total width of distal end of forearm	46
Total width of proximal end	41

Diagnosis of genus. Skull low, slightly asymmetrical. Premaxillae at proximal part of rostrum somewhat broader than maxillae; posteriorly, intensely broadened forming an inclined and slightly compressed prenasal plate, slightly covering the upper jaw. Maxillae nearly horizontal along entire length and slightly enlarged along the sides posteriorly, as a result of which the frontal part from the supraoccipital ridge to the preorbital groove it relatively long. The supraorbitals noticeably bulged in a longitudinal direction and inclined toward the premaxillae. Fossae maxillaria extremely deep. Their sharply raised posterior margins almost straight and extended in a posterolateral direction. The preorbital groove deep. The rectangular postnasal plate is horizontal and rises considerably above level of posterior margins of fossae maxillaria. Supraoccipital nearly vertical, forming a right angle with the posterior margin of the postnasal plate. The posterior ventral surface of the rostrum forms a broad and low ridge not bounded by a longitudinal groove. The nasal opening triangular. Teeth cone shaped, slightly compressed in basal portion of crown. There are three teeth per centimeter length of tooth row. Centrum of lumbar vertebrae elongated, transverse processes narrow.

Description and comparison of material. Skull (Fig. 5, Plate IV) incomplete. Occipital portion greatly damaged. Left preorbital process and much of left maxilla damaged. Only the posterior portion of rostrum preserved (roughly a third of the entire length).

Skull narrow, slightly asymmetric. Premaxillae in the proximal

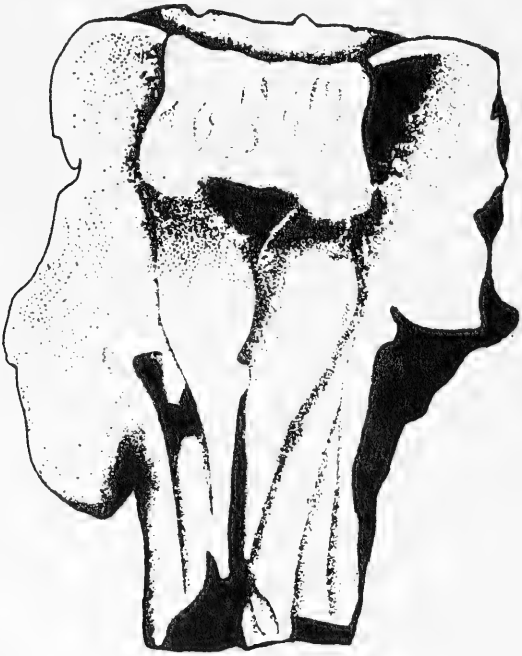

Fig. 5. *Iniopsis caucasica* Lyd. Skull, dorsal view.

part of rostrum broader than maxillae. Posteriorly, they expand to form an inclined, slightly compressed prenasal zone, partly covering the maxillae. Premaxillae nearly horizontal up to the anterior margin
32 of the nasal opening and then rise sharply, even beyond the posterior margin of nasal opening, constricting to a minimum and again becoming horizontal.

Premaxillae clearly divided by a broad cleft right up to the anterior margin of the nasal opening.

The postnasal plate is rectangular and formed of nasal, frontal and, evidently, the intensely constricted proximal ends of premaxillae.

The plate is noticeably raised above the rest of the skull. Its posterior margin falls somewhat above the posterior margins of the maxillae. The latter are horizontal all along the length and only slightly enlarged along the sides posteriorly, as a result of which the frontal part of the skull from the supraoccipital ridge to the preorbital groove appears relatively long. Supraorbital portions of these bones noticeably bulged in a longitudinal direction. Fossae maxillaria extremely deep. Their sharply rising posterior margins slightly rounded and elongated in a
33 posterolateral direction. Supraoccipital is vertical and forms a right angle with posterior margin of postnasal plate. Nasal opening trian-

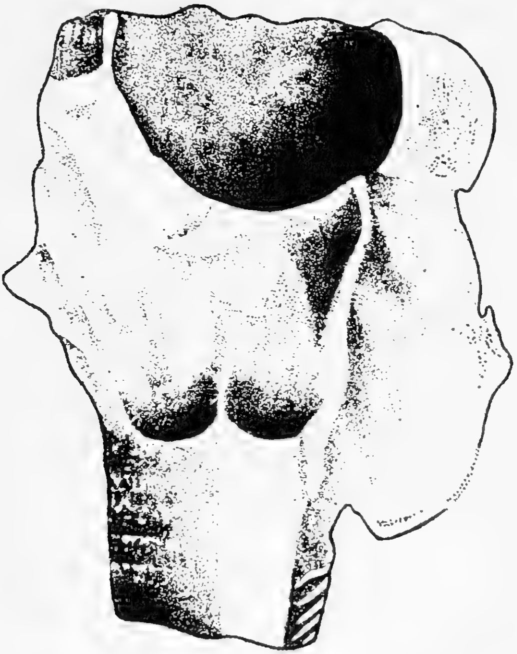

Fig. 6. *Iniopsis caucasica* Lyd. Skull, ventral view.

gular. Ethmoid plate distinct. Orbits considerably shifted forward. Distance between the posterior margin of orbits and anterior margin of the nasal opening almost equal to the length of orbits. The posterior ventral surface of rostrum forms a broad and low ridge not bounded by longitudinal grooves.

Brief characteristics of the skull under description were first given by Lydekker (1892). Along with this skull and some vertebrae, he attributed an isolated fragment of an upper jaw not having anything in common with *Iniopsis* to this animal.

Additional cleaning of the skull revealed a cone-shaped tooth from the right side of the posterior section of the upper jaw not corresponding in shape or size of the alveoli located on the isolated fragment of
34 the upper jaw (crown length of teeth found on the skull 9 mm and diameter 2.5–3 mm; there are three teeth per centimeter length of tooth row on the jaw; length of alveolus in the isolated fragment of upper jaw 7–9 mm and width 1.5–2.5 mm; there are 1.5 teeth per centimeter length of tooth row of the isolated fragment). If this is added to the clear difference in the proportions between the above fragment of the upper jaw and of the same bone in the skull, it becomes clear that these specimens were erroneously placed by Lydekker in the same genus.

By assuming the above fragment as a part of the upper jaw of *Iniopsis,* Lydekker brought the latter close to such members of the family Platanistidae as *Pontistes, Inia, Stenodelphis* and *Saurodelphis* (Lydekker, 1892, p. 63).

All the above listed genera are known from geologically much younger formations than *Iniopsis*; the boundary of their range does not fall below the Pliocene (Simpson, 1945), while I have dated the horizons containing the remains of *Iniopsis* as Miocene. Lydekker sees a striking similarity with *Pontistes* (in the shape of maxillary fossae, in the nature of their posterior margins, and also in the presence of elongated and large laterally compressed alveoli). However, this supposed affinity is based on an isolated fragment of jaw, which belongs in all probability to a member of the genus *Cyrtodelphis.*

Iniopsis differs from *Stenodelphis* by its cylindrical teeth set much deeper in the fossae maxillaria with highly elevated margins, presence of a quadrangular postnasal plate, etc. Insofar as its similarity with *Inia* is concerned, which prompted the author to call the new genus *Iniopsis* or *Inia*-like, it should be pointed out that the similarity is only in the presence of a quadrangular postnasal plate and deep fossae maxillaria with straight posterior margins. At the same time, *Iniopsis* differs from *Inia* in the absence of a high process posterior of the nasal opening, less elevated margins of maxillary fossae, form and size of nasal opening and teeth (Flower, 1866, Plate 25, Fig. 1). It differs from *Cyrtodelphis sulcatus* Ger. (Dal Piaz, 1903) in the angular posterior margins of the maxillary fossae, more horizontal proximal parts of upper jaw bones, weakly developed frontals, low medullary region of the skull, and in the morphology of the dental apparatus.

35 A comparison of the skull of *Iniopsis* with that of the present-day dolphin *D. delphis* (specimen No. 85–07, M.G. collection) showed the following differences: upper jaw bones of *Iniopsis* are horizontal all along their length. Fossae maxillaria deep with fairly angular and elevated posterior margins, preorbital process distinct and significantly long (it is less distinct and broader among members of *Delphinus*); premaxillae broadened towards prenasal plate and sharply constricted only at the level of posterior margin of nasal opening (the sharp constriction of these bones among members of *Delphinus* is noticed even in the anterior margin of the nasal opening). They are also distinguished by the shape of the postnasal plate and the structure of the ventral surface of the basal part of the rostrum.

Iniopsis differs from *Kentriodon pernix* Kell. (Kellogg, 1927) in the shape of the postnasal plate, depth of fossae maxillaria and the proximally highly elongate premaxillae. The similarity between them is seen in the development of the preorbital process, in the presence of a somewhat straight posterior margin of maxillary fossae, in the structure of the lower surface of the basal part of the rostrum, in the form of the nasal opening, and also even in the general shape of the entire frontal surface of the skull.

The *Iniopsis* skull differs from the skull of the Sarmatian dolphin *Leptodelphis stavropolitanus* Kirp. (Kirpichnikov, 1954) in the shape and size of the frontal bulge (i.e. postnasal plate) development of proximal parts of maxillae and premaxillae, form of maxillary fossae, contour of posterior margin of maxillae (arched in *Leptodelphis* and angular in *Iniopsis*) and the parallel margins of the basal part of the rostrum (Figs. 5 and 6).

The midthoracic vertebrae (Plate IVa*, Figs. 1, 2, 5 and 6) are characterized by a fairly long centrum and considerably enlarged articular surfaces. The shape of the articular surfaces is close to the cordiform (Upper margin straight and lower arched or slightly pointed).

Lumbar vertebrae (Plate IVa*, Figs. 3, 4, 7 and 8) are characterized by a long centrum and enlarged circular shape of articular surfaces. Judging from the preserved remains, the transverse processes
36 were evidently narrow and long, slightly resembling those of *D. delphis*
L. Relative to the articular surfaces, the transverse processes occupy

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*Plate IVa not included in the Russian original book—General Editor.

a midposition. The neural canal is considerably broadened. On the ventral surface of the centrum is a well-developed ridge characteristic of lumbar vertebrae.

37 **Table 15. Skull dimensions (in mm) of *Iniopsis caucasica* Lyd.**

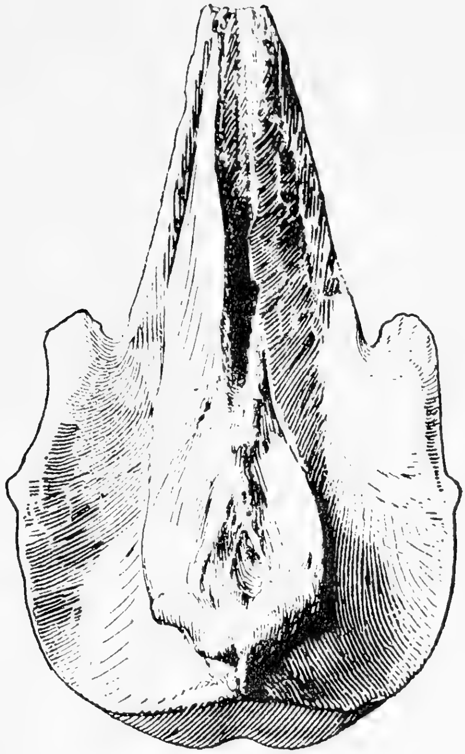
Length of preserved portion of skull	158
Length of skull from supraoccipital ridge to anterior margin of preorbital process	122
Maximum width of skull at anterior margin of orbits	124
Width of fossa maxillare in the posterior part	45
Maximum width of prenasal plate	50
Width of upper jaw bone in the proximal part of rostrum	15
Width of premaxilla in the same portion	16–17 (left)
Area of postnasal plate	52 × 34
Width* of skull in preorbital part	102 × 144
Length of nasal opening along midline	21
Maximum width of nasal opening	24
Width of rostrum in basal part	60

*Correct as per original, but should read *area.*

37 **Table 16. Dimensions (in mm) of vertebrae of *Iniopsis caucasica* Lyd.**

	Midthoracic	Lumbar	Anterior caudal
Length of centrum	33	36	41
Width of anterior articular surface	30	27	30
Width of posterior articular surface	31	28	29
Height of anterior articular surface	24	24	25
Height of posterior articular surface	23	25	26
Width of neural canal	19	11.5	4
Width of transverse process at base		17	20
Width of groove on ventral surface			11

The next vertebra, evidently the caudal, unlike that described above, is characterized by an intensely constricted neural canal, presence on the ventral surface of the centrum of a broad sulcus bound by well-developed ridges and also by the very low position of the transverse processes.



36 Fig. 7. *Leptodelphis stavropolitanus* Kirp. Skull, dorsal view (after Kirpichnikov).

38 Family ACRODELPHIDAE Abel, 1905

Genus Champsodelphis Gervais, 1848

Champsodelphis cf. *fuchsii* Brdt.

Material. The first, second and third cervical, one thoracic, one lumbar, ten caudal vertebrae, scapula, sternum and fragments of radius and ribs (specimen No. D1–D16, AKM collection).

Site. Armavir (Northern Caucasus), left bank of Kubana River (waterworks).

Geological age. Middle Sarmat.

Description and comparison. Vertebrae. Of the first cervical vertebra (Plate V, Figs. 1 and 3), lateral parts and the ventral arch are well-preserved. Surfaces for articulation with the condyles are pear-shaped, very deep and medially inclined. Their outer margins are arched and the inner noticeably straightened.

The neural arch was evidently not particularly high. Lower transverse processes thin, directed downward and sideways. The posterior articular surfaces are oval, the hypophysial process short, wedge-shaped. Ventral side of arch has an oval surface for articulation with odontoid process of epistropheus (axis).

The atlas of the Armavir dolphin is quite similar in form to the corresponding vertebra of the North American *Kentriodon* (Kellogg, 1927, p. 35) from which it, however, differs in the following features: the anterior articular surfaces of *Kentriodon* are more reniform while these are pyriform in the Armavir dolphin; the lower ends of the articular facets of the atlas in our form are wider set than those of the *Kentriodon* [the distance between them in it (Armavir) is almost equal to the length of the articular surface itself, while in *Kentriodon*, the distance is equal to only one-half the length of the articular surface].

This species differs from *Anacharsis orbus* Bog. (Bogachev, 1956) in its large dimensions (see Table 20) as well as in the shape of the articular surfaces (Plate VI, Fig. 1). The posterior articular surfaces and the transverse processes as a whole among *Anacharsis* are inclined medially, while in the Armavir dolphin, these are located on the same plane.

The species described above differs from *Cyrtodelphis sulcatus* Ger. (Dal Piaz, 1905) in having a very narrow neural arch, in the shape of articular surfaces, shape of neural canal, etc.

39 The second cervical vertebra (Plate V, Figs. 2 and 4) was fully preserved. It is characterized by a fairly massive centrum on which are seen the anterior oval and posterior elliptical articular surfaces. In the middle of the posterior articular surface are located two cavities surrounded by distinct concentric lines. The odontoid process is well-developed and has an oval area on the ventral surface for articulation with the preceding vertebra. Transverse processes are short, directed backward. Bases of neural spines are broad, the spine high and slightly bifurcated at the apex. A serrated ridge runs from the dorsal margin of the transverse process to the apex of the neural spine; on the medial side of it, almost at midheight of the neural arch, there is a circular flattening.

This vertebra differs from the corresponding one of *Kentriodon pernix* Kell. (Kellogg, 1927) in the high neural spine, high centrum and the shape of articular surfaces.

The epistropheus of *Anacharsis orbus* Bog. (Bogachev, 1957), differs in the shape of the posterior articular surface (elliptical in mine and triangular cordiform in *Anacharsis*, Plate V, Figs. 2 and 4) and in the considerably larger dimensions (see Table 22).

It differs from the epistropheus of *Araeodelphis natator* Kell. (Kellogg, 1957) in the serrated edge of radices apophysi and in some structural details of the centrum.

Maximum similarity can be seen with the epistropheus of members of the genus *Champsodelphis*, in particular *C. fuchsii* Brdt. (Brandt, 1878), which it resembles in an identical form of transverse processes, in the structure of anterior articular surfaces, shape of neural canal, and the development of the neural spine and also in the presence of a serrated ridge on the base of the neural spine (Plate V, Fig. 2).

The next vertebra of the cervical region is evidently the third or the fourth (Plate V, Fig. 5). It has a highly flattened centrum with elliptical articular surfaces. The bases of the transverse processes are attached at three-fourths of the height of the centrum's sides. Attention should be further drawn to the fact that although a considerable length of the transverse process is preserved, there is not even a trace of the existence of an opening for the blood vessel. Therefore, it should be assumed that the opening for blood vessels in this species was either located in the part of the transverse process quite separated from the centrum of the vertebra or that the vessels ran under the process, which is, however, less probable. The length of the centrum is
40 7 mm, the width of the posterior articular surface 29.5 mm, height 21.5 mm and width of neural canal, 17 mm.

The thoracic region of the vertebral column is represented by only one vertebra (Plate V, Fig. 6)*, evidently the fifth. The length of its centrum is slightly smaller than its width. The anterior articular surface is oval, the posterior more triangular. The base of the neural spine covers the entire length of the dorsal surface of the centrum.

The lumbar vertebra (Plate VI, Figs. 1 and 2) is characterized by a high and comparatively short centrum. The anterior articular surface is circular, and the ventral margin of the posterior articular surface noticeably pointed. The neural spine is located close to the anterior margin. Its base covers two-thirds of the length of the vertebra. The anterior articular process is short, the neural canal moderately wide and triangular in cross-section. Transverse processes are long and broad with parallel anterior and posterior margins. Bases of transverse processes cover about five-sixths of the length of the lateral margin of the centrum. The process occupies the midposition, relative to the anterior articular surface. On the ventral surface of the centrum is a distinct ridge, characteristic of lumbar vertebrae, and the moderately wide grooves for blood vessels run aslant from it.

The centrum of the seventh caudal vertebra (Plate VII, Fig. 1) is noticeably shortened. The anterior articular surface is considerably broader compared with the posterior. Transverse processes are in the form of rather low ridges covering more than half the length of the

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*Fig. 6 shows the last cervical vertebra—General Editor.

centrum. They are placed close to the anterior edge of the centrum. The neural spine is evidently low (it is not fully preserved). The neural canal is greatly constricted, almost slit-like.

On the ventral surface of the vertebra is a distinct wide groove with sharp and high longitudinal ridges. Running across the dorsal and ventral surfaces of the transverse processes are additional longitudinal ridges. They run the entire length of the centrum, parallel to the base of the transverse process, and are perforated by small canals running downward and forward on to the upper ridge and downward and backward on the lower ridge.

The next vertebrae, eighth and ninth (Plate VII, Figs. 1 and 2), have nearly the same features as the ones described above, but are smaller.

The tenth vertebra (Plate VII, Figs. 1, 2) differs considerably from the preceding one. Primarily, it has no transverse process, as a result of which the vertebra as a whole becomes narrow, and the 41 relative constriction of its posterior part is scarcely noticed; the groove on the ventral surface is noticeably constricted. The neural spine is, nevertheless, present but very low; its dorsal margin is inclined backward.

The neural spine of the eleventh vertebra (Plate VII, Figs. 1, 2) is greatly reduced, additional longitudinal ridges almost wholly disappear; the groove on the ventral surface is median and shortened.

The twelfth vertebra (Plate VII, Figs. 1, 2) is the last of those in which the length of the centrum still predominates over the width. The neural canal is a narrow groove. Additional ridges as well as processes (transverse and neural) are wholly absent. Articular surfaces still rounded.

The shape of the next vertebrae differs sharply from that described above. The thirteenth vertebra is clearly wider than long. All processes are totally reduced. The groove on the ventral surface becomes deeper; at its bottom is a very faint sharp longitudinal ridge. The anterior articular surface is rounded and the posterior distinctly elliptical.

The width of the fourteenth vertebra (Plate VII, Figs. 1, 2) is more than twice its length. Articular surfaces are elliptical. The dorsal surface of the vertebra is rounded and the ventral nearly flat; transverse processes are also flattened. A distinct groove is on the ventral surface, bounded by sharp ridges. Additional ventral ridges are distinct, as a result of which the entire ventral surface of the vertebra acquires a quadrangular outline.

The anterior articular surface is compressed and the posterior noticeably convex (faint procoelous type of vertebral structure).

Such a structure of articular surfaces is also characteristic of anterior caudal vertebrae, but this is more distinct on the fourteenth, fifteenth and sixteenth, i.e. on the vertebrae of the posterior caudal region.

The next, fifteenth, vertebra (Plate VII, Figs. 1, 2) is even more shortened. Its articular surfaces are greatly expanded. The dorsal and ventral surfaces of the centrum are quadrangular.

The sixteenth vertebra has a short low broad centrum. The entire surface of the centrum is rectangular.

The scapula (Plate VIII, Fig. 2) is almost entirely preserved. A negligible part of the vertebral edge has been damaged. The length of blade is twice its height. The blade is elliptical. The vertebral margin was evidently rounded. The anterior margin, unlike the scapula
42 of the present-day dolphin, is somewhat rounded and the posterior edge straight and inwardly inclined.

The coracoid is narrow, long and uniformly wide all along its length and has a rounded tip. The acromion is flat, greatly broadened and bent dorsally and medially. The spine of the scapula is weakly developed, but, nevertheless, is stronger than in present-day dolphins. In my specimen, it almost reaches the vertebral margin, while this spine in modern forms reaches up to only half the height of the scapula. Moreover, the spine in modern forms is considerably shifted toward the anterior margin as a result of which the prespinous fossa of the scapula is greatly constricted; in the Armavir dolphin, the spine of the scapula is noticeably separated from its anterior margin and the prespinous fossa is, therefore, more visible than in present-day forms. The glenoid cavity is very deep and oval. The height of the scapula is 110 mm, maximum width (distance between anterior and posterior angles) 135 mm, length of anterior margin 92 mm, length of the coracoid process 27 mm, width 10 mm, length of acromion 47 mm and width 25 mm.

The sternum (Plate VIII, Fig. 1) is extremely massive and spatulate. The body is almost of the same length as the sternebrae. It is considerably enlarged and quadrangular. In the anterior part, the body is bent, forming a distinct downward angle. The jugular notch is extremely deep, while the clavicular notch is faint. On the dorsal body surface, almost at the center, there are two crescentic symmetrical cavities. The lower angles of the body are intensely flattened and project as processes. The articular facets for the first pair of ribs are located on the body. Articular surfaces for the second pair of ribs are located in an angle formed between the body and sternebrae (angulus ludovici). Sternebrae considerably narrower than body. On it, the articular facets for the third and fourth pairs of ribs are located one behind the other. The distance between the facets of the third and fourth ribs is double the distance between the articular facets for the preceding ribs. The posterior end of the bone is concave. The maximum length of the sternum is 145 mm, length of body 74 mm, width of body 92 mm, width of sternebrae in the midportion 54 mm, thickness of bone 18.5 mm and width of jugular notch 32 mm.

In the collection studied, ribs of the right side, I, III, V, VI, VII, VIII, IX and X are preserved and on the left, only the first, third
43 and fourth. Ribs of the first pair are shorter than the rest and highly arched. Length of succeeding ribs increases gradually, reaching the maximum in the sixth or seventh, and then the sizes decrease again. The minimum radius of arc (along the inner surface) is in the first rib and maximum in the tenth. Each rib is in the form of an arched bone with a flattened head on the upper end for articulation with the two adjoining vertebrae; the head is followed by a distinct neck with a ventral tuberculum articulating with the transverse processes of the corresponding vertebra. The distal ends (rib) are straightened in almost all the specimens. The angles are sharp, especially in the third, fifth, seventh and eighth ribs. The tuberculum is quite distinctly separated from the angle, even in the first rib, and the distance between these parts gradually increases caudally.

The distal part of the radius and two metacarpals available in the collection evidently belong to this species.

The radius is relatively long and thin. Of the articular surfaces of the distal end, the medial is longer than the lateral and is quadrangular; the lateral is triangular.

In the structure of the first and second cervical vertebrae and also in the form of lumbar vertebrae, especially their transverse processes, the Armavir dolphin differs sharply from *Kentriodon*. It differs from *Anacharsis*, described by Bogachev from the Sarmatian formations in the vicinity of Stavropol', in the structure of the cervical, lumbar and caudal vertebrae as also in the features of the sternum.

Less elongated lumbar vertebrae, the structure of transverse processes and also much larger dimensions distinguish the dolphin (Armavir) described from the Sarmatian *Imerodelphis thabagarii* Mch. The Armavir dolphin differs from *Cyrtodelphis* (Dal Piaz, 1903) in the shape and structural features of cervical vertebrae as also in the nature of development of the cervical region itself as a whole (cervical region of vertebral column among Armavir dolphins is relatively more massive than in *Cyrtodelphis*). Differences in the structure of the lumbar vertebrae of *Cyrtodelphis* are also significant. The articular surfaces of
44 lumbar vertebrae of *Cyrtodelphis* are oval and very broad; the transverse processes long, lamellar and constricted at the base. The lumbar vertebrae in my form, as already pointed out, have circular

articular surfaces, long and broad characteristically curved transverse processes.

The similarity in the structure of cervical, lumbar, and caudal vertebrae, sternum, and scapula with *Champsodelphis*, however, is quite significant. This prompts me to consider the Armavir form as belonging to one of the representatives of this branch of dolphins, *Champsodelphis fuchsii* Brdt. (Brandt, 1887).

44 **Table 18*. Dimensions (in mm) of first cervical vertebra of** *Champsodelphis* **cf.** *fuchsii* **Brdt.**

Total height of vertebra from midventral surface to apex of dorsal surface (approximate)	56–57
Anteroposterior thickness of lower half (including ventral† tubercle)	23
Anteroposterior thickness of lower half (without ventral tubercle)	16
Maximum width of vertebra—distance between tips of lower transverse processes (approximate)	90
Maximum distance between outer margins of anterior articular facets	72
Maximum distance between the inner angles of articular facets	40
Distance between ventral ends of facets	24.5
Maximum length of left articular facet	33.5
Length along inner margin	28
Maximum width of its surface	18
Maximum length of right articular facet	31
Length along inner margin	28
Maximum width of articular surface	21.5
Area of left posterior articular surface	20×16
Length of ventral tubercle	11
Area of articular surface for odontoid process of epistropheus	14×11

*There is no Table 17 in the text; apparently this is an inadvertent jump—General Editor.

†Ventral tubercle should read as hypapophysis—General Editor.

45 **Table 19. Dimensions (in mm) of second cervical vertebra of** *Champsodelphis* **cf.** *fuchsii* **Brdt.**

Total height of vertebra	67
Maximum width (distance between tips of transverse processes)	82
Length of centrum along ventral surface	20
Area of right articular surface	20×16
Area of left articular surface	19×14
Height of posterior articular surface	21
Width of posterior articular surface	28.5
Length of transverse processes	12
Height of neural spine from dorsal surface of neural arch to apex of spine	28
Distance from base of neural arch to apex of spine	46.5

45 **Table 20. Dimensions (in mm) of first cervical vertebra of fossil dolphins**

		Kentriodon pernix Kell.	*Anacharsis orbus* Bog.	*Ch.* cf. *fuchsii* Brdt.
Height of vertebra from midventral surface to the apex of dorsal surface		37.6	40–42	57
Anteroposterior diameter at the ventral half, i.e. anteroposterior thickness		15	17	28
Maximum width of vertebra (distance between tips of transverse processes)		60 (67)	80	90–92
Distance between articulator surfaces	between inner edges of upper end	27	—	42
	between outer edges (maximum)	48.4	58	71–72
	between lower angles	84	20	26

46 **Table 21. Dimensions (in mm) of vertebrae of *Champsodelphis* cf. *fuchsii* Brdt.**

	Cervical IV	Thoracic V	Lumbar vertebrae	Caudal									
				VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI
Length of centrum	7	20.5	35	33	29	28.5 29	29.5	26.5	28.5	20	15.5	12.5	10.5
Maximum width of vertebra (between tips of transverse processes)	—	—	133	39 34	37 31.4	34 28.5	29 26.5	25.5 24	24 23	22.5 22	24 23	27 27	25.5 26.5
Width of anterior articular surface	29.5	26.5	30	30	31	28.5	27	23.5	22	21	22	22.5	20
Height of anterior articular surface	21.5	20	30	27	27	27	26	28.5	22	21	19	15.5	12.5
Width of posterior articular surface	—	25	32	29	28	26.5	24.5	23	21.5	21	22.5	21.5	18
Height of posterior articular surface	—	24	33	32.5	26.5	26	25.5	23	21.5	20	18	15	12
Width of neural canal	17	18	10.5	3	3	3	3	3	2	—	—	—	—
Length of transverse process	—	—	51.5	—	—	—	—	—	—	—	—	—	—
Width of transverse process	—	—	26	—	—	—	—	—	—	—	—	—	—

47 **Table 22. Dimensions (in mm) of second cervical vertebra of fossil dolphins**

	Kentriodon pernix Kell.	*Anacharsis orbus* Bog.	*Ch.* cf. *fuchsii* Brdt.
Maximum height	57.7	—	67
Length of centrum along lower contour	16.7	15	20
Maximum width	62.5	59	82
Area of right articular surface	—	17×12	21×16
Area of left articular surface	—	—	19×14
Width of posterior articular surface	—	23	29
Height of posterior articular surface	—	17	21
Length of transverse process	—	9	12
Height of transverse process	—	7	10.5
Thickness of transverse process	—	3.5	8

Champsodelphis cf. *letochae* Brdt.

Material. A fragment of left ramus of lower jaw (postsymphysial specimen No. 018, collection of AKM).

Site. Armavir. Left bank of Kubana River, ravine at Akhtamar.

Geological age. Middle Sarmat.

Description of material. The fragment of lower jaw corresponding to the postsymphysial part (Plate VI, Fig. 3) is noticeably curved along the long axis, the ventral edge rounded in the anterior half and angular in the posterior. The upper and lower edges are curved dissimilarly. The outer surface of the jaw is flat and the inner somewhat convex. Nine fairly distinct alveoli are preserved on the fragment. The interalveolar partitions are almost vertical. Alveoli are shifted toward the outer surface, and there are two teeth per centimeter length of jaw. Length of fragment 63 mm, height 18 mm, thickness 9 mm, diameter of alveolus 3.5 mm and thickness of interalveolar partitions 1.25 mm.

The size, characteristic curvature of lower jaw and also the shape, size and disposition of alveoli leads us to identify the jaw as that of *Champsodelphis* cf. *letochae* Brdt.

48 *Champsodelphis* sp.

Material. Two incomplete limbs and scapula.

Site. Armavir, left bank of Kubana River, ravine at Akhtamar.

Geological age. Middle Sarmat.

Description of material. Scapula triangular. Vertebral margin elongated and gently curving (almost straight); anterior, evidently straight (slightly damaged). Posterior margin in the upper section straight, in the lower (closer to the articulation) curved. Posterior angle rounded. Acromion flat. Coracoid process flattened, expanded distally, with a rounded tip. Glenoid cavity deep and elliptical. On the inner surface of the scapula, there are four faint oblong ridges; spine of scapula maximally shifted toward the anterior edge; there are three radial cavities to the right of it on the upper surface.

Humerus of right limb characterized by fairly long, flattened and curved shaft. The head of humerus hemispherical and located on the medial side; lateral to it is an unpaired tubercle on which two protuberances are noticed; one is ridge-like and the other conical. Between them is a horizontal plate, which is continued into a small cavity on the lateral surface of the bone. The lines surrounding the head are well-expressed even in the region of the tubercle. Deltoid ridge faint. On the lateral surface, roughly in the midportion of the bone, is an oval depression. At the distal end, articular facets for ulna and radius are distinct.

The bone described is characterized by its large dimensions: length 67.5 mm and width at the distal end 39 mm.

Ulna expanded at ends. Medial margin more gently curved than the lateral. Olecranon process well-developed; surfaces for articulation with the humerus, the medial margin of the radius and the carpals are also well-developed. At the ends, especially the proximal, the bone is very thick.

Radius flat and curved. Of the proximal row of carpals, only the ulnare and intermedium are present. The distal row has a single carpal having the shape of an 8 formed by the fusion of Ca (4) and Ca (2+3). We do not come across anything like this carpal in any of the
49 known fossil forms. In the present-day dolphin (*D. delphis*), however, such a feature has been observed as an extreme rarity.

Ulnare is pentagonal, its distal angle being more acute than the other. Lateral margin flattened, medial comparatively thick. Maximum length of bone 15 mm and width 23.5 mm.

Intermedium hexagonal with rounded angles, with a considerable right-angle lateral projection. Maximum length of bone 18 mm, width 28 mm and thickness 11.5 mm.

The surface of Ca (4) and Ca (2+3) are rounded dorsally. From the ventral side, the angles are more distinct and form a hexagon.

Humerus of the left limb long, almost equal to that of the forearm. Head of humerus tapering longitudinally. Unlike the humerus described above, the tubercle is considerably rounded and the boundary between it and the head eroded away, as a result of which the head has been gradually transformed into a tubercle. Deltoid ridge indistinct. A broad, long, distinct tubercle is present on the anterior margin of the bone. At the distal end, articular facets for forearm bones steeply inclined and the angle between them more acute than in the right limb.

The radius is almost similar to that of the right limb, but somewhat narrower and of uniform thickness all along its length. The shape of the ulna is quite typical. The proximal margin of the bone in the right limb is even, medial and angular. In the left limb, the medial angle is rounded and the proximal tapered. The prominent feature of the carpals is the greater development of the intermedium and its more rounded form compared to the right limb. In spite of all these differences, I have placed both the limbs tentatively in the same species since their similarity is quite significant.

Genus Cyrtodelphis Abel, 1900

Cyrtodelphis sp.

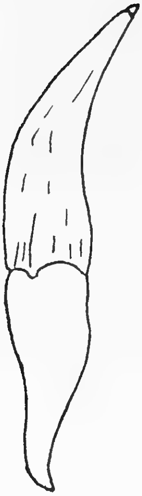
Material. Two teeth from the midsection of jaw (specimen No. A1-A2, collection of IPB).

Site. Armavir, left bank of Kubana River.

Geological age. Middle Sarmat.

Description and comparison. The tooth from the midsection of jaw (Fig. 8) is typical. Crown conical. In the basal part, it (crown) is
50 almost vertical, compressed anteroposteriorly and weakly constricted. In the midportion, crown intensely curved (almost geniculate) and in the upper part, sharply constricted and terminating in an apex. Enamel smooth. At the junction of root and crown, the tooth is noticeably constricted. Root highly compressed laterally, broad and long (although still shorter than the crown). There are two very distinct projections on the lateral surface of the upper part of the root. Below the tubercles, the root gradually tapers in the lower one-third of length sharply tapering and ending in a reversely directed tip. The crown and root bend in different directions and are flattened in mutually perpendicular planes (root flattened laterally and bent backward and the crown anteroposteriorly and bent lingually).

The second tooth is considerably damaged. The apex of crown and the lower one-third of root broken. The preserved portion of tooth reveals the very same features as were shown for the preceding specimen. The teeth described here somewhat resemble the posterior teeth of *Kentriodon pernix* (Kellogg, 1927, p. 33) and are also charac-
51 terized by a cone-shaped, pointed and inwardly bent crown, smooth enamel and, at times, even by the presence of tubercles on the roots. However, the teeth of the Armavir dolphin differ from those of *Ken-*



50 Fig. 8. *Cyrtodelphis* sp. Tooth from midsection of jaw ×^{4}, buccal surface.

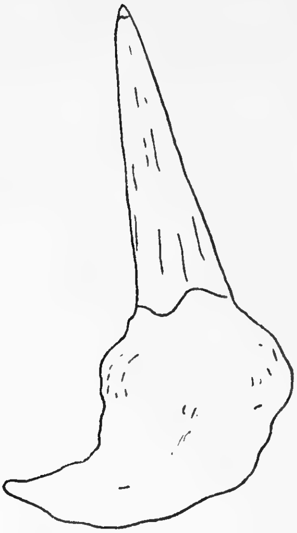


Fig. 9. *Cyrtodelphis* sp. Tooth from midsection of jaw ×^{4}, lingual surface.

triodon in the presence of a sharp constriction at the boundary of the crown and root, a typically pointed and intensely bent crown, type of root flattening and also even the dimensions (see Table 23).

The teeth of the Armavir dolphin differ also from those of members of the genus *Champsodelphis* (Brandt, 1873) in having a thick, low, slightly bent crown with hook-shaped tip and thick, nearly cylindrical roots.

The teeth described here differ from those of *Anacharsis orbus* Bog. (Bogachev, 1956) in their large size, absence of bulge at the boundary of crown and root, general shape of crown and the characteristic root structure.

There are significant differences also from the teeth of the Sarma-

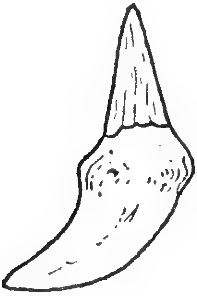


Fig. 10. *Cyrtodelphis sulcatus* Ger. Tooth from midsection of jaw ×^{2} (after Dal Piaz).

tian dolphin *Imerodelphis thabagarii* Mch. (Mchedlidze, 1959) as shown by the small size and sharply pointed root and crown.

The high, conical and inwardly bent crown and also the typical form of root bring these teeth close to those of the midsection of the jaw of *Cyrtodelphis sulcatus* Ger. (Dal Piaz, 1905, p. 213). However, the intense constriction, typically pointed crown and the relatively short root with tip sharply bent backward also differentiate them from those of *Cyrtodelphis.*

52 **Table 23. Dimensions (in mm) of teeth of fossil dolphins**

	Anacharsis orbus Bog.	*Kentriodon pernix* Kell.	*Champsodelphis* sp.	*Imerodelphis thabagarii* Mch.	*Cyrtodelphis sulcatus* Ger.	*Cyrtodelphis* sp.
Total tooth height	9–10	15	7	10–11.5	2.7	14.5
Length of crown	5–6	6.5	5	5.5	10	8
Diameter of crown	2	2.9	—	1.75–2	5.5	2.5–3
Diameter of root	1.5	3.2	—	1–1.5	—	4–3
Diameter of root tip	—	0.8–1	—	—	—	—

Cyrtodelphis bogatshowi Mch., sp. nov.

Type species. Incomplete skull (specimen No. 222, collection of Zardabi EIM).

Site. In the vicinity of Perekishkyul village, left bank of Sumgait River.

Geological age. Miocene.

Diagnosis of species. Skull low. Maxillae nearly horizontal all along their length. Width of rostral base hardly more than one-half the width of cranial portion of skull. Premaxillae almost as wide as maxillae and extend beyond the line of posterior margin of nasal opening. Prenasal plate slightly compressed and bordered by the sides of elevated medial margins of maxillae. Postnasal plate broad, trapezoid and noticeably caudally inclined. The highest point of skull shifted forward and approaches the posterior margin of nasal opening.

Along the sides of the postnasal plate, the frontal and, partly, the parietal form relatively broad bands, separating the supraoccipital from the maxillae along its entire length (almost as far as the temporal regions). Orbits located in the anterior part of the skull. Ventral surface of rostrum in the posterior portion flat, without ridges and lateral grooves.

Description and comparison. The skull is incomplete (Figs. 11 and 12). The rostrum and supraorbital part of maxillae broken. In 53 the occipital region, only an insignificant part of the supraoccipital with a well-developed ridge preserved. Rostral base greatly enlarged. Its margin forms an angle of 45° with the line joining the preorbital grooves. In the proximal part of the rostrum, maxillae are broader than premaxillae. Part of maxillae from the preorbital groove to posterior margin of fossae maxillare noticeably laterally inclined.

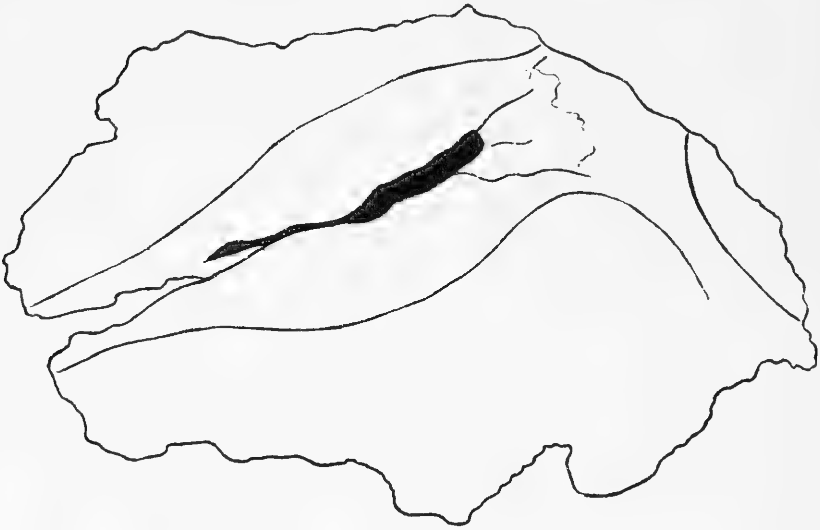


Fig. 11. *Cyrtodelphis bogatshowi* Mch. Skull, dorsal view.

Their posterior margin arched (of dolphin type). Premaxillae separated by a broad, distinct cleft all along the length of the preserved portion of rostrum right up to the anterior angle of nasal opening. The premaxillae broadened in the prenasal region and form a greatly inclined, elliptical prenasal plate. The lateral margins of the plate, unlike those of *D. delphis* L. and *Iniopsis caucasica*, do not rise above the maxillae. They are somewhat compressed and bordered from the sides by the raised medial edges of the maxillae. Premaxillae flank both sides of nasal orifice and reach beyond the line of its posterior margin abutting the frontals. Nasals damaged. They are placed between intensely constricted horizontal portions of premaxillae. Nasal opening oblong-triangular.

54 Postnasal plate broad, not rectangular. Anteriorly, it is relatively narrow and posteriorly greatly expanded. Lateral margins somewhat curved, general form close to a trapezium. Along the sides, the postnasal plate merges into relatively broad bands separating the supraoccipital and maxillae all along the arch of the skull (almost as far as the temporal regions). These bands are formed mainly of frontals and partly also of parietals. Postnasal plate inclined caudally, unlike all other known fossil and modern forms. Therefore, the apex of skull is shifted forward and is close to the posterior margin of the nasal opening.

The lower surface of the posterior part of the rostrum is low and flattened without a ridge and lateral grooves.

The characteristic features of this form are the highly developed ridges on the medial margins of the maxillae, presence of a broad band of frontals between supraoccipital and maxillae, typical form and nature of inclination of postnasal plate and also the forward location of orbits in the skull. This, along with the slight shift of occipital elements on to the frontal portion and relative flattening of the skull as a whole, clearly point to its antiquity.

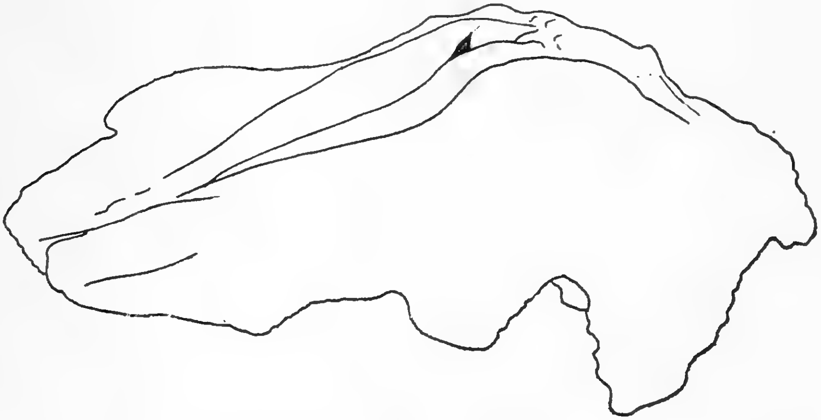


Fig. 12. *Cyrtodelphis bogatshowi* Mch. Skull, lateral view.

In the arcuate posterior margins of its maxillary fossae and the significant width of preorbital grooves and shape of the preorbital process, the skull described here somewhat resembles that of the skull of *D. delphis* L. The former differs from the latter, however, in the
55 orientation of the lateral margins of the rostrum and the structure of the prenasal plate (the latter in *Delphinus* overlies the maxillae in the rear) and also in the small, elongated nasal opening, extremely cons-

tricted and horizontal posterior part of premaxillae, the form of postnasal plate and presence of broad bands of frontals on the roof of the skull, reaching almost to the temporal regions.

The structure of the ventral surface of the rostrum, its broad basal part, and also the position of its lateral margins, presence of broad clefts between the premaxillae and several other features bring the form under description somewhat close to *Leptodelphis stavropolitanus* Kirp. (Kirpichnikov, 1954). However, the former differs from this species in the greatly broadened maxillae, raised medial margins of maxillae, shape of maxillary fossae, structure of prenasal plate, structure of postnasal part, the greatly inclined supraoccipital, etc.

Similarity with *Iniopsis caucasica* Lyd. is noticed in the fairly horizontal disposition of the maxillae all along the length, in the shape (but not disposition) of the prenasal plate, in the presence of a broad cleft between the premaxillae, in the formation of a broad postnasal plate, in the nature of the palatal surface, and also in its fairly low and flattened skull. However, the dolphin described differs from *Iniopsis* in a whole series of important features. Thus, for example, the maxillary fossae are less deep than in *Iniopsis*, the posterior margins of the maxillae are curved and the medial margins form a bed for the slightly compressed prenasal plate. The corresponding margins of the maxillae of *Iniopsis* are overlaid by the margins of the prenasal plate. The postnasal plate is trapezoidal and not elevated above the level of the posterior margins of the maxillae, while in the skull of *Iniopsis*, the same region is rectangular in shape, horizontal and noticeably elevated above the level of the posterior margins of the maxillae. The form described here differs from *Iniopsis* also in the presence of a broad band of frontals in the arch of the skull, this being a characteristic feature of the genus *Cyrtodelphis* (Dal Piaz, 1905, p. 196/10).

With the greatly enlarged rostral base and the structure of its ventral surface, the form of the posterior margin of the maxillary fossae, considerably enlarged maxillary bones in the orbital region, presence
56 of a broad cleft between premaxillae reaching up to the anterior margin of nasal opening, form of prenasal expansion of premaxillae and the extent of their expansion to the posterior of the nasal opening, as well as the form of postnasal plate, the skull described here is closer to that of *Cyrtodelphis sulcatus* Ger. (Dal Piaz, 1903). However, the presence of such features as the greatly developed medial margins of maxillae, slope of the broadened portions of the same bones, the presence of very broad, long and characteristic bands of frontals on the arch of the skull, and also the relatively flattened and low skull noticeably distinguished this species from the widely known dolphin *C. sulcatus* Ger.

Therefore, we place the dolphin under description as a new species of the genus *Cyrtodelphis* in honor of the earliest investigator of fossil cetaceans of the Caucasus, V.I. Bogachev.

A comparison of the skull of *C. bogatshowi* with those of various dolphins helped in making the following observations.

Generally, the frontal region of the skull of most dolphins, at the midlength of the prenasal plate, rises sharply and forms a distinct angle with the occipital. Later the broadened portions of the maxillae become horizontal in the orbital region, the prenasal plate rising with its lateral margins above the maxillae slightly bending around the midsagittal line. The frontal bulge forming a quadrangular postnasal plate in some forms is most often horizontal or slightly inclined forward.

In *C. bogatshowi*, the frontal region of the skull rises gradually and imperceptibly, while the maxillae take a horizontal position all along their length. Along the midsagittal line, the skull is slightly elevated, as a result of which the maxillae are inclined laterally which is especially distinct in the prenasal region. The postnasal plate, however, as pointed out above, is inclined caudally. The inclination of postnasal and prenasal plates relative to the vertical plane running through the
57 apex of the skull is almost identical. Therefore, the high point of the skull seen in most forms at the level of the supraoccipital ridge is shifted to the level of the posterior margin of the nasal opening.

The structural features of the skull of *Cyrtodelphis bogatshowi* Mch. pointed out above, viz. the elevation of the frontal region along the midsagittal line, caudal inclination of postnasal plate and the forward shifting of the apex of the skull associated with it, i.e. proximity to the nasal opening, evidently facilitated the elevation of the spiracle. In my opinion, such a structure could serve as a unique adaptation to aquatic respiration for forms with such a flattened and low skull as that of *C. bogatshowi.*

Family MONODONTIDAE Gray, 1821

Genus Delphinapterus Lacépède, 1804

Delphinapterus sp.

Material. Four caudal vertebrae (specimen No. S19, collection of IPB).

Site. Tsasri village (Chiatur region).

Geological age. Karagan.

Description and comparison. The centrum of caudal vertebra perceptibly longer than wide. Centrum constricted in the middle and expanded at articular surfaces. Articular surfaces oval and slightly wider. Concentric lines distinct on them.

Table 24. Dimensions (in mm) of caudal vertebrae of some Delphinapteridae

	Delphinapterus fockii Brdt. (after Brandt)	*Delphinapterus nordmanii* Brdt. (after Brandt)	*Archaeocetus fockii* Brdt. (after Makarovici)	*Delphinapterus* sp.			
				1	2	3	4
Length of centrum	84	85	75–60	67	60.5	67	—
Width of posterior articular surface	81	64	55–45	59	56	63	—
Height of posterior articular surface	63	54	55–45	56	56	53	—
Width of anterior articular surface	72	69	67–47	60	—	60	55
Height of anterior articular surface	60	55	65–47	54	54	55	48

Base of transverse process arises almost from the very edge of the posterior articular surface and occupies more than one-half the length of the lateral surfaces of centrum.

Bases of neural spine poorly preserved. Width of neural canal insignificant. The ridge on the midventral surface smooth, but evidently bifurcated at the ends. Bases of transverse processes perforated with round foramina.

In its structural features, this vertebra resembles closely the caudal vertebrae of some Delphinapteridae *Delphinapterus fockii* Brdt., *Delphinapterus nordmanni* Brdt., and *Archaeocetus fockii* Brdt. (Makarovich and Oesku, 1942); in these forms the vertebrae are, however, somewhat smaller.

58 Suborder MYSTICETI Flower, 1864

Family CETOTHERIIDAE Cabrera, 1926

Genus Imerocetus Mch. gen. n.

Type species *Imerocetus karaganicus* Mch. sp. n.

Material. Incomplete skull and the right tympanic bulla (specimen No. 146, collection of IPB).

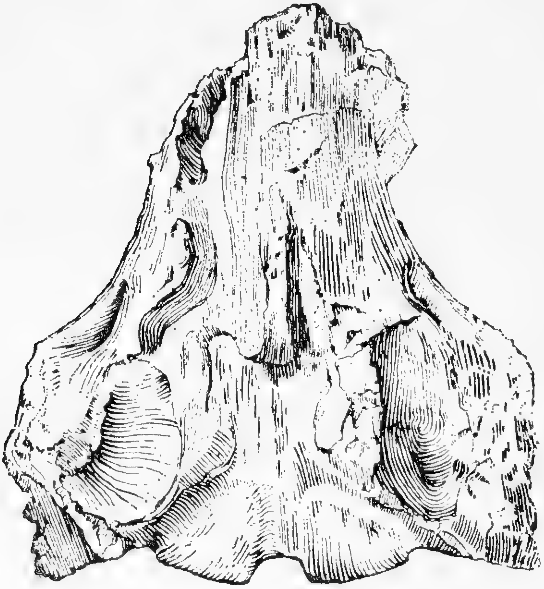
Site. Sachkher region, Dzhalaurt village.

Geological age. Karagan.

Diagnosis of genus. Small sized animal. Skull fairly horizontal. Cranial part of skull narrow and oblong. Supraoccipital shield greatly inclined caudally and arched. The anterior angle of shield reaches only to the middle of temporal fossae. Lateral ridges [of occipital shield. Ed.] are in the form of wing-like lobes. Ventral portions of occipital condyles situated almost on the ventral surface of skull. Lateral walls of cranium high. Their dorsal margins are close to midsagittal line. The lateral wall of skull is formed of parietal, squamosal and pterygoid bones. The highly developed parietal covers the entire 59 length of the lateral wall as far as the posterior angles of the skull. Squamosal is displaced ventrally and is in the form of a narrow strip. Suture between parietal and squamosal parallel to the lateral ridge [of the occipital shield. Ed.]. Distance between anterior angle of occipital shield and base of nasals hardly more than the height of skull from the upper edge of the foramen for the exit of second cranial nerve to the apex of the occipital shield. Base of occipital bone broadened. Basisphenoid not covered over by vomer. The posterolateral angles of skull set ventrally and backward.

Humerus long; edges of radius and ulna parallel all along the length of shaft.

60 Fig. 13. *Imerocetus karaganicus* Mch. Skull, dorsal view.



61 Fig. 14. *Imerocetus karaganicus* Mch. Skull, ventral view.

Description and comparison of material. The skull represented by cranium with well-preserved occipital region. Rostrum and zygomatic arch completely lost (Figs. 13 and 14).

The cranium, unlike that in most Cetotheriidae, is narrow and elongated. The supraoccipital shield is triangular without the medial ridge and oval fossae. Surface of shield considerably inclined caudally and depressed. The lateral ridges greatly elevated, flattened from the sides and wing-like. In the anterior half, the ridges are horizontal, later descend sharply downward and extend back to the level of the ventral margin of the occipital foramen. Exoccipitals short and slightly curved laterally. The posterior margin of the skull, at the level of the posterolateral angles of the occipital shield, unlike Upper Miocene whales, is considerably constricted. Anterior angle of occipital bone very pointed and reaches only up to the middle of the temporal fossae.

Occipital condyles slightly bulged and half-moon shaped. Lower half of condyles expanded and turned ventrally so much that they partly occupy the ventral surface of the skull, forming a part of the skull base. Ventrally, the condyles are distinctly set off from the adjoining sections of the occiput by an elevated margin and their pointed upper half is almost fused with the rest of the occipital surface.

The medial margins of the ventral part of the condyles are straight, separated by a broad groove. Occipital foramen oval and high.

In most Cetotheriidae, nasals commence roughly at the level of the exits of the second pair of cranial nerves; in this form, they occupy a considerably more anterior position (distance between the bases of
60 nasals and a point above nerve openings is equal to the height from the dorsal border of foramen magnum to the apex of skull).

The posterolateral angles formed by exoccipitalia of occipital bone were missing in my specimen, but judging from the portions preserved, they could not have been particularly massive and were directed downward and backward (in specimens of Cetotheriidae known to me, these angles were set sideways, hardly backward).

Lateral wall of cranium is high and long, formed of parietal, squamosal and pterygoid. Of these, the oblong parietal extending to the middle of the supraorbital ridge of the frontal constitutes the largest part. Parietals situated wholly posterior to nasals and descend in a line 45 mm long.

61 The squamosal, as a result of the abnormal growth of the parietal, is displaced towards the ventral margin as a narrow band. Sutures between these bones are parallel to the lateral ridge of the shield; while in almost all members of the Cetotheriidae known so far, they are perpendicular to the lateral ridge of the occipital shield and are

bent ventrally. The squamosal occupies the posterior half of the lateral wall.

The triangular pterygoid is wedged between the parietal and squamosal in the posterior border of the foramen for the second cranial nerve. In this species, it occupies not the ventral, but the lateral position. The pterygoid and parietal border the posterior side of the opening for the above nerve.

The frontals form a fairly broad band in the interorbital space. The distance between the anterior angle of the occipital shield and the base of the nasals is noticeably large, being nearly equal to the height of the skull at the anterior angle of the occipital shield.

Basioccipital broad and massive. Tubercles for muscles somewhat
62 damaged, comparatively small, but intensely convex. The medial angles of these tubercles not closely placed.

Basisphenoid not covered by the flattened posterior plate of the vomer. Here vomer reaches only to the level of posterior margins of the oval foramina; while in most Cetotheriidae it almost completely covers the basisphenoid and reaches back to the posterior angles of the muscle tubercles. Ridge of vomer high and greatly flattened posteriorly. Palatine plates thin and placed close together medially toward the ridge of the vomer in the anterior as well as posterior sections.

The alisphenoid canal is parallel to the base of the skull and runs close to the lateral margin of the ventral surface of the cranium.

The above description shows that the elements of the posterior as well as the posterolateral parts of the skull (squamosum, exoccipitalia, and also con. occipitalis) in my specimen are located posteroanteriorly, while in the Upper Miocene members of Cetotheriidae known to me, they are located in a fairly dorsal position.

These features of *Imerocetus* are evidently associated with a weak shifting of the occipital elements on to the frontal region of the skull. On more intense shifting of the occipital elements, the above bones are evidently gradually displaced upward and forward.

Consequently, the shifting of occipital elements and interlocking of the medial-rostrals in *Imerocetus* stand at a much lower level than in the Upper Miocene members of the Cetotheriidae.

The skull of *Imerocetus* resembles in several features the members of the genus *Plesiocetus* from the Upper Miocene of California (Kellogg, 1934, p. 232). In both forms, the parietals occupy a significant area of skull surface and extend anteriorly to the middle of the supraorbital ridge of the frontal; the lateral walls of the cranium are high and relatively vertical; their upper margins are placed close together sagittally. There is great similarity in the structure of the occipital condyles and also in the entire axial region of the skull base; the basioccipital in both forms is enlarged and the basisphenoid not covered by the flattened plate of vomer.

However, in the Californian species, the parietals are not as inten-
63 sely developed as in *Imerocetus*. In it, they do not reach the posterior margin of the lateral wall, the squamosal is not displaced ventrally and the suture between the parietal and squamosal is perpendicular to the lateral ridge.

The occipital shield of *Plesiocetus* was evidently broader with a weakly pointed anterior angle than in my forms. On the whole, the cranium of Dzhalaurt *Cetotherium* is much longer than in *Plesiocetus*.

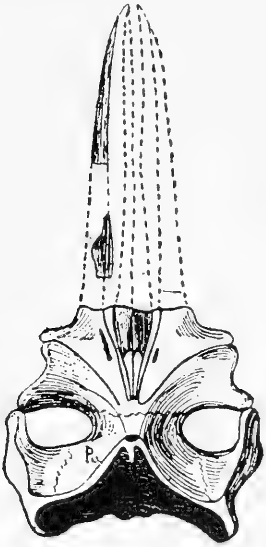


Fig. 15. *Cetotherium rathkei* Brdt. Skull, dorsal view (after Brandt.)

The Dzhalaurt *Cetotherium* differs from other members of the genus *Cetotherium*—*C. maicopicum* Spass. (Spasskii, 1951), *C. vandellii* Brdt. (Brandt, 1874), *C. rathkei* Brdt. (Brandt, 1874), etc. in the structure of the occipital shield, the highly developed pterygoid, lateral ridges of occipital, posteriorly inclined occipital shield, shape of foramen magnum, characteristic structure of the comparatively small occipital condyles, structure of lateral walls of cranium, the intensely developed parietal and ventrally displaced squamosals, and also in the structure of the axial part of the ventral surface of the skull. In all the skulls of the Upper Miocene Cetotheriidae, the basisphenoid is covered
64 over by the flattened plate of the vomer, but in the skull described by me, the vomer does not form a plate covering the sphenoid.

The skull of the Dzhalaurt whale differs from that of the Upper Oligocene *Cetotheriopsis linziana* Brdt. (Brandt, 1874) in having an elongated, intensely pointed occipital shield and laterally curved posterior angles of the skull. However, there is also some resemblance between the two in the highly developed lateral ridges of the occipital shield and in the horizontal disposition of the cranium. The latter feature in this form sharply distinguishes it from the known Upper Miocene forms as also from the present-day whalebone whales.

Auditory bone. This is represented by the right tympanic bulla. Its dorsal surface is pear-shaped and slightly rugose along the lateral margin. The medial margin is a low distinctly arcuate ridge. The ventral surface is smooth, slightly angular and convex, unlike *Plesiocetus,* which has a flattened ventral surface (Zittel, 1894, p. 181). The lateral angle of its anterior end is spherically bulged and the medial somewhat flattened. The medial part of the posterior half forms a wedge-shaped surface.

A comparison of the skull of my Middle Miocene whale with those of typical members of Upper Oligocene (*Cetotheriopsis*), Miocene (*Cetotherium*) and Upper Miocene or Pliocene (*Plesiocetus*) genera showed that the Dzhalaurt form differs from them significantly.

With such features as the highly developed parietals, ventral disposition of squamosals and the posterior angles of the skull, the highly developed lateral ridges of the shield and the horizontal disposition of the cranium, the species described above may be regarded as a new genus of the family Cetotheriidae.

Evolution of whalebone whales is known to have proceeded toward an increase in the volume of the oral cavity (the change over to plankton feeding brought about the curvature of the skull and curving of the rami of the lower jaw (Kellogg, 1928, p. 185). In my view, considering this feature, the horizontal disposition of the cranial part of the skull, characteristic of the form described, and also the weak shift-
65 ing of the occipital elements on to the frontal portion should point to the antiquity of the structure compared with the known members of the genus *Cetotherium.* This is also confirmed by the geological age of my find and its proximity to the Upper Oligocene *Cetotheriopsis.*

In my view, the incomplete skeleton of the forelimb discovered by me in the very same formations two km south of the above site belongs to this same form (specimen No. 551, No. 52, collection of IPB).

The skeleton of the forelimb consists of humerus, radius, three metacarpals and phalanges (Plates XI, XII). The humerus constitutes two-thirds of the length of the forearm. The humerus is characterized by a fairly flat and considerably elongated shaft. The radial and ulnar margins are parallel almost all along the length of the bone (including also the proximal end). The lateral surface of the shaft faintly but uniformly bulges, the medial surface in the distal half is

Table 25. Basic skull measurements (in mm) of *Imerocetus karaganicus* **Mch.**

Length of skull from condyles to base of nasals	235
Length from condyles to anterior angle of occipital shield	175
Height of condyles	60
Width of occipital condyles at lower margin	28
Width of occipital condyles at midheight	31
Width from condyle to condyle	95.5
Width of foramen magnum	38
Height of foramen magnum	43
Approximate width between posterolateral angles of occipital shield	185
Length of lateral occipital ridge along the arch	195
Width of occipital shield at bend of ridge*	
Height of lateral walls	115
Height of parietal	93
Height of squamosal	21
Maximum width of basioccipital	60
Width of basisphenoid	36
Length of basisphenoid	60
Width at the anterior end of basisphenoid	27
Width at the posterior end of basisphenoid	30

*No figure given for this entry—Editor.

66 flat but, in the proximal, commencing from the lower edge of the tubercles to the middle of the ulnar region, bears a transverse protuberance. The radial margin of the shaft is slightly pointed, while the ulnar margin on the contrary is thickened. The thickness of the ulnar margin is equal to one-half the width of the distal end. The ulnar half of the bone is noticeably thicker than the radial.

The head of the humerus is spherical, without a neck, and is slightly inclined downward. Tubercles are located almost along a horizontal line. The greater tubercle is poorly developed and located close to the head of the humerus, while the lesser is better developed and noticeably laterally recurved. Its apex falls considerably below the proximal margin of the bone. The boundary between the head and the lesser tubercle is completely smooth. The groove between the greater tubercle and the head is very distinct. Sulcus bicipitatus is very faint between the tubercles.

The articular surfaces at the distal end are considerably damaged. Judging from the preserved portions, the angle between these surfaces is weakly pointed.

The characteristic features of this humerus are the considerable length of the shaft, parallel ulnar and radial margins, slight inclination of head, flattening of ulnar margin and the presence of an oblong blunt ridge on the inner surface. Length of humerus 183 mm, length of shaft 123 mm, width at distal end 81, width of shaft at the proximal end 74, thickness of bone at middle 48 and area of articular surface of head of humerus 78×71 mm.

The radius is greatly flattened and long. The medial and lateral margins are sharp all along the length of the bone, excluding the proximal and distal ends of the medial margin. The medial margin is straight, lateral margin in the upper portion arcuate and parallel to the medial in the lower portion. The bone as a whole is intensely flattened at the middle and somewhat thickened at the ends. Articular surfaces of distal as well as proximal ends are triangular-oval. The lateral surface is convex, the medial correspondingly concave. The length of the bone is 278 mm and width at the proximal end 50 mm.

Of the metacarpals, II, III and IV are preserved. Mtc II is expanded at the proximal and narrowed at the distal end. Mtc III is considerably elongated. Mtc IV is expanded at the distal end and, on the whole, somewhat flattened. The proximal ends of all metacarpals are thickened. The second digit has two phalanges and the
67 third and fourth, five (the end phalanges of these digits have not been preserved). Thus, the phalanx formula of the species described should be as follows: II—2, III—5–6, IV—5 and V—3.

The phalanges of the third digit, unlike those of others, are long, expanded at the ends and slightly flattened.

Judging from the bones described, the length of flipper, as a whole, should roughly measure 90 cm.

The humerus described here mostly resembles that of the genus *Plesiocetus* (Zittel, 1894, p. 181) and also that of modern gray whales *Eschrichtius* (Tomilin, 1951, p. 343).

Here it is appropriate to deal with the remains of other limbs of Cetotheriidae found by me in the neighborhood of Dzhalaurt. Attention should particularly be paid to the extremely large dimensions of the distal portion of the humerus (specimen No. S48, collection of IMP). The shaft of bone was considerably elongated, thickened and slightly expanded at the distal end. At the middle, its outer surface carries an oblong tubercle below which the bone is noticeably flattened. The articular facet for the radius is rounded-oval. The ulnar facet, which also includes the facet for the olecranon process, consists of three plates located in different planes.

The proximal part of the humerus is also very large with a well-preserved spherical head (specimen No. S36, collection of IPB). The head is not separated from the shaft by a distinct neck and is slightly inclined relative to the long axis of the bone. In general, this bone is similar to the humerus of the limb described above (specimen No. S51, collection of IPB), but differs from it only in its much larger dimensions.

The shaft of the humerus (specimen No. S49, collection of IPB), obviously belonging to a young specimen, is also worth noting. It has a noticeable thickening of the ulnar margin and a crestate radial margin. The ulnar and radial margins of the shaft are parallel. It differs from the upper arm bones described above in its relatively small width and flattening.

Note. The upper arm bones of Middle Miocene (Karagan) whalebone whales of Western Georgia studied by us are characterized on the whole by a significantly long and broad shaft, faintly inclined
68 terminal head, parallel radial and ulnar margins all along the length of the shaft and shortening of olecranon facets. Thus, these cetaceans are characterized by a typical combination of progressive (weakly developed olecranon process) and primitive (considerable elongation of humerus) features of limb structure.

Genus Cetotherium Brdt., 1843

Cetotherium cf. *mayeri* Brdt.

Material. Six thoracic vertebrae, scapula, fragments of humerus and ribs belonging to the same specimen (specimens No. S104, S105, S106 and S107).

Site. Dzhalaurt village (Sachkher region), left bank of Rkviani River.

Geological age. Konksk epoch.

Description and comparison of material. Of the cervical region, only 5, 6 and 7 and impressions of centrum of third and fourth vertebrae are preserved.

Vertebrae are greatly shortened, have a discoid centrum and circular articular surfaces. Articular surfaces of vertebrae of thoracic region triangular-rounded or rounded, neural foramen considerably broadened in them. The ventral surface of the centrum is smooth.

The scapula was found together with a part of the humerus. The margins of the scapula (vertebral, anterior and posterior) are some-
69 what damaged. However, it is nevertheless possible to reconstruct the general contour of this bone based on the preserved parts. The scapula was evidently flabelliform. The spine of the scapula very weakly developed, almost smooth. The coracoid rudimentary. Acromion was lost.

The humerus is incomplete. The proximal end is greatly damaged. The distal section, comprising roughly a third of the total length of the bone, is quite well-preserved. The shaft was evidently somewhat elongated.

The epiphysis of the distal end of the humerus as well as the epiphyses of all the above described vertebrae are incompletely fused.

68 **Table 26. Measurements (in mm) of vertebrae of *Cetotherium* cf. *mayeri* Brdt.**

	Cervical vertebrae			Thoracic vertebrae				
	No. 5	No. 6	No. 7	No. 2	No. 3	No. 4	No. 5	No. 6
Length of centrum	12	13	18	32	33	35	35	37
Width	47	48	—	—	56	57	58	—
Height	45	46	—	48	50	48	55	—
Width of neural spine	35	35	—	—	30	27	—	—

In the basic structural features of the preserved parts of the skeleton, the form described stands close to *C. mayeri* Brdt. (Brandt, 1873, Plate XI), but the structure of the slightly elongated humerus is somewhat similar to the Karagan forms.

I also found innumerable fossil remains of whales in the Middle Miocene (Karagan ?) and Upper Miocene (Lower Sarmat) formations of the Terdzhol' region (Zemo-Sazano and Rupoti), but the unsatisfactory state of preservation of the material does not permit me to ascertain their taxonomy.

Cetotherium maicopicum Spass.

Material. Incomplete skull, fragment of left ramus of lower jaw, humerus, vertebrae and scapula belonging to different individuals (specimens No. S144, S131, S141, S142, S152, S125, S126, S128 and S130, collection of IBP).

Site. Maikop town.

Geological age. Middle Sarmat.

Diagnosis[1]. Animal of moderate dimensions. Brain case slightly wider. Occipital shield with medial ridge and fossae at anterior angle. Lateral ridges [of occipital shield. Ed.] nearly straight. The anterior angle of the shield reaches only up to the posterior margin of the temporal fossae. Lateral walls of skull almost vertical. The angle formed by the ascending process of the maxilla almost forms a right

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[1] Diagnosis was based on the data of Spasskii (1951) and of the author.

angle. Occipital condyles intensely convex. Mandibular rami faintly curved with flat, vertical lingual surface. Shaft of humerus flattened, 70 radial and ulnar margins parallel and the angle at the distal end of the bone slightly pointed.

The vertebrae show faint pachyostosis. Articular surfaces of lumbar and caudal vertebrae with three broad concentric bands.

Description and comparison. The cranial portion of the skull (Plate XIV) has been preserved. Rostral portion missing at the level of nasals; supraorbital ridges of frontals and the zygomatic processes are also missing.

The roof of the cranium formed by the supraoccipital is in the form of an isosceles triangle. Anterior angle of supraoccipital shield reaches only to the posterior margins of the temporal fossae. The middle portion of the skull roof is damaged as a result of which the broad cavity of the cranium is exposed. On the preserved portion of the occipital shield, commencing from the anterior angle, a medial vallate ridge runs, along the sides of which oval depressions lie close to the tip. The lateral portions of the occipital are flattened and somewhat rounded and directed posteriorly and sideways as a result of which a line running along the sides of the ridges of the shield is curved posteriorly. The surface of the bone slopes considerably caudally.

Occipital condyles comparatively small, highly convex and sharply raised in the lower as well as upper parts. The condyles are separated from the adjoining sections of the occipital bone by a sharp carinate edge. Height of condyles roughly one-half the height of the cranium. Their lower ends are quite widely separated by a groove. Condyles and posterior angles of supraoccipital shield are located on the same line. Foramen magnum oval, noticeably expanded in width. Lateral walls of cranium are formed of parietal and temporal bones of quadrangular form. Parietals occupy much of the lateral surface. In the posterior portion, they are located almost vertically and in the anterior, relatively displaced. Parietals not displaced from the roof of skull. They converge along the medial line of the surface of the brain case in front of the occipital shield (the length of line of contact is 33 mm).

The temporals take part in the formation of the lateral walls as well as the ventral surface of the skull. The glenoid fossa of the temporal is very shallow and the zygomatic process massive, directed backward and sideways. Its anterior surface is convex and the posterior flattened.

71 The basioccipital is slightly expanded. Tubercles for muscles triangular, somewhat shortened and placed close together. Directly abutting them is the posterior flattened portion of the vomer, covering the sphenoid and reaching up to the level of the medial angles of the

Table 27. Main dimensions (in mm) of skull of *Cetotherium maicopicum* **Spass.**

	My specimen	Spasskii's specimen
Width of skull with process	260	270
Length of lateral process	190	285
Height of cranium	110	
Height of condyles	68–70	
Width of condyles	33	
Width from condyle to condyle	100	
Width between posterior outer angles of muscle tubercles	74	
Maximum height of skull	107	
Distance between anterior angle of occipital shield and base of nasals	35	
Length of occipital shield along mid-sagittal line	115	
Length of nasals	72	
Maximum width of nasals	10	

muscle tubercles. A part of the sphenoid in the shape of a triangle emerges from under the parietal, posterior to the foramen for the second cranial nerve; the posterior margin of this foramen is formed by the lower portion of the parietal.

Only the bases of the flattened plates of the palatines, which in the natural position partly cover the vomer, are preserved.

The oval foramina are somewhat separated away from the lateral edges of the lateral skull surface.

The nasals were not completely preserved. They were evidently greatly elongated and expanded anteriorly.

The skull of *Cetotherium maicopicum* described here differs from that of *Cetotherium* aff. *mayeri* Brdt. from Derbent (Spasskii, 1954) in the
72 following features: lateral walls of cranium of Maikop *Cetotherium* are more vertical and the region between the temporal fossae more constricted than in the Derbent specimen: the angle formed by the ascending processes of the maxillae more sharp. The supraorbital processes of frontals more inclined. Moreover, these species differ from each other in the form of temporal arch (angular in Derbent and smoothly arcuate in Maikop), and also in the volume of brain case (length of cranial cavity of Derbent *Cetotherium* 144 mm and height 85 mm; the corresponding measurements in the skull of my specimen are 105 and 75 mm). The anterior angle of occipital shield in Maikop *Cetotherium* is less shifted forward than in the Derbent and the supraorbital process of frontals is wider.

The Maikop species differs also from *C. rathkei* Brdt. (Brandt, 1873) in several features of the skull. In the lateral portion, the occipital shield of *C. rathkei* Brdt. is notably constricted anteroposteriorly, the lateral ridges more inclined and medially intensely bent; while in my species, these ridges are considerably bulged. The posterior angles of the shield descend beyond a line drawn through the occipital condyles, sharply differing from the corresponding feature in *C. maicopicum* in which the condyles and posterior angles are located on the same line.

The parietals of Maikop *Cetotherium* are more perpendicular than in *C. rathkei* Brdt. The two species under comparison also differ from each other in the shape of the foramen magnum (round, slightly elongated in *C. rathkei* and oval and expanded in *C. maicopicum*) and in the features of the occipital condyles.

The Maikop *Cetotherium* differs from *C. helmersenii* Brdt. (Brandt, 1873, Plate 6), distinguished by its extremely scanty skull remains, in the more constricted anterior part of the cranium and the form of the occipital shield.

C. linziana Brdt. (Brandt, 1873, Plate 19, Fig. 1) with its intensely elongated and pointed shield, also differs from the Maikop form in the features of the lateral ridges (in *C. linziana* these are highly developed and the middle part of the shield is perceptibly deepened; while the ridges in the Maikop species are low and the middle part of the shield hardly bulged). Occipital condyles of *C. linziana* are less differentiated from the adjoining occipital area, while the condyles of *C. maicopicum*, as pointed out above, are sharply differentiated by sharp wedge-shaped edges.

73 The Maikop *Cetotherium* also greatly differs from *C. cuvieri* Brdt. (Brandt, 1873, Plate 20, Fig. 1) in the acutely pointed occipital shield shifted up to the orbital line, absence of medial ridge and slightly bulged surface of cranium.

C. cortesii Brdt. (Brandt, 1873, p. 153, Plate 21) differs from the Maikop species in its extremely broad intertemporal portion and less vertical lateral walls of cranium and also in the absence of a medial ridge.

C. vandellii van Beneden (Brandt, 1873, Plate 23) differs from the Maikop species in the presence of a medial ridge and oval depressions in the anterior angle of the shield, more vertical parietals, intensely posteriorly curved angles of exoccipitalia and the more sloping supraorbital processes of the frontals.

The left ramus of the lower jaw (Plate XV, Figs. 1 and 2) is incomplete. The anterior one-fourth and the posterior part up to the beginning of the coronoid process are missing. The jaw is long, anteriorly slightly narrow and slightly curved. The coronoid process is in the form of a long low flattened projection of the dorsal margin of the jaw and is bent medially in its posterior part. The outer surface of the jaw is considerably bulged, the inner flattened all along the length of the fragment. Height of jaw is gradually reduced anteriorly. The upper region of the jaw is very much sharper than the lower. The maximum bulge of the outer surface of the jaw is in front of the coronoid process. A shallow groove with faint depressions set at regular intervals runs along the inner surface of the posterior half of the jaw. Anteriorly, the groove gradually disappears and the faint depressions are replaced by sharp elongated alveoli.* The latter are seen on the outer as also the inner surfaces of jaw. However, on the former, they are more distinct; additionally, they are located at a relatively lower level than on the inner surface. In places, the depressions on both the surfaces are set in pairs (across the jaw), especially in the anterior part.

The jaw described is similar in many features to that of *C. maicopicum* (Spasskii, 1951) to which it probably belongs.

74 In lower jaw structure, *C. maicopicum* greatly differs from *C. mayeri* Brdt., the latter having a greater curvature of the rami of the jaw as well as an intensely convex outer and less flattened inner surface. Moreover, unlike the Maikop form, the rami of the lower jaw in *C. mayeri* are thicker and higher.

Along with the jaw described, I also found some fragments of lower jaws, evidently that of a young *C. maicopicum*, in the neighborhood of Maikop town, on the left bank of the Belaya River.

Table 28. Main dimensions (in mm) of the left ramus of the lower jaw of *Cetotherium maicopicum* Spass.

Length of fragment	750
Maximum thickness	45
Maximum height	67
Height of coronoid process	150
Distance between the outer row of alveoli and upper margin of jaw	17
Distance between the inner row of alveoli and upper margin of jaw	6

The scapula is flabelliform, sharply constricted and extended caudally. Dorsal margin of the blade straight. The cranial margin is flattened, extremely shortened and, in the posterior portion, notice-

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*These are probably foramina—Editor.

ably inwardly bent compared with the other margins. The posterior margin is almost equal to the dorsal in length and is also flattened. The anterior and posterior angles are rounded. The lateral surface is smooth and flat. The spine of the scapula is rudimentary, notably displaced toward the cranial margin. Judging from the preserved basal part, the acromion was evidently much flattened. The lateral margins of the process are parallel to each other: the lower margin is raised and the upper one occupies a horizontal position. Base of acromion massive and somewhat thick. Coracoid process projects close to the inner surface almost at the margin of the glenoid fossa. In my specimen, only the basal part of this process was preserved; but all the same, it showed that its dorsal margin lay almost on the 75 same line as the lower margin of the acromion. Between the spine of the scapula and the anterior margin of the bone lies the 25–28 mm wide rudimentary supraspinous fossa (fossa supraspinata). The poor development of this fossa evidently points to the reduction of the group of muscles associated with it, evidently due to a shift in the functions of the forelimbs (it is understood that the forelimbs in these animals were modified from organs of locomotion to organs of steering). The supraspinous region is smooth and flat without any trace of ridges or fossae, which also suggests a reduction of associated muscles. The medial surface of the blade has four radially diverging lines dividing the surface into an equal number of fairly raised bands (the first three from the anterior margin are particularly raised).

The above structural features of the medial surface of the scapula are evidently associated with the significant development of musculus subscapularis. Commencing from the vertebral margin of the scapula, this muscle gradually merges into a tendinous plate and is inserted onto the tubercle of the humerus. On contraction, it brings the shoulder close to the scapula and turns it inward, thus effecting movements necessary for accomplishing steering functions.

The glenoid cavity of the scapula is elliptical and slightly deepened.

On the caudal margin of the scapular blade, below the base of the articular head, is a distinct, triangular tuberositas infraglenoidalis.

The scapula described here differs from that of *C. maicopicum* Spass. (Spasskii, 1951) in the straight vertebral margin, nature of development of lines for muscles and also the pointed posterior angle and horizontally extended articular head, differentiated from the blade. At the same time, the scapula assigned by Spasskii as belonging to *C. maicopicum* shows great similarity with the scapula in Derbent's *C.* aff. *mayeri* Brdt., differing from it only in the slightly thickened central part and reduced supraspinatous portion (Spasskii, 1954). All of this compels us to assume that it would perhaps be more correct to place only the scapula described here as that of *C. maicopicum* and not Spasskii's specimen which belonged, perhaps, to *C.* aff. *mayeri* Brdt.

76 **Table 29. Main dimensions (in mm) of scapula of** *Cetotherium maicopicum* **Spass.**

Length of vertebral margin	270
Length of anterior margin	165
Length of posterior margin	200
Height of bone	192
Width of base of acromion	60
Width of base of coracoid	40
Maximum diameter of glenoid cavity	55

The humerus (Plate XVI) has an intensely shortened and flattened shaft. The radial margin of the shaft is slightly convex and the ulnar margin correspondingly concave. The head of the humerus is massive and spherical, considerably inclined toward the ulnar margin, forming a distinct, nearly right angle with the latter. The radial and ulnar margins are parallel to each other. The distal end is insignificantly enlarged. The articular surfaces for the forearm bones are slightly deepened, comparatively narrow and form an obtuse angle between them. The facet for the olecranon process is broad and high (occupies almost a third of the total length of the shaft).

The lesser tubercle (tub. minus) is highly developed, conical and forms the tip of the radial margin of the bone. Its apex is slightly raised above the level of the upper edge of the head. The greater tubercle is insignificant and conical, located on the inner surface of the bone and almost directly adjoining the head of the humerus. The groove between the tubercles is completely obliterated; the collum anatomicum is well-developed all along the periphery. An oval impression lies distal to the neck, close to the ulnar margin. The humeri of *C. maicopicum* Spass. differ from those of other Cetotheria in a more flattened and narrow shaft, mutually parallel ulnar and radial mar-
77 gins (the ulnar margin of other forms, for example of *C. mayeri* Brdt. or *C. priscum* Brdt., commences from the upper angle of the olecranon, rising obliquely and indistinctly merging with the lateral surface of the head). The dimensions of this bone in *C. maicopicum* are somewhat less than in other species.

Note. While describing the remains of the Maikop *Cetotherium*, Spasskii (1951) pointed out that the ten humeri available to him were similar in structure to those of *C.* aff. *mayeri* Brdt. from Derbent. In my view, however, three groups of humeri could be distinguished in the collection of the Maikop Regional Museum. One of these consists of specimens actually belonging to *C. mayeri* Brdt., another to specimens similar to the humerus of *C. priscum* Brdt. and the third evidently belonging to *C. maicopicum* Spass. and differing sharply from both the preceding groups.

The vertebrae are represented by two dorsal, one lumbar and one caudal belonging to different individuals of this species.

The anterior dorsal vertebra of an adult specimen has a short, nearly discoid centrum and elliptical articular surfaces. Its posterior articular surface is more expanded than the anterior and has a slightly angular ventral margin, which is obviously due to the presence of a ridge on the ventral surface of the vertebra. On the posterior articular surface at the base of the ventral surface of the transverse processses, there are facets for articulation with heads of corresponding ribs. The transverse processes are broad and bear facets on their greatly thickened ends for articulation of the tuberculum of the rib. Evidently, the presence of both the above articular surfaces on this vertebra suggests its similarity to the vertebra of the anterior thoracic region.

The neural spine is missing. The neural arch and the base of spine are preserved.

The anterior articular processes are short, somewhat pointed. The neural canal is low, triangular and wider than high; the bases of the transverse processes are constricted and noticeably thick.

78 The lumbar vertebra is represented by one of the first vertebrae of this region. The articular surfaces are elliptical, the posterior surface considerably expanded. Three distinct concentric bands on the epiphyses distinguish my specimen from the vertebrae of several other Cetotheriidae in which these epiphyses are covered by narrow concentric lines. Based on this feature, as also some other features, the vertebra described here resembles the vertebra of *C. mayeri* Brdt.

The caudal vertebra has oval articular surfaces. As in the case of the epiphyses of the lumbar vertebra, there are three concentric bands here too. The centrum is short. The width of the articular surfaces is greater than the length of the vertebra. The ventral surface has an oblong-quadrangular depression on the anterior and posterior margins, on which are located paired symmetrical tubercles. Of these, the posterior ones are more developed. The vascular sulcus is distinct on the anterior as well as posterior parts of the ventral surfaces of the vertebra. Vascular sulci are also present on the corresponding parts of the dorsal surface of the centrum close to the bases of the transverse processes. The latter are short, expanded and directed downward. They are slightly pachyostotic. The neural canal is triangular anteriorly and flattened posteriorly, almost slit-like.

Table 30. Dimensions (in mm) of vertebrae of *Cetotherium maicopicum* Spass.

	Thoracic	Lumbar	Caudal
Length of centrum	18	58	71
Total width with transverse processes	203	254	193
Height of anterior articular surface	56	49	67
Width of anterior articular surface	68	65	87
Height of posterior articular surface	53	54	69
Width of posterior articular surface	73	78	85
Length of transverse process	73	92	62
Width of transverse process	45	58	73
Thickness of transverse process	25	31	33–34

Thus, the general features of the vertebrae of *C. maicopicum* Spass. are the prominent pachyostosis on the transverse processes of lumbar and caudal vertebrae, the presence of three broad concentric bands 79 on the epiphyses of the articular surface and the wider than longer centrum.

The vertebrae of *C. maicopicum* differ sharply from the corresponding bones of *C. mayeri* Brdt. in form and structure of the articular surfaces and in the considerably ventrally inclined and thick transverse processes. In these features, they more closely resemble *C. priscum* Brdt. although they differ from the latter in the much thicker transverse processes bulged at the base.

The species *C. maicopicum* was established by Spasskii in 1951 based on material from the Middle Sarmatian formations in the vicinity of Maikop. Beginning in the year 1945 the Regional Museum at Maikop often received remains (vertebrae, fragments of skull, lower jaws, etc.) of fossil whalebone, but there were neither complete skeletons nor sets of vertebrae in their natural state. Unfortunately, the sites of most remains were not precisely indicated. Therefore, I have no basis to dispute their possible origin from the different Sarmatian strata.

In 1950, while building the Maikop Hydroelectric Power Station, a nearly complete whale skull was recovered, which together with the earlier collected bones served as material for separation of a new species, *C. maicopicum* Spass.

While describing the remains of a new species of *Cetotherium*, Spasskii gives only a brief description of the skull and casually refers to the rest of the skeletal parts. At the same time, as he himself states (Spasskii, 1951), apart from the two skulls sketched by him, he had fifty vertebrae, ten ribs, six scapulae and ten humeri.

Detailed processing of old and new collections of the Maikop museum, and also a study of the material collected by me around Maikop, revealed that the remains of *Cetotherium* assigned by Spasskii as belonging to the same species of *C. maicopicum* in fact belongs to a new member of the genus *Cetotherium.*

A comparison of the skulls of *C. maicopicum* specimens one and two (Figs. 16 and 17) given by Spasskii (1951) helps to establish the following differences between them.

The difference in the form of the occipital shield is striking at first sight. The lateral ridges of the occipital shield of skull No. 1 are some-
80 what straight and converge gradually anteriorly to form an acute angle. The lateral ridges of skull No. 2 are bent like an S. At the level of the posterior margin of the temporal fossae, they are outwardly directed in a marked degree, as a result of which the posterior part of the shield in this skull is far wider than in skull No. 1. The apex of angle of the supraoccipital shield of skull No. 1 is located at the level of the midtemporal fossae and in skull No. 2 it is shifted almost to the level of the orbital line. In the middle part the anterior margins of the

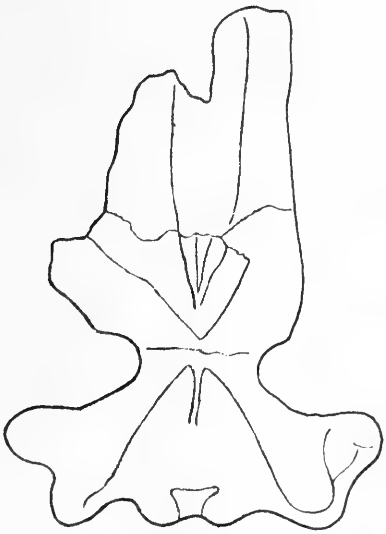

Fig. 16. *Cetotherium maicopicum* Spass. No. 1.
Skull, dorsal view (after Brandt).

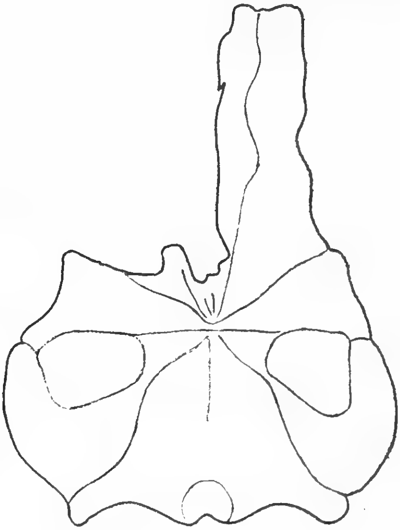

Fig 17. *Cetotherium maicopicum* Spass. No. 2.
Skull, dorsal view (after Spasskii).

supraorbital processes of the frontals of skull No. 1 are greatly bent and form a right angle. In skull No. 2, they are straight and form an obtuse 120° angle. Particular attention should be paid to the ratio of the distance between the anterior angle of the occipital shield and the base of the nasals to the length of the occipital shield. For skull No. 1, this ratio is 1/2 and for skull No. 2 1/11. The ratios of zygomatic width to the length of the occipital shield also differ (3.2 for skull No. 1 and 2.5 for skull No. 2).

Spasskii points out that the ascending processes of the maxillae in *C. maicopicum* form a more acute angle than in *C.* aff. *mayeri* Brdt. 81 from Derbent. However, it is not clear whether he considered the features of both the skulls for this purpose. The point is that one of them (No.1) differs distinctly in this feature from the Derbent *Cetotherium*, but the second resembles the Derbent form. Moreover, judging from Spasskii's description, skull No. 1 should be regarded as a type specimen of his species.

It is interesting, however, that the distinctive features of the structure of skull No. 1 are also characteristic of the skull described here (specimen No. S144, collection of IPB) from the Sarmatian formations in the vicinity of Maikop and also for the skull from the neighborhood of Goryachie Klyuchi (collection of the Krasnodar Regional Museum) also assigned by me to *C. maicopicum* Spass.

All of this no doubt indicates the constancy of the examined features of skull No. 1.

Thus, it follows from the above discussion that differences between skulls No. 1 and No. 2 run beyond the range of individual variability and, of the two skulls of *C. maicopicum* depicted in the work of Spasskii, only one, i.e. No. 1, should be placed in this species.

Insofar as skull No 2 is concerned, it belongs to some other species of *Cetotherium*, but without studying the material, I cannot hazard any further guess.

Cetotherium mayeri Brdt.

Material. Cranial part of skull, fragments of lower jaws, vertebrae and humeri of different individuals (specimens No. S145, S133, S128, S139 and S140).

Site. Maikop town.

Geological age. Middle or Upper Sarmat.

Description. The skull is represented mainly by the cranial part (Plate XVII). Anteriorly, it is broken at the level of the anterior margin of the temporal fossa; the zygomatic process of the squamosal is also broken. The occipital region of the skull with distinct condyles and the foramen magnum is well-preserved. A markedly developed

supraoccipital forms the roof of the cranium. The lateral ridges of the supraoccipital give it the appearance of an isosceles triangle. In spite of considerable damage, the boundaries of the ridges are distinct. The anterior angle of the occipital shield extends up to the anterior border of the temporal fossa. The surface of the shield is slightly arched (in the region from the upper border of the foramen magnum to the ante-
82 rior angle), smooth, without the median ridge and depressions, characteristic of *C. maicopicum* Spass. The foramen magnum is oval, somewhat longer than wide. The occipital condyles are large and very typical. In the lower portion, they are greatly enlarged, almost merging with the surface of the basioccipital. In the upper portion, however, they constrict and fuse with the surface of the supraoccipital. The exoccipital processes are directed backward and sideways and fall on the same line together with the condyles. The lateral walls of the cranium are formed of parietal and temporal, and unlike those in *C. maicopicum*, are less inclined, considerably short and curved medially. The line of descent of the parietal at the apex of the skull is 22 mm.

The temporal also takes part in the formation of the ventral surface of the posterior angle of the skull. The postglenoid process is considerably less developed than that in *C. maicopicum* Spass.

The greatly expanded basioccipital occupies the center of the ventral surface of the skull. The occipital condyles are massive, triangular, with their apices directed upward. The condyles are highly convex and, in the rear portion, shifted somewhat sideways. The posterior part of the vomer is greatly flattened and enlarged, its posterior margin almost totally covers the central portion of the sphenoid and reaches back to the medial angles of the condyles. In the skull fragment's anterior region, the exits of the II pair of cranial nerves and the contours of the olfactory stalks could be clearly seen on the broken surface.

Thus, this skull differs from that of *Cetotherium maicopicum* in the following basic features: the form and flattening of the occipital shield, apex of shield reaching up to the anterior border of temporal fossae, absence of vallate ridge and oval fenestrae in the anterior angle of the shield; greatly shortened, medially bent side walls of cranium; enlargement of intertemporal section, intensely enlarged basioccipital, enlargement of vomer reaching back to the medial angles of condyle, structure of occipital condyles and foramen magnum; significant height of skull in the parietal region and the close disposition of ventral ends of condyles. It differs also from the skulls of *C. rathkei* Brdt., *C. helmersenii* Brdt. and *C. linziana* Brdt. in the shape of the occipital shield, absence of medial ridge, structure of side walls, etc.

83 The skull described resembles *C. cuvieri* Brdt. (Brandt, 1873) in the smooth surface of the slightly bulged supraoccipital, but it differs

from the latter in the nature of displacement of the occipital elements: the anterior angle of the occipital shield in *C. cuvieri* is very acute and extends up to the orbital zone, while the side walls of cranium are almost vertical.

The specimen described above resembles the skull of *Cetotherium mayeri* Brdt. (Spasskii, 1954), found in the Sarmatian formations in the neighborhood of Derbent town. Its resemblances include shape and dimensions of the slightly bulged supraoccipital, length of its lateral ridge, absence of vallate ridge and oval fenestrae on this bone, high and more inclined parietals in the posterior half and also the structural features of the basal portion of the skull. This together with the identical geological age of these finds suggests its inclusion as a member of the genus *Cetotherium*.

Table 31. Dimensions (in mm) of the skull of *Cetotherium mayeri* **Brdt.**

Width between exoccipitals	250
Width between pr. postglenoidales	215
Length of lateral ridge	190
Height of brain case	140
Height of occipital condyles	70
Width of occipital condyles	40
Width from condyle to condyle	96
Transverse diameter of foramen magnum	43
Width between posterior angles of muscle tubercles	94
Distance between lower margins of occipital condyles	8
Height of side wall	104
Length of shield from upper margin of foramen magnum to anterior angle	120

84 The fragment of lower jaw (Plate XVIII, Figs. 1 and 2) represents the posterior half of the right ramus. The articular condyles, posterior half of coronoid process and the entire anterior end are missing. The ramus is thick with a greatly bulged outer surface and considerably sharp margin. Its inner surface is flat (or slightly concave) and less vertical than in *C. maicopicum* Spass.

Coronoid process low with a carinate ridge on the outer margin. The opening of the foramen falls closer to the inner surface of the jaw. Height of jaw all along the length of fragment same. The groove on the inner surface faint. Traces of alveolar cavities* noticeable only at the very surface of fragment.

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*Probably foramina—Editor.

The humerus (Plate XIX, Figs. 1 and 2) has a short and slightly flattened shaft. Head of humerus large, hemispherical and greatly truncated relative to the long axis of the bone. The neck is faint, especially in adults.

Among the tubercles, pr. minus is less developed, conical and medially slightly bent as if forming the radial margin. P. majus is very faint. Radial and ulnar margins of shaft not parallel. The ulnar margin, commencing from the upper angle of the articular surface for the olecranon process and rising obliquely, merges gradually with the contour of the head not forming any perceptible angle. This feature is better seen in the humerus of adults.

Upper half of shaft somewhat expanded, while the lower half of the shaft is sharply constricted (radial and ulnar margins in this portion are greatly bent). Distal end of bone enlarged and noticeably flattened. The articular surfaces for the forearm bones are very broad, sharply inclined and converge at an angle of 110° (in *C. maicopicum* this angle is 130°). The articular surface for the olecranon process is well-developed. It extends one-fourth the length of the ulnar margin, but, nevertheless, is shorter than the corresponding surface of the humerus of *C. maicopicum*, which measures one-third the length of the ulnar margin.

85 **Table 32. Principal dimensions (in mm) of humerus**

Length of bone	152
Width at distal end	67
Width at proximal end	90
Maximum diameter of head	68
Minimum width of shaft	571

Vertebrae. Centrum of lumbar vertebra relatively short. Articular surfaces elliptical. Epiphyses covered with concentric lines with a vertical line—nucleus pulposus—at the center of the surface, distinguishing this vertebra from those of other species of *Cetotherium* (Spasskii, 1954). Transverse processes damaged, but judging from the preserved basal portion of the remnants, they were quite massive.

The material collected from the Sarmatian formations in the vicinity of Armavir town provides a clear picture of the structure of the vertebral column of this animal. This material comprises vertebral columns of *Cetotherium* from the second cervical to the second lumbar.

As a rule, the second cervical vertebra differs sharply from the rest of the vertebrae in its form and particularly in its large width. Of the process disposed at the center of the anterior surface, only the base of the odontoid process measuring one-third of its entire surface was preserved. On the sides of the odontoid process are located symmetrically arranged flat, crescent-shaped articular surfaces to which are joined the backward sloping massive wings of the transverse processes pierced by the vascular foramen (foramen transversarii). The posterior articular surface is elliptical, curved and highly expanded. The dimensions of this articular surface are considerably less than these of the anterior surface and, correspondingly, the posterior surface of the lateral bodies is larger than the anterior. The length of the centrum of this vertebra along the upper margin is 36 mm and of the lower, 40 mm; height of anterior articular surface 70 mm, total width of anterior articular surfaces with the odontoid process 134 mm, maximum width of vertebra 212 mm, height of posterior articular surface 60 mm, width 84 mm and diameter of foramen transversarii 8–9 mm.

86 The other cervical vertebrae have a discoid centrum and elliptical articular surfaces. The margins of the latter are elevated and rugose. The lower surface of the vertebrae at the bases of the processes is noticeably sunken. The increase of body length in the caudal direction is insignificant.

The thoracic region of the vertebral column is well-preserved (twelve vertebrae). The first and second vertebrae are fused in a natural state. The form of articular surfaces commencing with the third thoracic vertebra changes gradually from angular-oval to elliptical. The length of vertebrae increases sharply. The sharp elongation of the centrum of the eighth vertebra far exceeds the length of the preceding ones and is particularly striking. On its ventral surface are seen a vallate, oblong crest and vascular grooves which obliquely diverge from much of its width.

The rest of the vertebrae are even more elongated, their rugosity reduced and the margins of articular surfaces elevated. The ridge on the lower surface and the grooves for blood vessel are more distinctly formed. The separation of bases of transverse processes commences with the eleventh vertebra and is completed in the thirteenth.

The transverse processes and neural spines on all the vertebrae of this region are broken off. Transverse processes are located in the upper part of the centrum and evidently directed downward and forward. The articular surfaces are typically elliptical, a characteristic of this species (see Brandt, 1873, Plate X, Fig. 8).

Of the first lumbar vertebra, only the centrum with the bases of the transverse processes is presevred. On the ventral surface of the centrum, the vascular grooves are considerably sunken, slantingly located and joined roughly at the center of the vertebra. The anterior and posterior margins of the lower surface form tubercles.

The second lumbar vertebra is well-preserved (only the neural

Table 33. Dimensions (in mm) of vertebrae of *Cetotherium mayeri* **Brdt**

	Thoracic vertebrae												Lumbar	
	1	2	3	4	5	6	7	8	9	10	11	12	1	2
Length of centrum	25	30	31	39	43	46	—	—	58	61	65	73	75	77
Width of articular surface	78	79	80	72	77	80	—	—	83	91	83	80	84	85
Height of articular surface	68	67	68	60	57	52	—	—	63	61	58	64	63	60
Width of neural canal	—	—	—	—	33	32	—	—	—	30	29	23	—	24
Basal width of transverse process	—	—	—	—	—	—	—	—	—	60	—	50	57	55
Basal thickness of transverse process	—	—	—	—	—	—	—	—	—	24	—	—	—	—
Length of transverse process	—	—	—	—	—	—	—	—	—	—	—	—	93 (incomplete)	120

spine damaged). Its articular surfaces are elliptical. The centrum is
distinctly high. The bases of the transverse processes are located in
the upper half of the vertebra. They are noticeably inclined down-
ward, markedly long, slightly expanded at the ends and have a rounded
off tip. The neural canal is high and triangular. The structure of the
ventral surface of the centrum is the same as that of the first vertebra,
though the tubercles of the anterior and posterior margins on this ver-
87 tebra are already bifurcated; this, as well as the absence of articular
facets at the tips of the transverse processes, confirm that this bone came
from the lumbar region of the vertebral column.

Cetotherium sp.

Material. The fourth, fifth, sixth and seventh cervical, and first thoracic vertebrae (specimens No. 116-19, 116-34, 116-25 and 116-62, collection of MG) and rib fragments (specimens No. 116-52 and 116-8, collection of MG).

Site. Perekishkyul, left bank of Sumgait River.

Geological age. Miocene.

Description of material. Cervical vertebrae not fused (Plate XX). Centra discoid and short. Bases of the transverse processes are preserved along the sides of the upper and lower surfaces of the vertebrae, and these impart a quadrangular contour to the vertebrae. Articular surfaces elliptical, their ventral margins are slightly horizontal and expanded far more than the dorsal margins. The anterior articular surfaces of all the vertebrae are slightly convex and the posterior correspondingly concave, resembling the opisthocoelous vertebrae of terrestrial animals.

88 The centrum of the first thoracic vertebra is long and bears a triangular-oval articular surface. The dorsal part of the second left and fourth right ribs of *Cetotherium* with well-preserved capitulum and tuberculum (Plate XX) were exposed by further clearing of the material. The proximal ends of these bones are considerably flattened, rib angles close to the tubercles. Cross section of the its upper part is elliptical.

Table 34. Dimensions (in mm) of vertebrae of *Cetotherium* sp.

	116-19	116-34	116-49	116-25	116-62
Length of centrum	22.5	24.5	25	30	44
Height of anterior articular surface	52	60	58	51	52
Width of anterior articular surface	84	79	79	89	78
Height of posterior articular surface	54	60	55	52	58
Width of posterior articular surface	88	78	78	87	82
Width of neural canal	38	40	46	58	57

I also studied the fragmentary remains of vertebrae and skeleton of the forelimb of *Cetotherium* from the Sarmatian formations in the neighborhood of Kabala village (Kabristan, Azerbaidzhan Soviet Socialist Republic).

Chapter III

Geology of Some Sites of Fossil Cetaceans of the Caucasus

88 The geological age of Maikop cetaceans of Azerbaidzhan (Sjegren's collection) is not yet completely certain.

Lydekker pointed out that Sjegren's collection of fossil cetaceans was made along with innumerable remains of fish in highly gypsiferous clays of the Tertiary formations of the Caucasus, similar in lithology
89 to "London clays" (Eocene). However, based on an analysis of the cetacean fauna, he concluded that these collections belong to the Miocene age. Moreover, at the end of his note (Lydekker, 1892, p. 564) while referring to the work of Sjegren (Sjegren, 1891), he included them all the same in the Eocene.

It is known that Sjegren included the formations of the present "Sumgait series", which he discovered in the western part of the Apsheron peninsula (Uchtapa, Arbat and Perekishkyul) in the Eocene. Later, it transpired that he had included the lower portions of the Tertiary formations up to the Maikop (V.V. Veber, 1927) under the "Sumgait series". Sjegren does not refer to the cetacean remains in his work, but points out that "the stratum along with fish remains and petrified tree trunks contains vertebrae, ribs, jaws with teeth, some individual teeth of sharks and also several bones joined together, some of which are covered with crystallized gypsum" (Sjegren, 1891).

There is hardly any doubt that the reference is to the cetaceans described by Lydekker, but which is regarded by Sjegren as being that of sharks.

Regarding the age of this material, Abel writes: "the nature of the cetacean fauna does not enable accurate dating of their host rocks; nevertheless, they suggest that these strata with cetacean remains should not be placed either in the Eocene or the Lower Oligocene since the presence of *Cyrtodelphis* in this collection favors the Miocene age of these formations. On the other hand, the presence of the remains of such a lowly organized form as *Microzeuglodon* compels us to consider them as more antique." According to Abel, it would be more appropriate to place them tentatively in the Upper Oligocene (Abel, 1913,

p. 208). V.V. Bogachev also shares this view (1956).

Considering that the remnants referred to above should have been found in those strata in which, in 1928, V.V. Veber found almost a whole skeleton of *Zeuglodon*, A.N. Ryabinin places them in the Upper Maikop (Ryabinin, 1931, p. 141)*.

90 There is also no precise information on the sites of these remains. Some (Lydekker and Abel) merely state that the material was found in the Caucasus, while others (Ryabinin and Veber) placed them in the vicinity of Baku.

On the whole, among the localities examined by Sjegren, Perekishkyul (western part of the Apsheron peninsula) could be the only location of this material. Very rich material of fossil cetaceans was recently discovered there (Aslanova, 1961). Regarding the other areas studied by Sjegren, Uch-tapin yielded only insignificant finds, which were tentatively demarcated as cetaceans (Golubyatnikov, 1927); fossil cetaceans were not found at all in Arbat. This assumption is supported by the fact that, according to Sjegren, the site which yielded the collection to him was exceptionally rich. He wrote the fossil bones "could make a camel load." The Perekishkyul locality is known for its abundance as well as diversity of material.

For understanding the stratigraphic position of this material, let us study the geological conditions of the sites of *Microzeuglodon* aff. *caucasicum* Lyd., described by Ryabinin, and compare them with a Maikop section typical of the Apsheron peninsula.

A skeleton of *M.* aff. *caucasicum* Lyd. was found on the right bank of Sumgait River (Dzhengichai) three km northeast of Dzhengi guest house.

The section of Maikop stratum at Dzhengi, described by Veber, is given below:

Immediately under the gray marl with *Spirialis* (the base of the *Spirialis* horizon), the following are found from top to bottom:

1. Dark-chocolate-brown shales with efflorescences of jarosite. Thickness 20 m.
2. Siderite layer: dark-brown and brownish-black shales with siderite lenses. Thickness 34 m.
3. Chocolate-brown shales with efflorescences of jarosite, dark-brown on top and foliated. Thickness 21 m (evidently Riki horizon).
4. Chocolate-brown shales and platy clays with efflorescences of
91 jarosite and bands of platy dark-brown shales. The clays are underlain

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*As a matter of fact, Veber found the *Zeuglodon* not in the Upper Maikop beds, but in the beds disposed just above the Khadumsk horizon, i.e. stratigraphically much lower.

by characteristic spherical concretions of dolomite and limy sandstone. Thickness 93 m.

5. A thick bed of dark-chocolate-brown, chocolate-cinnamon shales with efflorescences of jarosite with insignificant bands of loose sandstone. Bits of petrified tree trunks are encountered. The lower half of this bed is underlain by three series of large lensoid concretions (thickness 1 m and length 12 m) of gypsiferous limy sandstone. Thickness 159 m (Veber, 1928).

Below them is a bed with alternating greenish-brown, greenish-gray and chocolate-brown clays evidently corresponding to the "transitional beds" of Gubkin or the Lower Maikop beds of Sahatski (Gubkin, 1950, p. 360).

Let us now get acquainted with a more complete Maikop section of the Apsheron peninsula at Uch-tapin drawn up by A.A. Putkaradze (A.G. Aliev and E. Daidbekov, 1952, p. 267).

The upper Maikop section is represented by the following strata (top to bottom):

1. Supersideritic horizon (MKR$_2^3$)—alternation of dark-gray, brownish-gray, chocolate and gray bedded clays with jarosite and fish remains. Thickness 14 m.

2. Siderite horizon (MKP$_2^2$)—alternation of dark, nearly black, chocolate-gray clays with jarosite, fish remains and bands of dark sandstone. Thickness 30 m.

3. Riki horizon (MKP$_2^1$)—chocolate-brown, thin-bedded, foliated, considerably gypsiferous clays with fish scales and remains of *Cedroxylon* and almost black bituminous fuel shales. Large concretions of marls are also encountered. Thickness 117 m.

Lower Maikop with horizons (MKP$_1^1$) and (MKP$_1^2$):

1. MKP$_1^2$—a band of dark-chocolate-gray clays with abundant jarosite, fish imprints and remains of *Cedroxylon*, more rarely greenish clays with marl bands. Thickness 351 m.

2. MKP$_1^1$—(transitional beds of Gubkin) frequent alternations of light-green, yellowish-gray, and brown book clays with bands of dense marl. Thickness 49 m.

92 A small bone of *M.* aff. *caucasicum* Lyd. was found in bed No. 5 of the Dzhengi section immediately above the "transitional beds" (Khadum stratum). This evidently corresponds to the upper level of the Lower Maikop Uch-tapin section of Putkaradze, or the lower level of the Middle Maikop (Middle Oligocene) of K.A. Ali-Zade (1959, p. 64), but not the Upper Maikop as assumed by Ryabinin (1931, p. 141).

Insignificant remains of cetaceans, corresponding to [those] of the supersiderite stratum (Upper Maikop–Lower-Middle Miocene or

Lower Miocene), were even found by Veber in bed No. 1 as also in bed No. 4, located under the beds corresponding to the Riki horizon.

The above data show that the remains of cetaceans in the Dzhengi section were discovered at different levels corresponding to different sections of the Maikop suite exposed in Uch-tapin. If the Uch-tapin section is regarded as typical of all the regions studied by Sjegren and Dzhengi, and if the Uch-tapin sections are assumed as identical, it may throw light on the geological conditions of the most abundant Perekishkyul cetacean fauna. This complex consists of forms, some of which (*Cyrtodelphis*, *Iniopsis* and *Cetotherium*) have a geologic range, based on the deposits in which they occur, extending to the Upper Maikop, corresponding to the Miocene epoch. Other forms include *Microzeuglodon* as well as large-sized fish in the lower portions [of the section] corresponding, evidently, to the Lower Oligocene or even to much older formations.

In bed No. 5 of the section at Dzhengi (Suprakhadum bed), a nearly complete skeleton of *Zeuglodon* was discovered. Moreover, cetacean remains were found, as pointed out above, in the upper and middle sections of the same exposure. In the upper part of Maikop, close to Perekishkyul, cetacean faunas were found with a predominance of forms pointing more to the Miocene epoch (members of Delphinidae, similar to present-day *D. delphis* L.) and characterized by the absence of large fish remains, which had been present in great quantity in Sjegren's collection.

Considering all the above facts, it can be concluded that Sjegren's material came from totally different horizons of the Maikop suite.

In my opinion, the remains of *Microzeuglodon* and large sized fish
93 should be placed in the lower Middle Maikop (i.e in the beds located immediately above the Khadum horizon) and regarded as belonging to the same age as the *Zeuglodon* of Ryabinin, though it is possible to place them in the Lower Oligocene. The dolphin members should evidently be placed in the upper parts of Maikop in the Miocene beds.

In the territory of western Georgia, I established the sites of Miocene cetaceans at the following places: Bzhinevi, Koreti, Sairkhe, Argveti, Chorvila, Dzhalaurta (Sachkher region), Mgvimeri, Shukruti, Tsasri, Usakhelo (Chiatur region), Kvaliti (Zestafon region) and Zemo Sazano, Rupoti (Terdzhol' region). In eastern Georgia, only one site, at Norno, is known.

The regions of Sachkher and Chiatura are most abundant in cetacean remains; the bones of these animals were discovered in primary formations as well as in the form of individual fragments washed out and scattered in maize fields. In some cases, even articulated bones were found there (for example, almost a complete limb of a whalebone whale at Dzhalaurta village).

The maximum amount of material came from the vicinity of Dzhalaurta village and villages Tsasri and Usakhelo adjoining it.

In all these localities, cetacean remains were confined to the Middle Miocene formations belonging to the Upper Karagan portion and possibly the lower portion of the Konk horizon.

In the above territory as well as in the extensive region of the entire Chiatur-Sachkher area, beds of the Karagan formations were characterized mainly by the alternations of clayey sandstones, limestones and oolites. Mollusks were collected from the outcrops of the Karagan beds examined by us, along with innumerable remains of cetaceans. These are represented exclusively by *Spaniodontella gentilis* Eichw., *Spaniodontella tapesoides* Andrus., *S. pulchella* Andrus., *Savanella andrussowi* Toula. (identified by E. Zhgenti). Moreover, on the surface of petrification and in rocks filling the hollows of bones, shells of *Savanella andrussowi* Toula. were most often encountered. This confirms the Upper Karagan age of these cetacean remains (Zhgenti, 1961).

94 In the vicinity of Dzhalaurta-Tsasri-Usakhelo, the beds of the Konk horizon, deposited above *Spaniodontella*-bearing limestones, are also bone-bearing. These beds are dark in color with gypsum-bearing inclusions, while the upper portion lodges gray sandy shales, cemented in places with limestone-oolite rock or often bits of platy limestone containing innumerable *Barnea* (*Barnea pseudoustiurtensis* Sinz. and *Barnea niratamica* Andrus.).

In the stratigraphically overlying Lower Sarmatian formations of western Georgia studied by me, cetacean remains are found in Kvaliti and Rupoti.

The Kvaliti sites are located right on the bank of the Kvirila River, between the estuaries of the Dzhoboura and Achkheta rivers. In the neighborhood of Kvaliti, according to the data of A.A. Chikovani (1960, pp. 126 and 127), the following sequence of Sarmatian formations is seen, from bottom upward:

I. Thin layer of silty marl, light gray with sparsely scattered inclusions of plagioclase and quartz with impressions of *Abra* and microfauna. Thickness 2.2 m.

II. Dense marl with fish scale and plant remains. Among the mollusks seen are *Mactra basteroti* Mayeri cf. var. *konkensis* Sok. and *Cardium* sp. Thickness 16 m.

III. Marls with *Abra* cf. *reflexa* Eichw., *Abra* cf. *alba* Wood; and according to O.I. Dzhanelidze, the microfauna in the Lower Sarmat are *Quinqueloculina reusii* Bogd., *Q. consobrina* d'Orb., *Nonion punctatus* d'Orb. and *Nonion angulatum* d'Orb. Thickness 4 m.

IV. Thin layers of gray marls on top with bands of platy light gray limestone. From this band were collected shells of *Cardium lithopodolicum* Dub., *C. lithopodolicum* var. *inflatum* var. n., *Cardium ruthenicum* (Hill) Lask., and *Cardium* ex. gr. *gracile* (Dub.) Pus.

V. The amount of siltstone gradually increases on top and at times silty marls appear. The latter form partings, lenses and "buns". Among the mollusks encountered are: *Mactra* cf. *eichwaldi* Lask., *Cardium* cf. *plicatiphitoni* Sinz., *Cardium kasikensis* Koles. and *Cardium* aff. *vindobonense* (Partsch) Lask.*

95 The Lower Sarmatian microfauna was identified from a sample of marl embedding a "bun" with a dolphin.

VI. Near the bridge on the left bank of the Kvirila, alternating calcareous sandstone is stratigraphically exposed on top, evidently also belonging to the Lower Sarmat (A.A. Chikovani, 1960).

A section of the Lower Sarmat on the Kvirila River near Zestafon, as drawn by A.A. Chikovani, is shown in Fig. 18.

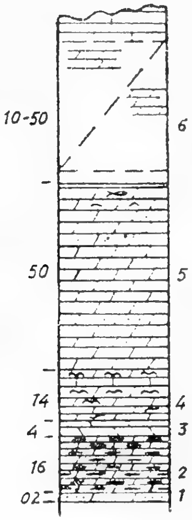

Fig. 18. Section of Lower Sarmat on Kvirila River near Zestafon (after Chikovani).

At Rupoti village, cetacean remains were found at a depth of 18–20 m from the soil surface (in a well) in gray clays, at places with ocherous coatings and bands of crystalline gypsum. Remains of fish skeletons, impressions of leaves and poorly preserved shells of *Abra* sp. were found in the clays housing whale bones. Microfauna, according to L. Maisuradze, are *Quinqueloculina reussi* Bogd., *Q. consobrina* d'Orb.,

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*V.I. Tabagari found the dolphin described by me in this very horizon.

Q. consobrina (d'Orb.) var. *nitens* Reuss, *Q.* cf. *complatana* Gerke and Issaeva, *Q. guriana* Dian., *Nonion subgranosus* Egger., *N. bogdanowieze* 96 Volosh. and *Elphidium* sp. Based on the presence of the above complex of fossil forms, the cetacean remains could be placed in the Lower Sarmat.

I studied the Miocene cetaceans around Maikop town from the material of the Regional Museum at Maikop town and my own collection made in 1958.

A significant part of the Maikop museum collection was found near a town in the Middle Sarmatian formations, exposed on the left bank of the Belaya River.

Here under a loamy soil is a bed of shingle and rubble followed by beds of greenish sandy clays, gray clays, greenish-black clays and light yellow sands. In these beds were found, from time to time, shells of Middle Sarmatian mollusks *Mactra podolica* Eichw., *M. vitaliana* d'Orb., *Donax* sp., *Solen subfragilis* Hörn., *Cardium fittoni* d'Orb. and *C. obsoletum* Eichw. (Spasskii, 1951).

I found the remains of cetaceans on the left bank of the Belaya River, 250–300 m away from the town bridge (downstream) in the Middle Sarmatian clays, crumbling easily after drying. At places, these clays contain bands of fine-grained sand and sandstone and also a large number of imprints of leaves. The total thickness of clay bands is 10–16 m.

The cetacean remains around Maikop town, according to the data of V.P. Kolesnikov (1953, p. 449; 1940, p. 279), are noticeable not only in the Middle Sarmatian formations, but also in the Upper Sarmatian. He points to the preponderance of bands of sandy-calcareous shells in the Upper Sarmatian formations around Maikop town with typical Upper Sarmatian *Mactra* fauna often intermixed with remains of fish and cetaceans.

Thus, I have reason to assume that a part of the cetacean remains collected in Maikop Museum must have also come from the Upper Sarmatian formations, which would perhaps explain such a wide diversity of the remains of Cetotheriidae in this material.

Around Armavir town, fossil remains of cetaceans are encountered on the left (Akhtamar, waterworks, corner of Khalturin and Gorkii streets) as also on the right bank of the Kubana River (on the slopes of the hill at the Forshtadt collective farm and at the brickworks).

97 On the left bank of the river, in gray-black clays deposited under the Serpulevo-Mshank limestones, workers of the Armavir Regional Museum found remains of dolphins and seals. The beds containing the bones of marine mammals at this point do not contain fossil mollusks; while the reef limestone, covering the bed containing the bones, is

characterized by the presence of diverse species of Middle Sarmatian mollusks. To the right of the ravine at Akhtamar, right on the bank of the Kubana River, I collected the following Middle Sarmatian mollusks in reef limestone: *Cardium laevigatoloveni* Koless., *Cardium renesium* Koless., *Tapes vitalianus* d'Orb., *Modiola fuchsii* Sinz., *Modiola incrasata* d'Orb. and *Hydrobia elongata* Eichwaldi.

Upstream, 1.5–2 km from the above site, a heap of dolphin bones was encountered 10 m below the surface while constructing the waterworks in 1957. A study of the site showed that beds of gray clays containing the dolphin remains here in all probability represented a continuation of the clays exposed at Akhtamar. In these clays, near the waterworks, I collected the shells of *Tapes gregarius* (Partsch) Goldf. and *Cardium obliquoobsoletum* Koless., thus confirming the Middle Sarmatian age of these formations.

According to the data of Kolesnikov (1940, p. 274) between Armavir and Ubezhensk station, Mshank limestones are considerably thick (up to 45 m) and more often lie in the bed of gray sands. More rarely, they are deposited directly on clays with *Tapes* shells (in Armavir).

The presence of Serpulevo-Mshank limestones is a characteristic of the extensive Armavir-Ternovka region surrounding the shallow-water facies zone of the Middle Sarmatian formations.

On the right bank of the Kubana River, overlying the eroded Middle Sarmatian formations, are diagonally bedded sands with innumerable remains of *Mactra* (Kolesnikov, 1940). In the 1–2 m thick clay bands, impressions of leaves of *Platanusineariloba* Koless. (E.F. Kutuzkina, 1958) as well as disarticulated fish remains are often found.

Kolesnikov points out that the adjoining Upper and Middle
98 Sarmatian formations contain large pebbles of limestone and a considerable number of imprints of the stones of nuts as also of trunks (Kolesnikov, 1940, p. 280). I have come across a similar phenomenon on the right bank around the foothill of "Bovkunov Cape". Here, in sandy limestones, I noticed petrified fruits of *Juglans*, *Corylus* and also the heartwood of trunks and impressions of leaves of *Phragmites*.

Massive gray sand and clay beds deposited over the above layer mostly contain shells of *Mactra*.

In the site under study, the transition of gray sands and clays into a bed of shells was marked by a 20 cm band of white sand. Following it is a layer of dense sandstone, a pipe of *Mactra* limestone of thickness 75 cm (*Mactra* shells, though few, were more intensely crystallized than in the overlying beds). On top is a 90 cm—at places 1.5 m thick—bed made up exclusively of cemented shells of *Mactra bulgarica* Toula. This is followed by a 2–5 m thick rocky sandstone topping the Upper Sarmatian formations.

The Sarmatian beds described here are overlain by fine-grained conglomerates and sands of the "Armavir suite" containing a rich Hipparion fauna.

Chapter IV

Burial Conditions of Fossil Cetaceans of the Caucasus

98 The cetacean remains could have been preserved in a fossilized state following the death of the animal in the open sea or its death on the shoals in the low tide.

As a rule, the carcasses of dead mammals in the open sea sink immediately to the bottom. In the normal oxygen regime at the bottom of the basin, after a brief submergence, they float on to the sea surface until waves or currents carry them to the coast. This would explain the fact that marine mammals are found mostly buried in the coastal sediments (Schäfer, 1955).

99 In the coastal belt, bones are usually found buried in a scattered condition since skeletons of dead animals easily disintegrate and are strewn over a wide area by the constant movements of high and low tide and waves. An example of such a burial is the cetacean fauna preserved in the Sarmatian limestones around Derbent. Here, the bones of cetaceans are found over a great distance all along the limestone quarry—sometimes as stray isolated bones and at other times heaped in a natural state. Quite often, parts of the same animal are scattered among the rocks over comparatively long distances far away from each other (Spasskii, 1954). An even more significant scattering evidently occurred during the burial of cetacean bones in the coastal parts of the Upper Karagan Sea, in the area constituted by the present-day Chiatur and Sachkher regions (Western Georgia).

However, in the relatively shallow regions of the basin, under conditions of intense sedimentation, preservation of even whole skeletons is possible as happened near the Icelandic coasts (Kellogg and Whitmore, 1957). Kellogg suggests that in such cases whole skeletons could be preserved under conditions of a progressively rising sea level accompanied by intense sedimentation.

Due to the absence of oxygen in the deeper levels of the sea, animals which died in the open sea are most likely buried in the ocean floor since its oxygen-free environment prevents the floating of carcasses up to the surface. Dismembered as well as whole skeleton could be buried in the floor of the sea. It should be assumed that more whole skeletons would have been buried in the deep water (settled) portions of the basin than in the coastal areas.

At times important clues to the burial conditions under which the cetacean fossils were formed are provided by the fish remains discovered along with them. Stray dead fish have little chance of preservation either at the bottom of the sea or on the coast, but are mostly preserved in the event of a massive allogenic death in bays contaminated with H_2S (Schäfer, 1955 and Danil'chenko, 1960). Instances of the occurrence of bones of birds, land mammals and plant remains together with cetacean fossils also help serve as indicators.

Therefore, while reconstructing the burial conditions of cetaceans, I naturally tried to take into account as much data as possible on the
100 other fossil forms also discovered with them, at the same time taking into consideration, the geology of the sites of fossil remains.

The latest finds of fossil cetaceans in the Apsheron peninsula are confined to the uppermost Maikop suites (Aslanova, 1961). The material is extremely well-preserved. Skulls with a full set of teeth and even articulated skeletal segments have been obtained. This as well as the type of their host rocks (dark-gray book clays) points to burial of these animals in deep water conditions. There is no doubt that having sunk to the ocean bottom in water contaminated with H_2S, the carcasses were buried *in situ*.

Cetacean remains recovered from somewhat more archaic formations of the same section (lower levels of the Upper Maikop) belonging to *Cyrtodelphis*, *Iniopsis* and *Cetotherium* suggest a more scattered type of burial. However, judging from the preserved remains, this was a less common occurrence, which can again probably be explained by deep water conditions and a relatively settled burial environment. It should be pointed out that almost entire skulls of *Iniopsis* and relatively well-preserved individual vertebrae (even parts of brittle transverse processes still existed in some of them) can be noticed here along with several vertebrae of *Cetotherium*: from III cervical to I thoracic inclusive. A part of Sjegren's collection studied by me (*Microzeuglodon caucasicum* and the remains of large fish), which I placed in the lower Maikop suite, can be seen as scattered and fragmented remains—fragments of a lower jaw with two whole and two broken teeth and a fragment of an upper jaw with few remains of teeth, one deformed humerus and broken and deformed vertebrae without processes—possibly point to a scattered burial in the shallow coastal sections of the basin. It should be pointed out that, according to Schäfer (1955), even a single find of cetacean and fish remains should suggest burial on the coast. Thus, in the lower parts of the Maikop section studied, dismembered and fragmented cetacean remains were seen, while in the overlying beds, dismembered, but better preserved bones than in the lower beds were found. In the uppermost portions of this suite, exceptionally well-preserved remains are buried.

101 This distribution of cetacean remains in the section of the Maikop suite at Perekishkyul and the nature of their preservation, in my view, should be associated with certain paleogeographic information of Apsheron. It is well-known that at the end of the Eocene, the sea boundaries in the region under study shrank considerably, and were then followed by transgressions. This sequence is suggested by the presence of a widely distributed basal conglomerate and angular nonconformity between the Eocene and Oligocene formations over a large territory of Azerbaidzhan (Ali-Zade, 1959). The subsequent marine regime is reflected in the accumulation of the thick Maikop suite sediments, which, in many cases, point to deposition under settled and relatively deep water conditions.

Based on this, it may be presumed that the shallow water of the late Eocene or Early Oligocene basin, at the bottom of which in my view were buried dispersed and fragmentary remains of cetaceans, was gradually buried deeper due to the transgression then taking place. In the sections where *Microzeuglodons* and large fish were buried, fairly deep-water formations began to develop. To these were added the disarticulated but already well-fossilized cetacean remains. With time, this part of the bottom of the Maikop Sea possibly underwent further burial, sedimentation was more intense and this ultimately promoted the rapid burial of whole skeletons of cetaceans.

The burial of Middle Miocene cetaceans in the Sachkher and Chiatur regions evidently occurred in the coastal belt or in the shallow water coastal belt of the basin adjoining the northwestern rim of the Dzirul' massif. This is supported by preserved bone material (for the most part bone fragments or disarticulated bones of cetaceans are found) as also by the geological structure of the formations (sandy limestones filled with various species of *Spaniodontella* predominate). This is also upheld by the discovery of remains of terrestrial mammals. From the Karagan formations in the neighborhood of Koreti village (Sachkher region), L.K. Gabuniya described the tooth of a typical fossil pig, *Listriodon* cf. *splendens* H.v.M. (a typical inhabitant of Middle Miocene forests—Gabuniya, 1959). In the Karagan formations of the same belt at Dzhalaurt, Usakhelo and Koreti, the teeth of
102 dinothere, mastodon, fragments of scapula of proboscideans and impressions of plant remains (impressions of leaves of *Cinamomum* sp.) were recently found.

As pointed out above, the study region reveals material that was widely scattered and then buried. Possibly here was a case of a massive allogenic death of these animals, though we have as yet no proof to support such an assumption. This could also be a wave-cut zone and skeletons of animals that died during the ebb tide were buried as disarticulated and often fractured and scattered remains. It is possible that there were also storms here, a theory which is supported by the finds of isolated teeth and bones of terrestrial mammals, which could have died in the high floods accompanying the storms. This is what happened during the burial of the Miocene fauna of Calvert County, Maryland (USA), where apart from cetaceans, some bones of mastodons, tapirs, rhinoceroses, horses, etc. were buried (Kellogg and Whitmore, 1957).

The burial of the remains of Middle Sarmatian cetaceans, found around Maikop town, evidently occurred in the relatively shallow water zone of the basin. Here, the beds containing the cetacean remains are delineated by light yellow clays alternating in places with bands of sandstone and layers of light yellow sands. The fossil remains are represented by disarticulated parts of skeletons with several bones polished smooth (in some cases, the bones have smoothened fracture edges). Evidently, at least some of the bones buried there in the shallow water zone of the sea were partly exposed to ebb-tide currents. The shallow water characteristic of these formations is also supported by the composition of fossil mollusks. Nevertheless, members of the lamellibranch mollusk species *Mactra vitaliana* d'Orb., *M. fabreana* d'Orb. and *Cardium fittoni* d'Orb. are found here on rare occasions. These forms, characterized by thick-walled shells, inhabit the shallow water regions of the Middle Sarmat Sea.

Around Armavir town, the remains of Middle Sarmatian cetaceans were evidently also buried in relatively shallow water regions of the basin, though considerably away from the coast. Complete skeletons were not found there, but articulated limb bones were discovered, some of them right up to the distal rows of the carpals, a few vertebrae with processes, whole ribs, etc. All of this points to burial in settled
103 parts of a shallow water basin, where no scattering of the skeleton over a vast area occurred.

Unlike Middle Sarmatian formations, the burial of Upper Sarmatian cetaceans is evidently confined to the coastal strip of the basin. Apart from the lithology of the formations and the nature of preservation of bone material (individual vertebral bodies or series in which mostly damaged processes were preserved), this is also supported in these formations by the presence of the remains of terrestrial mammals (*Hipparion*), fish (*Cyprinus*) and plants (*Corylus*, *Juglans* and *Phragmites*). As already pointed out above, simultaneous burial of marine mammals and fish occurs mainly in the coastal formations. Interestingly enough the present-day species of *Cyprinus* inhabit the estuaries of rivers colonized by *Phragmites*.

All of this provides a basis to assume that the burial of cetaceans occurred here in the coastal strip of the basin close to the estuary of the river, which then carried bones of terrestrial mammals along with leaves and fruits of several types of plants to the sea.

Chapter V

Biology and Evolution of Fossil Cetaceans

103 The paleobiological history of cetaceans, which secondarily became aquatic, is of much interest to science.

The return to water from land undoubtedly occurred with a gradual shift in the organization of the animal as a whole. During the course of adaptation to new living conditions, the cetaceans acquired several specific morpho-physiological features whose importance cannot be correctly interpreted without taking into account the data on studies of fossil as well as present-day forms.

Among the aquatic mammals, cetaceans are best adapted to live in this environment. Their present-day representatives have a torpedo-shaped body and a laterally compressed caudal stalk with a horizontal fluke typical of marine mammals. The body surface is smooth, without any projections to impede movement. The external ear is absent, forelimbs relatively short and modified into a streamlined fin-like structure, the hind limbs, as a result of changeover from a terrestrial
104 locomotor function to swimming, disappeared completely, the nipples are hidden in skin folds and the male reproductive organs are located in a body cavity (Kleinenberg, 1956, p. 100). The skin is devoid of a hair coat as well as sebaceous and sweat glands. The skin surface is covered with a special epidermal exudation, which enhances the passage of the animal in water. The upper epidermal layer did not undergo Keratinization, which also promotes excellent gliding through the water (Sokolov, 1955).

The modifications of cetaceans associated with their changeover to a new, aquatic medium are reflected mainly in the following skeletal features.

The frontal part of the skull is considerably extended forward as a result of elongation of the vomer, maxillae and premaxillae. In the proximal part, the premaxillae cover the extremely short frontals. As a result of the position of the pterygoids, close together at the midline of the skull, the bony palate has shifted posteriorly, thus displacing the choanae toward the larynx. As a result, the nares located at the highest point on the head permit air to pass through the nearly vertical respiratory tube without entering the oral cavity. The cranium became rounded and shortened. The occipital bone developed greatly as a result of giving anchorage to the massive dorsal musculature and is displaced toward the parietals; and in well-developed specimens, it is shifted onto the frontal part of the skull. The mandibles are considerably long and are either joined with ligaments (*Mysticeti*) or firmly fused (*Odontoceti*). The shoulder region is without a collar bone. All joints of the limb bones, except for the humerus, are immovable. The skeleton of the posterior limbs is vestigial and only some bones not connected with the vertebral column remained of the pelvic region.

The reduction of hind limbs among toothed cetaceans has progressed far beyond that in the toothless ones. This is indicated by the more primitive structure of the pelvic region among the toothless cetaceans (Tomilin, 1957, p. 343) and the frequent presence of vestiges of hind limb skeletons among them, i e. the phenomenon of atavism (Zem'skii and Berezin, 1961).

In the vertebral column, there are four instead of the five regions normal among terrestrial mammals. These are: cervical, thoracic, lumbar and caudal. The sacral is not differentiated as a result of the reduction of the pelvis. The cervical region is greatly abbreviated.
105 The reduction of the zygapophysis and pelvis enhanced the mobility of the posterior half of the vertebral column (Tomilin, 1957, p. 91). The vertebrae are short and, at times, even discoid (among dolphins) and somewhat compressed laterally. Transition to the caudal region is marked by the presence of hemapophyses.

A characteristic feature of cetaceans is the absence of hollow bones. The bones of the forelimbs, like all other bones of the skeleton, are spongy and impregnated with a large quantity of fat which greatly reduces the density of bone.

Based on the data of the fossil cetacean remains of Georgia, Azerbaidzhan and the Northern Caucasus and also the information contained in literature on the subject, I have tried to trace the evolutionary history of some morphological characteristics among the members of Cetacea available with me.

The Miocene members of the Odontoceti had evidently already possessed a streamlined body. This fact is supported by the presence among these animals of an extremely tapering frontal region of the skull (*Anacharsis*, *Champsodelphis*, *Iniopsis*, *Cyrtodelphis* and *Imerodelphis*) and the nature of changes in the size and shape of the vertebrae in the cranial-caudal direction (small in the anterior part of the vertebral column and with relatively short transverse processes; the greatest part of the body length as also the length of the vertebral processes are in the midportion of the vertebral column, i.e. in the lumbar region;

in the caudal region, however, the vertebrae decrease, processes shorten and totally disappear even at the middle of the caudal region. The caudal vertebrae of fossil dolphins have well-developed hemapophyses and compressed transverse processes). The structure of the caudal region of the skeleton points to the possession of a laterally compressed and massive tail in these animals. However, in spite of this, the tail and generally the entire vertebral column of these animals was evidently less supple than in the later, i.e., in all of the Miocene dolphins studied by me (*Champsodelphis*, *Iniopsis*, *Imerodelphis*, *Cyrtodelphis*, *Anacharsis* and *Kentriodon*), the vertebrae with the exception of the terminal caudal ones are relatively long. According to the data of Colbert (1944), the elongated vertebral bodies of the posterior part of the vertebral column constitute a primitive feature among the cetaceans.

The shortened, almost discoid vertebrae of present-day dolphins were evolved perhaps relatively late in the phylogeny of these animals.

106 The hind limbs in Miocene Odontoceti, as in present-day forms, are completely reduced, the pelvic region retained as curved tiny ossicles resembling short ribs (Bogachev, 1957).

The shoulder bones in the fossil forms are less shortened than in the modern. In many fossil dolphins, *Anacharsis orbus* Bog., *Champsodelphis letochae* Brdt., *C. fuchsii* Brdt., *C. karreri* Brdt., *Incacetus broggii* Colbert, *Imerodelphis thabagarii* Mch. and others, the humerus is as long as the forearm (Fig. 19). In the Pliocene and present-day *D. delphis* L. (Druzhinin, 1924 and Ryabinin, 1908) (Fig. 20), the humerus is relatively short. This phenomenon may be interpreted as follows.

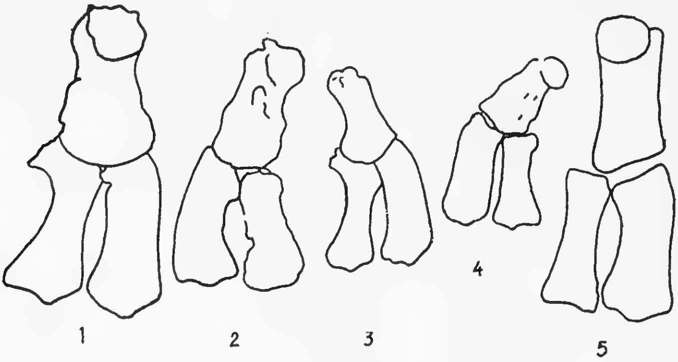
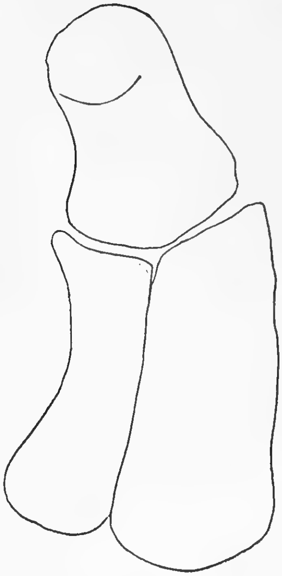


Fig. 19. Skeletons of the forelimbs of fossil dolphins :
1—*Champsodelphis fuchsii* Brdt.; 2—*C. letochae* Brdt.; 3—*C. karreri* Brdt.; 4—*Anacharsis orbus* Bog.; 5—*Incacetus broggii* Colbert.



107 Fig. 20. Skeleton of forelimb of present-day dolphin *D. delphis* L.

Modern dolphins are known to use their limbs only for altering direction or for a braking motion. It is also known that only their forearm projects fully beyond the trunk. The forearm bones are articulated with the humerus by a cartilaginous union to form a common axis. Efficiency depends on the surface area of the forearm and manus as a whole. If the entire limb is considered as a single axis, the shorter the limb the lesser the force required for rotation. It may, therefore,
107 be assumed that the control mechanism was perfected in the present-day forms (by forelimbs) by shortening the limb axis, which in turn is achieved by reducing the length of the humerus. While the limb as a whole was shortened, the length of the segment performing the effective work was not subject to any change.

The relatively greater width of the forearm and carpus in the fossil forms compared to the present-day forms is noteworthy. The medial margins of the forearm bones in the present-day *D. delphis* L. are straight, and the bones adhere closely to each other (Fig. 20). In most of the fossil forms, however (*Champsodelphis fuchsii* Brdt., *C. letochae* Brdt., *C. karreri* Brdt., *Anacharsis orbus* Bog., *Incacetus broggii* Colbert and *Imerodelphis thabagarii* Mch.), the ulna has a curved medial margin. The whole of the radius is curved as a result of which there is a broad space between the bones (*spatium interosseum*), making for a significant width of the forearm (Fig. 19).

The carpus of present-day forms consists of five bones of which the
108 radiale, intermedium and ulnare constitute the proximal row and the

other two, Ca(4) and Ca(2+3), the distal. However, exceptional instances were noticed of reduction (by fusion of two adjoining bones) as well as an increase in the number of carpals (Vokken, 1946). I examined only three complete wrists of fossil dolphins, and I could see the three types of structure in them: normal, with five bones (in *Anacharsis*); increased, with six bones (in *Imerodelphis*); and reduced as a result of fusion (in *Champsodelphis*).

The six-boned carpus of *Imerodelphis* was considered earlier (Mchedlidze, 1959) as a systematic feature. However, a further study of the material prompted me to reject this assumption. It may be possible that the six-boned carpus was characteristic of some Miocene dolphins; but in my view, it would be more correct to assume that this feature varied widely in the Miocene forms. Evidently, during the evolution of Delphinoidea, insignificant changes in the number of carpal bones were not of material importance to the animal (i.e. the reduction of their number did not give them any special advantage), and hence the feature which began varying even in the Miocene forms has not yet stabilized.

An extremely striking feature of present-day toothed cetaceans is the asymmetry of the skull. The bones in the left half of the skull are noticeably smaller than those in the right half. However, this asymmetry of the skull, seen so distinctly in present-day forms, is almost absent or hardly noticeable in the fossil members of the Delphinoidea (*Leptodelphis stavropolitanus* Kirp., *Sarmatodelphis moldavicus* Krip., *Iniopsis caucasica* Lyd., *Cyrtodelphis sulcatus* Ger., *Kentriodon pernix* Kell., *Cyrtodelphis bogatshowi* Mch., *Palaeophocaena andrussowi* Abel. and others), which have been identified from their well-preserved skulls. Of the current hypotheses which explain this phenomenon (Mekkelei, 1822, Khaast, 1874, Kuykental, 1908, Guild'ber, 1896, Winge, 1824, Beddard, 1910, Polinskii, 1909, Larzher, 1913, Lillie, 1910, Sleptsov, 1939, Narkhov, 1937, Shuleikin, 1941 and others*, the hypothesis of Shuleikin appears to me to be the most correct and scientific.

109 Analyzing the kinetics of motions of dolphins, Shuleikin came to the following conclusion. Having developed immense speed, the dolphins accelerated like a screw with a left-handed helix. Such a movement, i.e. "screwing" of the body, is achieved by two wave systems running from head to tail. One of them runs along the body of the fish in waves, i.e. by transverse oscillations in the horizontal plane and the other also by transverse oscillation, but only in the

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*The works of Mekkelei, Khaast, Kuykental and others are cited after Sleptsov (1939).

vertical plane*. The combination of these oscillations in mutually perpendicular planes points out that each transverse section of the dolphin body performs oscillations in the vertical as well as horizontal planes and, at a given point on the animal's body surface, makes an ellipse and, in a special case, a circle. According to him, the best conditions of rotation are realized when a growing wave (from head to tail), polarized in an elliptical or circular form, runs along the body. In the absence of skull asymmetry, the animal would be spinning around its own axis all the time and only asymmetry saves it from this rotation (Shuleikin, 1941, pp. 716–717).

The helical motion evidently evolved with the increasing speed of the animal, which in turn was undoubtedly associated with the perfection of the locomotor system. In my view, this perfection of the locomotor system should have occurred by the involvement of the entire trunk of the animal in the process of reciprocating motion. The reduction of zygapophyses, hind limbs and the pelvic region undoubtedly increased the elasticity of the vertebral column, though it was not an adequate adaptation to effecting the helical motion. Miocene
110 forms, in fact, had already a reduced pelvis, hind limbs and zygapophyses, but asymmetry was still absent in them and their long vertebrae did not permit helical motion. Consequently, long vertebrae are characteristic of fossil forms with poorly developed asymmetry of the skull or with asymmetry totally absent and, hence, it may be assumed that during the evolution of dolphins along with the development of asymmetry, the length of centra of vertebrae shortened, thus increasing the elasticity of the animal's body.

Thus, unlike present-day dolphins with extremely short discoid vertebrae, short shoulder bones and asymmetry of the skull, the Miocene animals had long vertebrae and relatively long shoulder bones, with almost a total absence of skull asymmetry. There is no doubt that all of these structural changes in the skeleton of Delphinoidea (skull, vertebrae and humerus) are associated with the same phenomenon, namely with the acceleration of movement, which was one of

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*Based on a study of morphology of the muscles of dolphins, Narkhov established that the ilio-costalis muscle raises the tail up and simultaneously draws it aside by unidirectional contraction, while the ischiocaudalis muscle by a similar action drops the tail downward and simultaneously also draws it aside. Consequently, these muscles clearly serve to effect simultaneous oscillations of the body not only in the vertical, but also in the horizontal plane. In spite of this, Narkhov continues to believe that the caudal fin vibrating in the vertical direction serves as a dolphin motor. In such an event, as correctly recognized by Stas' (1939) "the dolphin would have to develop such a high frequency of oscillations that it would be humming like a bumblebee."

the most important adaptations of marine animals feeding predominantly on rapidly swimming organisms (fish).

Judging from skeletal features, the Miocene dolphins were poor swimmers compared to their present-day counterparts. The tail was their prime propeller, helical motion was evidently not one of their distinguishing features and, even if it did exist at all, it played only an insignificant role in its reciprocating motion. This can also be proven by the absence of asymmetry in the skull of Miocene fossil members.

From this point of view, a study of Pliocene dolphins would be of much interest as they represent an intermediate stage between the Miocene and the present-day forms. Unfortunately, however, the scanty paleontological material on Pliocene dolphins comes in the way of tracing the structural changes in the skeleton.

Vertebrae of the Pliocene dolphin, described by Ryabinin (1908) from the Apsheron formations of Cheleken island were evidently slightly less shortened than in the present-day *D. delphis* L. The ratio of length to width of lumbar vertebrae in the Apsheron fossil dolphin was 0.9, while this ratio in the modern Mediterranean dolphin with which Ryabinin compared his own material (Ryabinin, 1908, p. 520) was 0.75. Moreover, the humerus of both Apsheron and present-day forms, according to the data of Ryabinin, were of equal size and, at the same time, noticeably shorter than the radius.

111 Unfortunately, the author did not come across indications of asymmetry in the skull. There is no information in available literature for other finds of Apsheron and Pliocene dolphins (Bogachev, 1938). Nevertheless, there is justification to regard the Pliocene dolphins as already fully comparable (in shape and dimensions of certain skull bones, structure of teeth and limbs) to the recent *D. delphis*, slightly differing from the latter in the relatively less short vertebrae.

During the course of adaptation of cetaceans to the aquatic environment, the hind limbs evidently were the first to lose their function and became reduced. Among the dolphins, throughout the Miocene, the locomotory function at this stage of evolution was performed evidently by the relatively flexible tail, though quite possibly the forelimbs, too, took part in this activity. The latter were possibly not fully specialized for performing the control function. The vertebral column, consisting of long vertebrae, was not adapted to executing the helical motion which, in my view, was in conformity with the absence of an asymmetrical skull among the Miocene forms. During subsequent stages of evolution, even in the Pliocene, some vital changes in the structure of the forelimbs took place: the shoulder bones were considerably shortened and adapted to a steering function with which, in my view, 111 **Table 35. Comparison of some dimensions of limb bones of Miocene, Pliocene and present-day dolphins**

	Palaeophocaena andrussowi Abel (Chokrak)	*C. c. letochae* Brdt. (Sarmat)	*D. delphis* L. (Apsheron)	*D. delphis* L. Mediterranean form	*D. delphis* L. Black Sea form
Length of humerus	35	67.5	56	56	41
Length of radius	32	66	72	72	58
Length of ulna	—	57	60	55	46

should also be associated the intensification of the locomotor function of the tail. The vertebrae compared with those of Miocene delphinoids were noticeably short, as a result of which the entire vertebral column 112 became considerably more elastic. However, even the Upper Pliocene Apsheron forms did not yet achieve the perfection of locomotion noticed in present-day dolphins, since their vertebrae were not as short as present-day ones.

Among the dolphins inhabiting the present Black Sea–Azov Basin (*D. delphis* L., *P. phocaena* L. and *T. tursiops* Fabr.), the cosmopolitan *D. delphis* L. stands closest to the Miocene forms.

The present-day dolphins listed above are typical ichthyophages, but some aspects of their feeding and the distribution of their food base differ widely. Thus, for example, the white-sided dolphin feeds mainly on pelagic fish, while Azov and bottle-nosed dolphins are bottom feeders; moreover, the Azov dolphin, unlike the bottle-nosed, feeds in the benthic zone in shallow water. The regular food bases of the latter two species are scattered in the sea and do not form large shoals. The species of interest to us (*D. delphis*) feeds mainly on relatively small fish forming dense schools (Kleinenberg, 1956).

Most authors (Danilevskii, 1871; Arnol'd, 1896; Silant'ev, 1903; and Dinnik, 1910)* regard anchovy (*Engraulis encrasicholus* L.) at the main food of white-sided dolphins in the Black Sea. But, apart from fish, the stomachs of these dolphins often contained cephalopods (Genshtel', 1937; Froind, 1932; and Kleinenberg, 1956), crustaceans (Mal'm, 1932), and at times, also a few gastropods and lamellibranchs: *Nassa reticulata* L., *Mactra subtruncata* Da Costa, *Venus gallina* L. and *Modiola adriatica* Lamarck. The latter, according to Kleinenberg (1956, p. 116), is not really considered as food for dolphins. They are simply swallowed along with fish when the latter sink to the ocean bottom on the coast (in spring and autumn) or enter the dolphins' stomach from fish feeding on these mollusks.

The steady and prolonged process of adaptation to catching food in water preceded the final changeover of cetacean predecessors to an 113 aquatic medium. The first inhabitants of the sea probably acquired their food in relatively shallow portions of the basin. Food specialization, involving catches consisting exclusively of fish, arose later when, after acquiring several other adaptations, it became possible for them to seek food at a greater speed in the open sea and to be able to dive to a considerable depth (for benthose feeding).

If the present-day white-sided dolphin is capable of feeding on

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*The above references of Danilevskii, Arnol'd, Silant'ev, etc. are cited after Kleinenberg (1956).

rapidly swimming shoals of fish with its unique adaptation for this purpose, the Miocene dolphins, in my opinion, were poor swimmers and were perhaps less adapted to such feeding. Various marine organisms (cephalopods, lamellibranchs, gastropods and crustaceans), which serve as accidental constituents of food of present-day forms, possibly constituted a significant portion of the food of Tertiary dolphins since these represent food relatively easy to obtain.

Apart from the information on the specific characteristics of whalebone whales given above, in a discussion of the general characteristics of cetaceans, attention should also be drawn to the following features of these animals. Firstly, the significant increase of skull size in relation to the total body length should be noticed (the skull of modern whales occupies one-fifth and at times one-third the total length). This is associated with the great increase in the volume of the oral cavity, which is a consequence of the characteristic mode of feeding of these animals (straining large amounts of water containing plankton).

If perfection of the method of acquiring food among toothed cetaceans necessitated a gradual increase in the speed of locomotion, then among the toothless forms, which remained relatively slow moving, the adoptation of the method of feeding proceeded toward an increasing volume of the oral cavity, facilitating the gulping of planktonic food in large quantities.

However, the history of evolution of whalebone whales bears some common features with the toothed cetaceans. For example, in the evolution of fossil whalebone whales, as also among the toothed forms, a tendency towards shortening of the humerus is clearly noticeable.

The limbs of whalebone whales found in the Chokrak formations of Otradnaya village (Northern Caucasus) have relatively long humeri; the same features are characteristic of the limbs of the Karagan whalebone whales of Western Georgia, though the humeri in them are
114 better proportioned than among those from the Chokrak. The humeri of the Sarmatian whalebone whales *C. maicopicum* Spass., *C. mayeri* Brdt. and *C. priscum* Brdt. (Northern Caucasus, Baku and Derbent) already have extremely short bones constricted in most cases at the middle of the shaft (Plate XIX).

An extremely interesting feature is that among present-day whalebone whales, right whales and finback whales have short humeri; while the rhachianectids, which are more archaic in the structure of skull, pelvis, lower jaws and in their habitat conditions (they colonize shallow coastal parts of the basin), have a considerably longer humerus resembling that of the fossil *Plesiocetus* (Tomilin, 1957).

The shortening of the humerus in the evolution of whalebone whales is undoubtedly associated, as in toothed whales, with the perfection of locomotor organs enabling the animal to come into the ocean.

Miocene dolphins, being relatively slow swimming forms, were not yet sufficiently specialized for catching rapidly swimming quarry, and their humerus was relatively long. It should be remembered that even these were associated more with the coastal section of the sea than the pelagic.

All of this compels us to assume that among Miocene cetaceans, the perfection of forelimbs proceeded more rapidly in the toothless than toothed cetaceans since the Sarmatian dolphins still had long humeri (shortening was noticed only in the Pliocene); while the whalebone whales of the same period (Cetotheriidae) already had significantly short humeri.

Among toothed cetaceans this slowing down in the rate of shortening of the humeri is explained possibly by the fact that the perfection of the motor mechanism was also effected in them by some changes in the structure of the skull and vertebral column. Yet among whalebone whales, which did not undergo corresponding changes in structure of skull and vertebral column, the perfection of the motor apparatus proceeded mostly by transformations in the forelimbs.

A study of the central nervous system of fossil mammals is one of the most important aspects of paleontology.

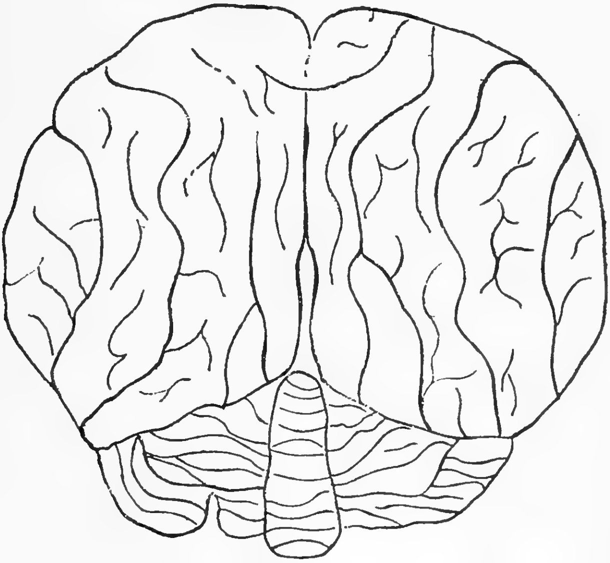
The natural and artificial endocranial casts of animals serve as
115 material for paleoneurological investigations. A cast corresponding closely to the brain of the animal (Orlov, 1949) has been preserved in only exceptional cases, and hence investigators more often come across casts corresponding to the brain plus the entire cranial cavity. The correlation of the cast of the cranial cavity with that of the brain is more complete if the brain presses against the bones underlying the skull base as also the other bones of the braincase, which is particularly typical of mammals and birds. The brain of most reptiles, amphibians and especially fish is separated from the braincase by cavities filled with a vascular network, and by gaps in the cranium. It is clear that, in such an event, the internal cast of the brain will not match in size and topography that of the brain of the animal.

Further investigations (Dechaseaux, 1961) revealed that the lack of correlation between the cast of the brain cavity and the brain is particularly characteristic of large cetaceans. By comparing the cranial cavities of present-day whalebone (*Balaenoptera musculus* L.) and toothed (*Phocaena phocaena* L.) cetaceans with their own brains, Dechaseaux (1961, p. 882) came to the conclusion that the brain of cetaceans does not fill the whole cavity of the cranium and that a part of the cavity is occupied by vascular bundles, causing a difference between the cranial cavity and the brain. Such a braincase structure is characteristic of large forms, i.e. members of the Mysticeti. In small cetaceans (Odontoceti), the development of the vascular network is so poor that they only insignificantly alter the general form of the brain.

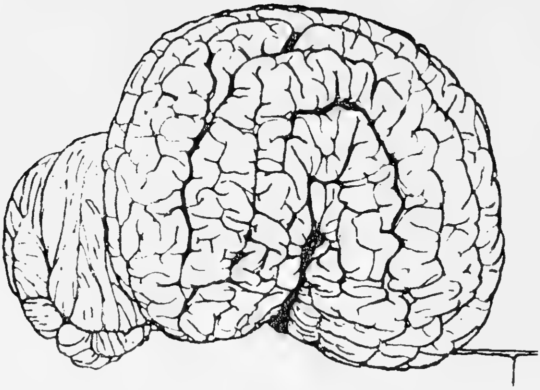
Before going over to a review of the cranial cavities of fossil cetaceans to explain some of their features, the central nervous system of present-day members of this group of animals should also be studied.

The brain of modern cetaceans is characterized by large, oval and intensely curved hemispheres. In view of the intense development of the temporal lobes of the hemispheres, the brain is considerably posteriorly enlarged. It is noticeably wider than long, particularly among the toothed cetaceans. The posterior part of the cerebral hemispheres is so intensely developed that it covers the anterior part of the cerebellum. The presence of considerably enlarged frontal lobes and the intense flexure in the region of the diencephalon impart a spherical
116 form to the brain as a whole (Breathnach, 1960). In the whalebone whales, the anterior end of the brain is almost vertical (Fig. 22) and relatively arcuate among the toothed (Fig. 23).

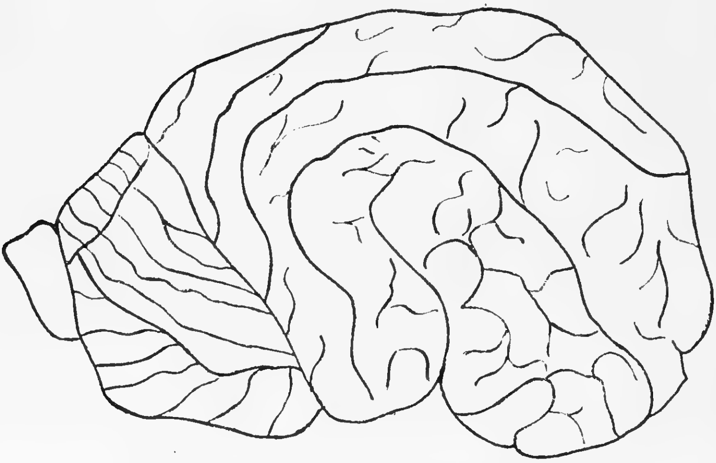
The characteristic features of the central nervous system of ceta-
117 ceans include the poor development (Mysticeti) or total absence



116 Fig. 21. Brain of adult present-day dolphin *D. delphis* L., dorsal view (after Sakharova).



116 Fig. 22. Brain of adult present-day whale *Balaenoptera musculus* L., lateral view (after Breathnach).



117 Fig. 23. Brain of present-day dolphin *D. delphis* L., lateral view (after Sakharova).

(Odontoceti) of olfactory nerves, bulbs, stems and the relatively well-developed V and VIII pairs of cranial nerves (Breathnach, 1960). Another feature is the intense development of the posterior lobes of the corpora quadrigemina which, unlike all other terrestrial mammals, are much larger than the anterior lobes in cetaceans. Such a phenomenon, apart from cetaceans, is also only characteristic of the members of the *Microchiroptera* and is evidently associated in both cases with the intensification of the role of auditory perception in the orientation of the animal. Groups of nerve cells vital for coordinating locomotor reflexes in response to auditory stimulations are located in the posterior lobes of the corpora quadrigemina.

According to the data of Sakharova (1941), during the ontogeny of the dolphin *D. delphis*, important changes in the shape and proportion of the brain could be traced. In the early stages of development of the embryo, the brain of the dolphin is similar to that of terrestrial mammals in form and proportion of individual sections. In particular, its length exceeds its width, as in the brain of terrestrial forms. However, during the growth process, this ratio becomes reversed; the width increases more than the length. The olfactory lobes, even during the middle stages of embryonic development, are located not in the anterior end of the large hemispheres as in terrestrial predators,
118 but on the ventral surface. The olfactory lobes are very small but nn. olfactorii are completely reduced.

During early stages of development, the flexure in the region of the diencephalon cannot be noticed. It is observable during the middle stages and gradually increases, imparting a spherical shape to the brain (Sakharova, 1941, p. 310).

Let us now attempt to compare the endocranial casts of some fossil dolphins with the brains of modern dolphins at different stages of development.

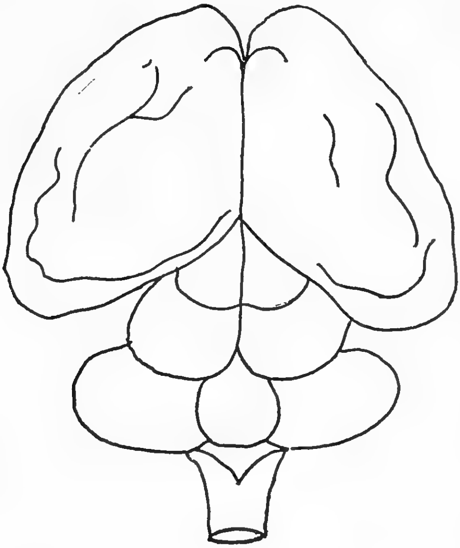


Fig. 24. Brain of a 20 cm embryo of present-day *D. delphis* L., dorsal view (after Sakharova).

By comparing the endocranial casts of *Cyrtodelphis sulcatus* Ger. (Dal Piaz, 1906, Plate 21) with the brain of the present-day dolphin at different stages of development (Sakharova, 1941), it may be noticed that in several features, the brain of *Cyrtodelphis* is comparable to that of embryos in early developmental stages and has much in common with the brains of terrestrial predators.

The length of the endocranial cast of the Miocene dolphin *Cyrtodelphis sulcatus* far exceeds its width. Anteriorly, the hemispheres are noticeably constricted; while posteriorly, they are considerably broad-
119 ened. All the same, they do not cover the anterior end of the brain. The olfactory lobes are well-developed, located at the anterior end of the brain, and are somewhat raised.

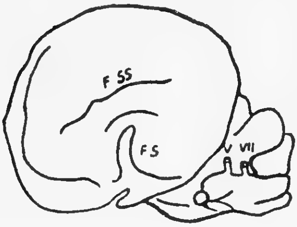


Fig. 25. Brain of a 20 cm embryo of present-day dolphin, *D. delphis* L., lateral view (after Sakharova).

Fig. 26. Endocranial cast of fossil dolphin, *Cyrtodelphis sulcatus* Ger., lateral view (after Dal Piaz).

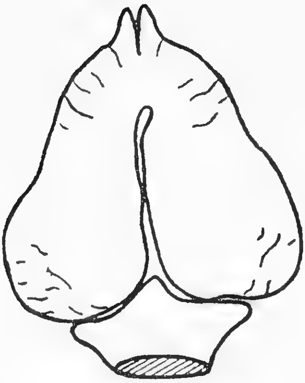


Fig. 27. Endocranial cast of fossil dolphin, *Cyrtodelphis sulcatus* Ger., dorsal view (after Dal Piaz).

Nearly the same structural features are also noticed in the endo-
cranial casts of other Miocene dolphins, *Palaeophocaena andrussowi* Abel
(Abel, 1905, p. 379). Although in this example, only an insignificant
part of the lateral surface of the cast is exposed, this material is of
much interest since it evidently represents the core corresponding
120 to the brain. A shallow Sylvian fissure, part of the posterior ectosylvian
fissure, as well as a slightly anteriorly inclined fissure separating the
olfactory lobes (fissura rhinalis) could be distinguished in the cast.

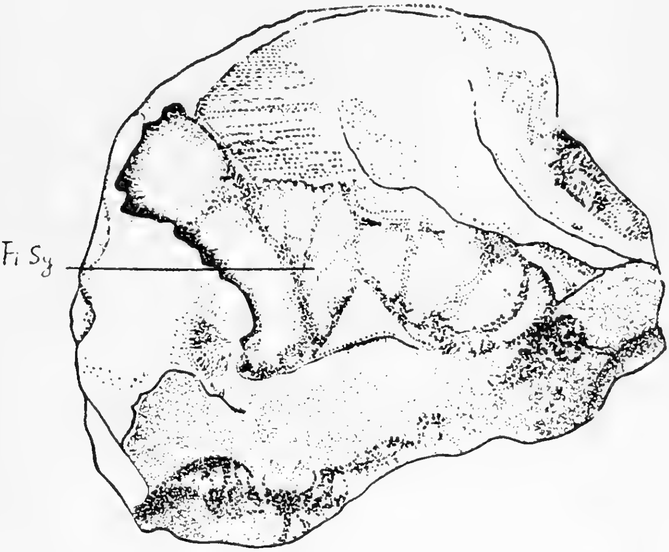


Fig. 28. *Palaeophocaena andrussowi* Abel. Skull with endocranial cast, lateral view (after Abel). Fi Sy=Sylvian fissure.

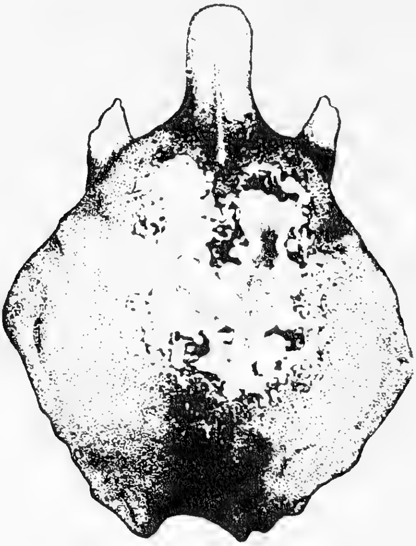
Judging from the exposed fragment of the natural cast of the brain of *Palaeophocaena*, the olfactory lobes in this form were well-developed and, as in *Cyrtodelphis*, located in the anterior end of the brain. As a whole, the brain was slightly flexed in the region of the diencephalon, which is supported by the presence of nearly straight convolutions and fissures on the cast.

The intense enlargement of the anterior part of the hemispheres (frontal lobes and anterior portion of parietal lobes) noticed among present-day toothed cetaceans is obviously associated with the complicated nature and diverse forms of locomotion of these animals. It is well-known (Kogan, 1959, p. 61) that the nucleus of the locomotor analyzer is mainly localized in the forecentral (gyrus centralis anterior), pericentral (gyrus paracentralis) and in the posterior section of the central and lower frontal convolutions (gyrus frontalis media et inferior). The 121 area of their location is quite developed in present-day members of cetaceans (Breathnach, 1960 and Sakharova, 1941). The enlargement of the temporal lobes of the hemispheres where the cortical sections of the acoustic analyzer are located (central part of the dorsal temporal convolutions, gyrus temporalis superior) as also the changes noticed in the structure of the corpora quadrigemina correspond undoubtedly to a maximum development in hearing.

Data available on the central nervous system of Miocene cetotheriids are scanty. Only some stray, extremely incomplete, endocranial casts of cetotheriids have been studied so far (Dechaseaux, 1961, p. 885). I prepared and studied a nearly complete endocranial cast of the Sarmatian whale *C. maicopicum* Spass. and a Middle Miocene Karagan member of the Cetotheriidae, *Imerocetus karaganicus* Mch.

The brain of the Karagan whale (Fig. 29) was evidently fairly long and triangular. Its posterior portion was relatively low and slightly expanded transversely. The hemispheres are almost devoid of a flexure in the region of the diencephalon. The frontal lobes are 122 small, slightly bulged and intensely constricted anteriorly. They gradually merge into the long and high olfactory lobes represented in the cast by the digitate process (Fig. 29).

According to the data of Edinger (1955), the anterior elongation of the cerebral cast of *Cetotherium* studied by her should correspond to



121 Fig. 29. Endocranial cast of *Imerocetus karaganicus* Mch., dorsal view.

the olfactory stalks enveloped in vascular packets. In my opinion, however, the digitate process, in the frontal portion of the cast of *Imerocetus*, represents the cast of a portion of the cranial cavity occupied by the greatly developed olfactory lobes and olfactory stalks partly diverging from them. My data given below on the changes noticed in the cerebrum of the present-day *Balaenoptera musculus* L., resembling in many features the structure of the skull of Miocene cetotheriids, led me to a similar conclusion.

The brain of present-day forms, as already pointed out above, is intensely flexed in the region of the diencephalon (see Fig. 22). As a result, the poorly developed olfactory lobes and the basal parts of the olfactory stalks are shifted onto the ventral surface of the brain and are located close to its center. Consequently, seen from above, only the anterior parts of the olfactory stalks run beyond the anterior end of the brain. It is, therefore, natural that the elongated process at the anterior end of the endocranium in present-day forms would correspond to the olfactory stalks with their vascular bundle.

Fig. 30. Endocranial cast of *Imerocetus karaganicus* Mch., lateral view.

Regarding the brain of Miocene fossil whales, my material shows no flexure at all (*Imerocetus karaganicus* Mch.) (Fig. 30) or flexed insignificantly (*C. maicopicum*) (Fig. 31). As a result, the olfactory lobes, 123 which were well-developed in them, should have occupied the anterior part of the hemispheres. Therefore, in my view, the forward growth of the frontal lobes in the endocranial casts of Miocene forms should correspond to the olfactory lobes and possibly partly to the olfactory stalks.

The cranial cavity of the Middle Sarmatian whale *C. maicopicum* is so transversely expanded in the region of the temporal lobes that its total width is far greater than the length. This may be due to the intense development in the temporal region of vascular packets of pro-

Fig. 31. Endocranial cast of *Cetotherium maicopicum* Spass., lateral view.

liferation on the dura mater of the cerebrum, particularly in the posterior portion of the accessory processes. The frontal lobes, unlike those in the Karagan form, are considerably enlarged, expanded in the anterior part and bent relatively downward. Their bulged surfaces are directed forward, and the longitudinal axes of these bulged formations lie mutually parallel to each other (the same surfaces in Karagan *Imerocetus* are laterally directed, and their axes diverge forward at an angle). The olfactory lobes in the Sarmatian form are

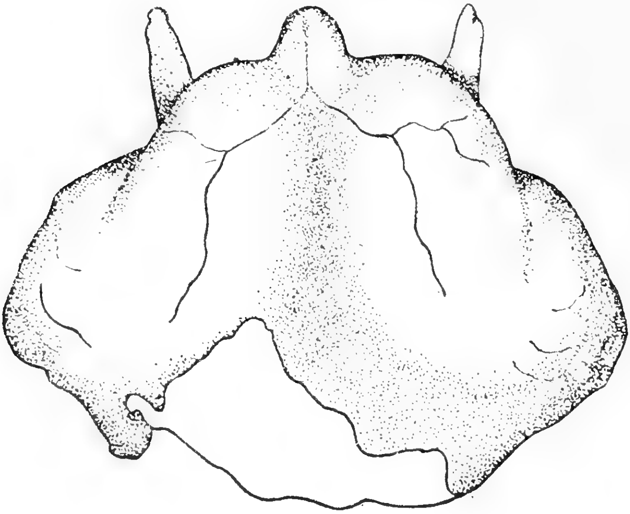


Fig. 32. Endocranial cast of *Cetotherium maicopicum* Spass., dorsal view.

greatly reduced; consequently there is a considerable ventral shift of the olfactory lobes on the flexure of the hemispheres, which has already commenced. All the same, they are still located at the anterior end of the brain.

I assume that the frontal lobes and the cerebral sections adjoining them in the Miocene forms were not covered by any significant accessory formations, which could cause a difference between the anterior portions of the brain and the corresponding sections of the endocranium. This is supported by the presence in the endocranial cast of
124 distinct arteria meningea media with its anterior and posterior rami. This artery could not have left any trace on the inner surface of the skull in the presence of (any significant) accessory formations, which usually fall between the dura mater and the cranium.

To what degree of embryonic development does the brain of modern finback whales correspond to the brain of the Miocene cetotheriids? This question could be answered by comparing the fossil material with the brain of a 72 cm embryo of *Balaenoptera musculus* (Friant, 1957). On the ventral surface, this brain is triangular and laterally bean-shaped. The anterior portion of the hemispheres is already considerably expanded. On the whole, the brain is relatively elongated. Its height is less than its length—unlike the brain of adults in which an inverse ratio prevails (Breathnach, 1960). The flexure in the region of the diencephalon is fairly well-developed, as a result of which the relatively broad olfactory stalks lie completely on the ventral surface without their ends emerging beyond the anterior end of the hemispheres (Fig. 33).

125 As could be seen from the above discussion, in some structural features, the brain of the embryo of finback whales at midstage of

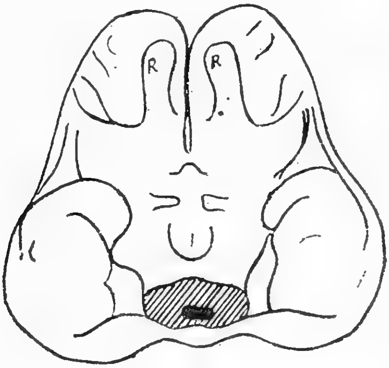


Fig. 33. Brain of a 72 cm embryo of *Balaenoptera musculus* L., ventral view (after Friant).

development (proportion of some parts of brain, disposition of olfactory stalks, etc.) evidently stands relatively at a much higher level than that of the Miocene forms.

In spite of the fact that no precise information is yet available about the phylogenetic affinities between Archaeoceti and Mysticeti, it would be quite interesting to compare the endocranial casts of whalebone whales studied by me with those of some members of the Archaeoceti since, according to Abel (1903), the ancestors of the cetotheriids are to be found possibly among the Archaeoceti. Dart (1923) having studied a series of casts of members of the Archaeoceti established that, among the Eocene Zeuglodontidae, the reduction of olfaction proceeded gradually and, at the same time, parallel with the exceptional development of the trigeminal complex and hearing organs, enabling these animals to achieve a perfect adaptation to their habitat.

The brain of Miocene cetotheriids differs sharply from that of *Prozeuglodon stromeri*, a member of the Archaeoceti, in its general form as well as in the development of olfactory organs and the proportion of different parts of the brain. The brain of *Prozeuglodon* is greatly elongated and acutely triangular in shape, the olfactory lobes, stalks and bulbs very well-developed, and the cerebral hemispheres are relatively only slightly enlarged. In the Miocene cetotheriids, however,
126 the general form of the brain is nearly rounded (especially among the Upper Miocene members of this family), the olfactory organs are considerably reduced and the cerebral hemispheres noticeably enlarged.

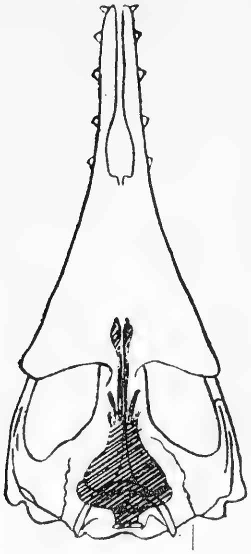


Fig. 34. *Prozeuglodon stromeri* Andrews, skull with endocranial cast (after Dart).

Thus, a comparison of the endocranial casts of Miocene cetotheriids with the endocranial cast of *Prozeuglodon stromeri*, a member of the Archaeoceti, justifies the assumption that in the course of evolutionary divergence of Mysticeti from Archaeoceti, their brains underwent several vital changes. This is seen in a significant increase of the size of the hemispheres, conversion of the triangular shape of the brain into a spherical one, and a more substantial further reduction of the olfactory lobes of the brain, stalks, bulbs and their displacement onto the ventral surface.

From the above discussion, it emerges that the reduction of the olfactory faculty and, hence, the corresponding parts of the brain was evidently an extremely prolonged process, commencing soon after the changeover of these animals from land to an aquatic medium and continued throughout the Tertiary period.

127 However, comparing the level of principal changes of the brain of Middle Miocene forms with those of the Eocene, and the Upper Miocene with the Middle Miocene, it is inevitably concluded that the rate of evolution of the brain of toothless cetaceans was not uniform throughout these epochs. Presumably, this process proceeded somewhat at an accelerated tempo from the Karagan epoch to the Middle Sarmat.

The acceleration of the tempo of reduction of olfactory organs, noticed between the Middle and Upper Miocene, coincides with the commencement of the exceptional development of the hemispheres of the cerebellum and their flexure, these being characteristic of modern cetaceans. It may be assumed that at this stage of phylogenetic development of these animals, the acceleration of progressive development of the brain was evidently associated with the emergence of these animals in the open expanses of the basin. This, in turn, was accompanied by fairly important changes in the structure of the limb skeleton (shortening of humerus and mobility of shoulder joint) at the junction of the Middle and Upper Miocene.

In my view, all these progressive structural changes among cetotheriids were also responsible for their exceptionally wide distribution in the oceans of the Upper Miocene.

Conclusions

127 1. Much of the material covered in the study came from new sites discovered in Georgia and the Northern Caucasus. Sites of fossil cetaceans in Western Georgia were established around the villages Kvaliti (Zestafon region), Rupoti (Terdzhol' region), Perevisa, Tsasri, Usakhelo (Chiatur region) and Dzhalaurta, Bzhinevi, Chorvila and Koreti (Sachkher region); in Eastern Georgia, around the village of Norio; and in the Northern Caucasus, Armavir and Maikop towns.

2. The following cetaceans have been described in this work:

ARCHAEOCETI—*Microzeuglodon caucasicum* Lyd.
Zeuglodon sp.
ODONTOCETI —*Iniopsis caucasica* Lyd.
Cyrtodelphis bogatshowi Mch.
Cyrtodelphis sp.
Champsodelphis cf. *fuchsii* Brdt.
128 *Champsodelphis* cf. *letochae* Brdt.
Champsodelphis sp.
Delphinapterus sp.
MYSTICETI —*Cetotherium maicopicum* Spass.
Cetotherium mayeri Brdt.
Cetotherium sp.
Imerocetus karaganicus Mch.

Among the above forms, there are two new genera and species and one new species.

3. Based on a study of paleontological material and analysis of data available in the literature on the subject on fossil cetaceans, it could be concluded that this group of mammals played an important role as a constituent of the marine fauna of the ancient basins ever since the Eocene. The faunal composition shows that in the Oligocene, the Caucasian basin was colonized most probably by predominantly archaic cetaceans, Archaeoceti; in the Miocene, whalebone whales of the family Cetotheriidae and also toothed cetaceans of the families Delphinidae and Acrodelphidae colonized there extensively. In the Pliocene, the basin covering the territory of the present-day Caspian

Sea was colonized by dolphins similar to the present-day Black Sea white-sided dolphins.

4. A study of the geological conditions of the sites of fossil cetaceans in the Caucasus provided accurate information on the stratigraphic position of many interesting finds. The sites and stratigraphic position could be successfully established as one of the best known complexes of fossil cetaceans described by Lydekker, based on material from the Tertiary formations of the Apsheron peninsula and erroneously placed by him in the Eocene. The geological age of some members of this fauna could be established accurately. It was evident that Sjegren's collection, forming the basis of Lydekker's studies, was taken from altogether different horizons of the Maikop suite at Perekishkyul village. The remains of dolphins, contained in this fauna, belong to the upper layers of the Maikop corresponding in age to the Miocene formations. The remains of *Microzeuglodon* evidently came from the lower Middle Maikop belonging to the Oligocene.

5. The deposition of Middle Miocene members of cetaceans in the Sachkher and Chiatur regions evidently occurred in the shallow
129 coastal strip of the basin adjoining the northwestern rim of the Dzirul' massif. The deposition of Lower Sarmat cetaceans in Western Georgia (at least in the Zestafon region) occurred in fairly deep parts of the basin under conditions of intense sedimentation, but not far away from the coastal zone. Around Armavir town, the deposition of Middle Sarmat cetaceans occurred in the shallow parts of the sea, though undoubtedly quite far from the coast. The Upper Sarmat forms known to us were, however, buried in the coastal belt close to the river estuary which carried the bones of terrestrial mammals and also leaves and fruits of different plants found together with the remains of cetaceans to the sea.

6. A study of dentition of several members of the family Zeuglodontidae established fairly constant differences between the upper and lower molars of these animals. For example, it was clear that the upper molars of *Zeuglodon* have a relatively low crown compared with the lower.

7. At present, it is not worthwhile to separate Microzeuglodontidae into a separate family as proposed by Abel, since the presence of diastemata between the lower molars cannot serve as an adequate basis for isolating a family.

It would be more correct to regard *Microzeuglodon* as a separate genus which together with the genus *Zeuglodon* constitutes the family Zeuglodontidae.

8. A comparison of the remains of "Microzeuglodon", described by Ryabinin from the Maikop of Kabristan (the region falling west

of Apsheron peninsula), with the known Zeuglodons *Z. isis* Beadn., *Z. cetoides* Str. and *M. caucasicum* Lyd. shows that in the structure of the teeth as well as dimensions, it stands closer to *Z. isis* than to *M. caucasicum.*

9. The structural features of the bone tissue of the humerus of *Microzeuglodon* provide justification to assume that the animal had a poorly developed cranial cavity. This feature of *Microzeuglodon* is positively archaic for the cetaceans and points to the histological structure of the bone, which to some extent brings this animal close to its terrestrial ancestors.

10. The most important changes in the skull structure, forelimbs and vertebrae during the delphinids' evolution were associated with the increasingly complex mode of locomotion, resulting in a significant increase in the rate of swimming which, in turn, was an extremely 130 important adaptation to living in the open seas and feeding mostly on rapidly moving organisms (fish).

11. The shifting of occipital elements onto the frontal portion of the skull is fainter among Middle Miocene cetotheriids than among their Upper Miocene counterparts.

The evolution of whalebone whales proceeded toward an increase in the size of the oral cavity brought about by the curvature of the skull and of the rami of the lower jaw. It should, therefore, be assumed that the horizontal position of the cranial portion of the skull, characteristic of Middle Miocene *Imerocetus*, as also the slight shifting of the occipital elements point to the antiquity of this form (in this case, this is also confirmed to some extent by its affinity to the Upper Oligocene *Cetotheriopsis*).

12. A study of the material from Maikop on Cetotheriidae showed that their remains, placed by Spasskii in *C. maicopicum*, actually belonged to some other species of the genus *Cetotherium*, possibly even to those from various Sarmatian horizons.

13. Miocene delphinids are very similar in several features of brain structure to terrestrial predators which, in the level of evolution of certain characteristics of the central nervous system, corresponds to the early stages of embryogeny of modern dolphins.

In the course of evolution of cetaceans, a sharp increase in the volume of the cerebral hemispheres (especially their anterior part) took place and the brain, as a whole, gradually acquired a spherical form; the olfactory bulbs, stalks and olfactory lobes were reduced. Simultaneously with this, the hearing and trigeminal complex were accentuated.

The reduction of olfaction was an extremely prolonged process, commencing soon after the changeover of the ancestors of cetaceans from land to an aquatic medium and proceeded far more intensely among members of the Odontoceti than the Mysticeti.

14. The reduction of olfactory lobes, stalks and bulbs among cetotheriids proceeded at an accelerated tempo in the period from Karagan to Middle Sarmat. Undoubtedly, at this stage in the evolution of cetotheriids, there was accelerated progressive development of the brain—evidently associated with the invasion of these animals into the open expanses of the basin. This, in turn, is associated with fairly significant changes in the skeleton of the forelimbs at the juncture of the Middle and Upper Miocene periods.

Résumé

131 This book on the Tertiary cetaceans of the Caucasus describes in considerable detail fourteen fossil forms (listed on p. 112) found in the Upper Oligocene and Miocene formations of the Caucasus.

Other important aspects covered in this book include a review of the history of studies on the Caucasian Tertiary cetaceans, geology of host rocks in which the bones are embedded, conditions of fossilization and the biology and evolution of cetaceans in general.

The steering function of Cetotheriidae and Delphinoidea improved by the shortening of the humerus and of the whole limb during the course of evolution. Miocene dolphins possessed long vertebrae, long humeri and a symmetrical skull and, undoubtedly, swam slower than present-day forms which have short vertebrae, short humeri and an asymmetrical skull.

Miocene forms are much similar to terrestrial predators in a number of features of the brain. The Miocene whalebone whales correspond to the early stages of development of present-day forms insofar as the evolutionary level of some brain characteristics is concerned.

The increasing complexity of the mode of locomotion, the accentuation of hearing and, at the same time, a weakening of the olfactory faculty during the evolution of cetaceans are reflected in the phylogenetic changes in their brains. The frontal and temporal lobes of the hemisphere areas, where the locomotor and auditory analyzers are located, have been enlarged; the olfactory organs which have shifted to the ventral surface have been partly reduced in the whalebone whales and totally so in the toothed ones.

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Plates

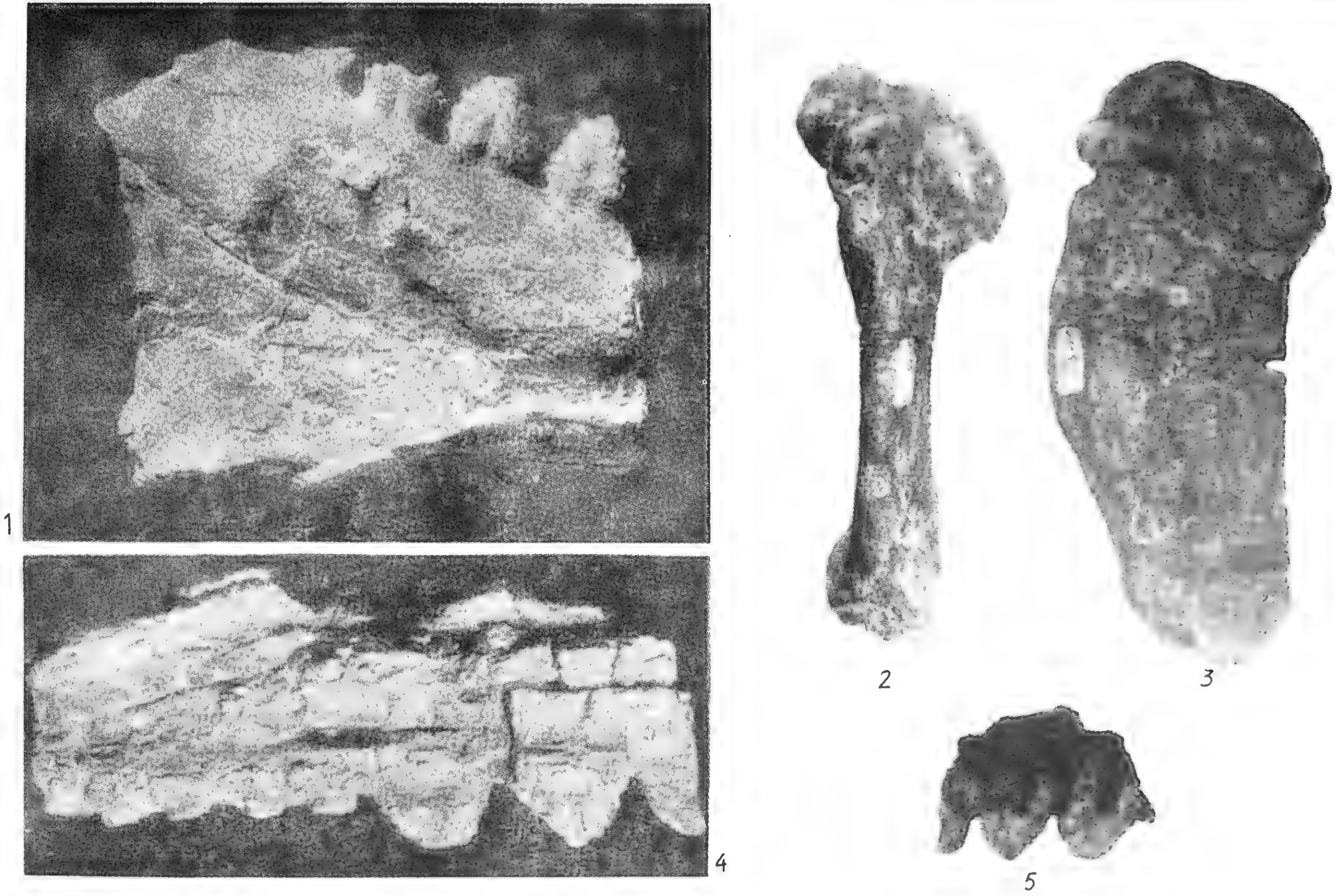

PLATE I

Microzeuglodon caucasicum Lyd.

1. Fragment of the right ramus of lower jaw. Natural size. 2. Humerus, radial margin. Natural size. 3. Humerus, dorsal view. Natural size. 4. Fragment of upper jaw, lingual surface. 5. Upper molar teeth. Natural size.

PLATE II

1. Skeleton of *Imerodelphis thabagarii* Mch. embedded in rock.

1

2

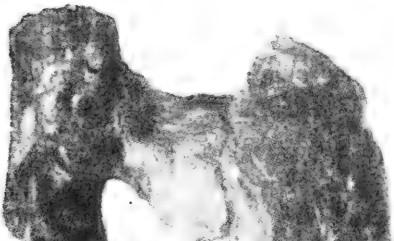

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PLATE III

1. Skeleton of forelimb of present-day dolphin *Delphinus delphis* L. Natural size.

2. Skeleton of forelimb of Sarmatian dolphin *Imerodelphis thabagarii* Mch. Natural size.

3. *Imerodelphis thabagarii* Mch. Lumbar vertebra. Natural size.

PLATE IV

1. *Iniopsis caucasica* Lyd. Skull, dorsal view. Natural size.

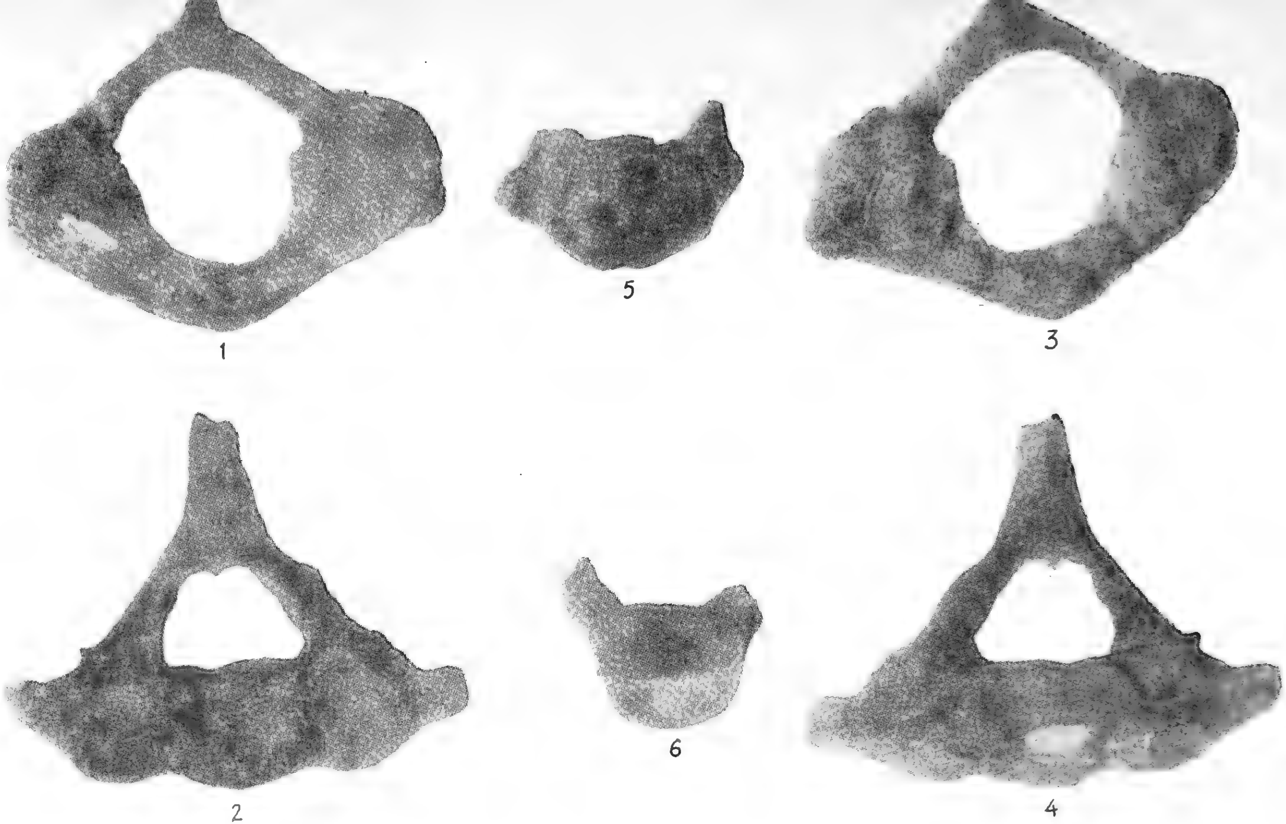
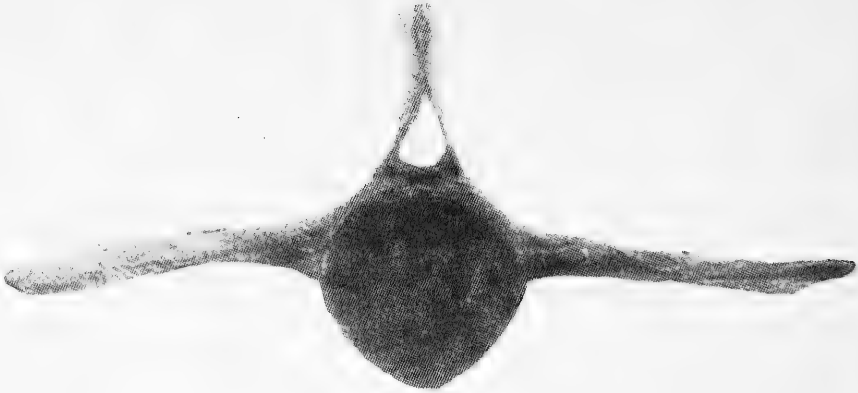


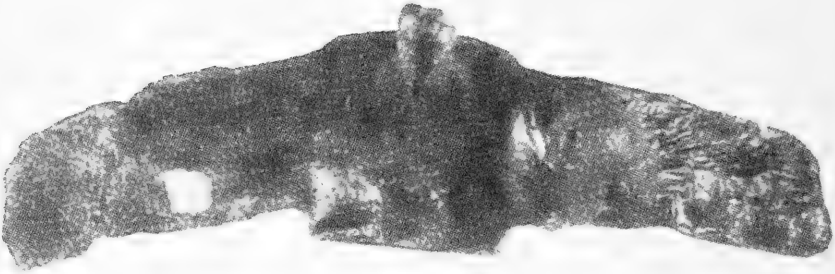
PLATE V

Champsodelphis cf. *fuchsii* Brdt.

1. First cervical vertebra, cranial view. 2. Second cervical vertebra, cranial view. 3. First cervical vertebra, caudal view. 4. Second cervical vertebra, caudal view. 5. Third cervical vertebra, cranial view. 6. Last cervical vertebra, cranial view.
(all bones of natural size)



1



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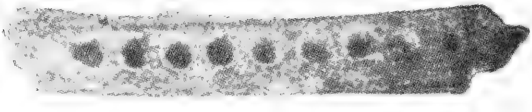


3

PLATE VI

Champsodelphis cf. *fuchsii* Brdt.

1. Lumbar vertebra, cranial view. Natural size.

2. Lumbar vertebra, dorsal view. Natural size.

3. Lower jaw fragment of *Champsodelphis* cf. *letochae* Brdt. × 1/2.

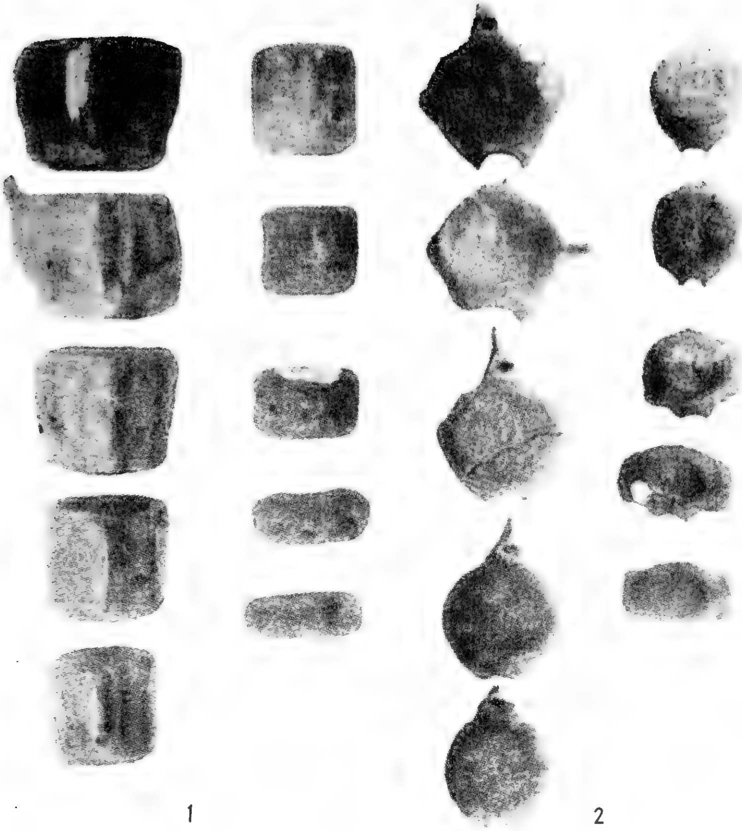


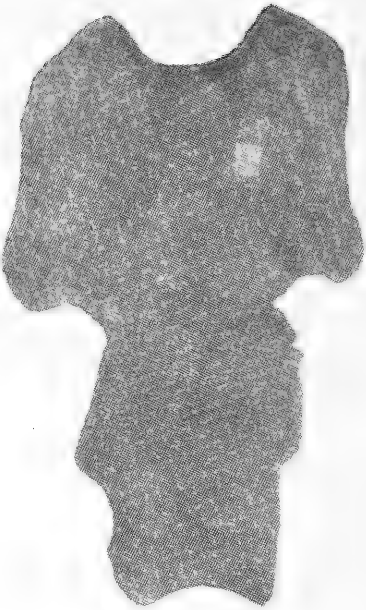
PLATE VII

Champsodelphis cf. *fuchsii* Brdt.

1. Caudal vertebrae, dorsal view. Natural size.

2. Caudal vertebrae, cranial view. Natural size.

2



1

PLATE VIII

Champsodelphis sp. *fuchsii* Brdt.

1. Sternum, dorsal view.

2. Scapula.

1

2

3

PLATE IX

Champsodelphis sp.

1. Scapula, about 3/4 of natural size.

2 and 3. Skeletons of forelimbs, about 2/3 of natural size.

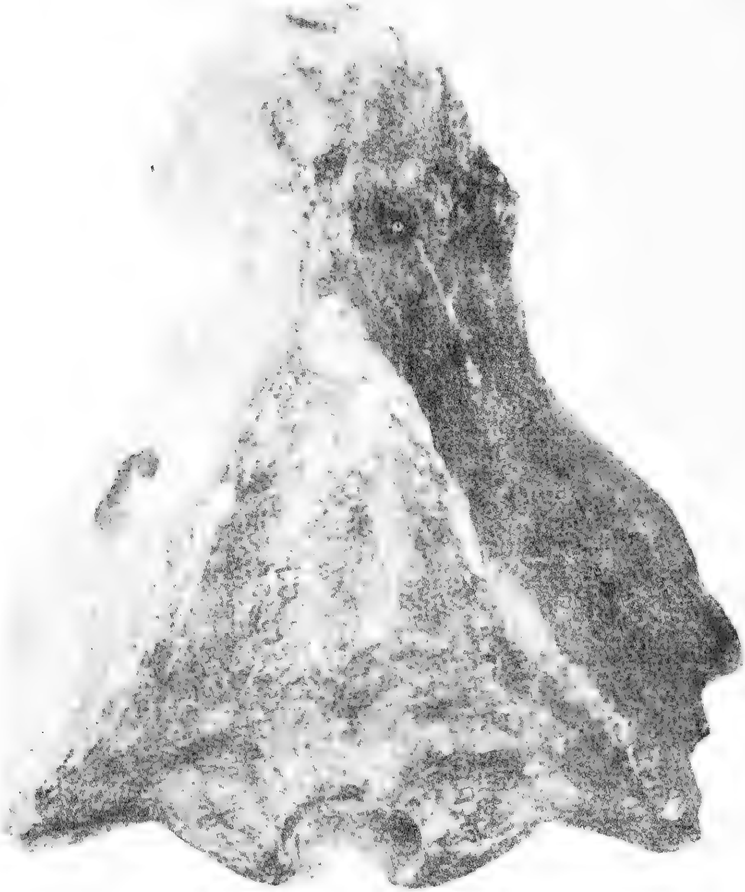


PLATE X

Imerocetus karaganicus Mch.

1. Cranial portion of skull, dorsal view.

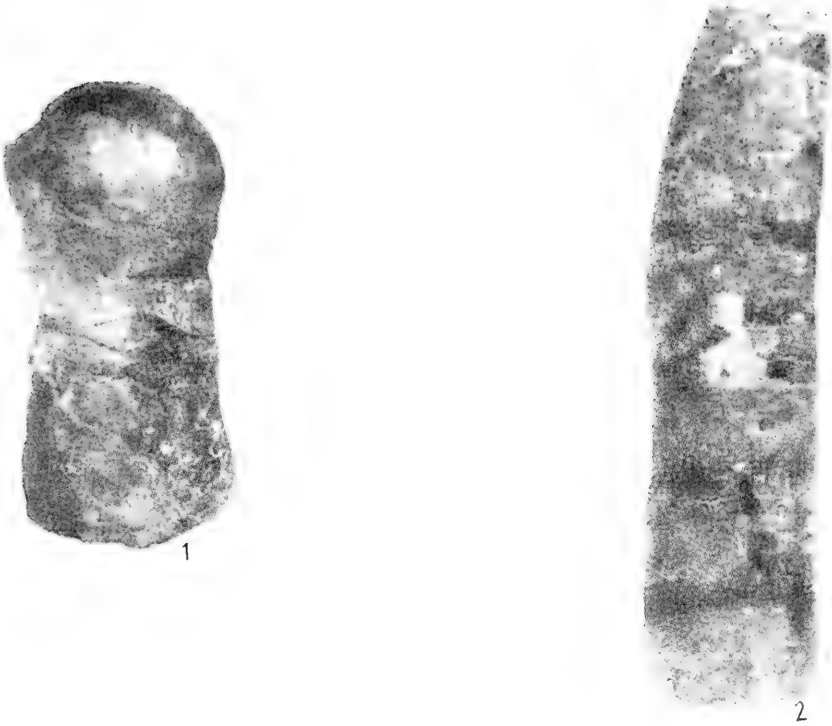


PLATE XI

Imerocetus karaganicus Mch.

1. Humerus.

2. Radius.

PLATE XII

Imerocetus karaganicus Mch.

1. Manus. Natural size.

PLATE XIII

1. Humerus and proximal portion of radius of Middle Miocene Cetotheriidae from vicinity of Zestafon town. Natural size.

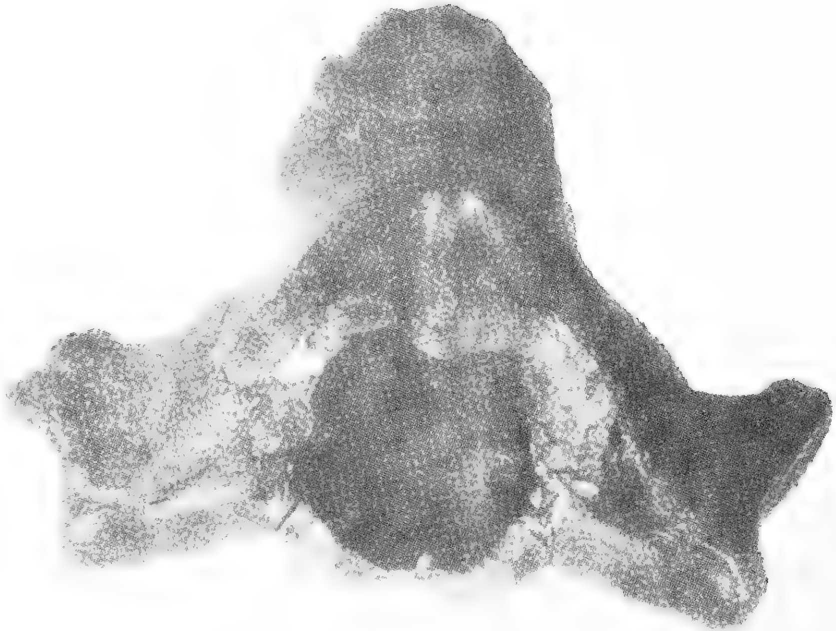
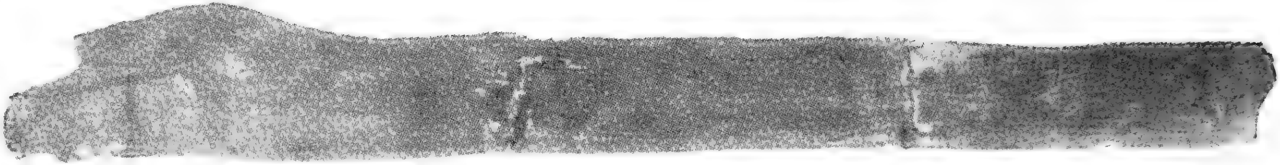


PLATE XIV

Cetotherium maicopicum Spass.

1. Skull, dorsal view.

1



2

PLATE XV

Cetotherium maicopicum Spass.

1. Lower jaw, inner (lingual) surface.
2. Lower jaw, outer (buccal) surface.

PLATE XVI

Cetotherium maicopicum Spass.

1. Humerus, about 2/3 of natural size. Dorsal view.

PLATE XVII

Cetotherium mayeri Brdt.

1. Cranial part of skull, dorsal view (Maikop town—Sarmat).

1

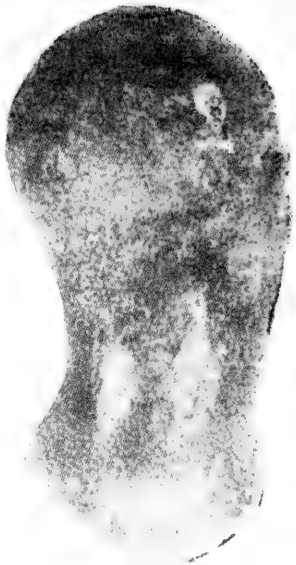
2

PLATE XVIII

Cetotherium mayeri Brdt.

1. Fragment of lower jaw, inner surface.
2. Fragment of lower jaw, dorsal view.

1



2

PLATE XIX

Cetotherium mayeri Brdt.

1. Humerus, about 2/3 of natural size. View from ulnar margin.

2. Humerus, about 2/3 of natural size. Dorsal view.

PLATE XX

Cetotherium sp.

1. Thoracic vertebrae and rib fragments (from Sjegren's collection).