Archaeomeryx (Archaeomerycidae, Ruminantia): Morphology, Ecology, and Role in the Evolution of the Artiodactyla

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Dedicated to the memory of Wladimir Kowalevsky (1842–1883),
the great founder of evolutionary paleotheriology

"It can be proposed that some small species
of Eocene ungulates can show us relationships
about which now we have even no presumption."

W.O. Kowalevsky (1873–1874)

Abstract—The morphology of the skull and postcranial skeleton of the primitive ruminant artiodactyl *Archaeomeryx optatus* Matthew et Granger, 1925 from the Middle Eocene Shara Murun Formation of the Ula Usu locality in Inner Mongolia of China is described in detail. In addition to the type collection housed at the American Museum of Natural History, extensive fossil material collected by the Joint Soviet–Chinese Paleontological Expedition in 1959 and stored at the Paleontological Institute of the Russian Academy of Sciences is studied. The material of the type collection, including, among other fossils, one complete articulated and two fragmentary skeletons, is supplemented by 14 additional skeletons. The appearance and ecology of *Archaeomeryx* are specified. It is shown that, in morphology and ecology, this animal was close to primitive eutherians. New morphological evidence of the early evolutionary stages of the suborder Ruminantia and the order Artiodactyla and comparisons with other primitive artiodactyls and ungulates show that the order Artiodactyla undoubtedly appeared much earlier than was registered in the fossil record and that its roots perhaps go back to the Late Cretaceous. This conclusion supports the hypothesis first proposed by W. Kowalevsky in the 19th century. The adaptatiogenesis and the major principles of macroevolutionary processes are traced based on Ruminantia evolution.

INTRODUCTION

Archaeomeryx is a unique extinct artiodactyl of the infraorder Tragulina that can be a key to understanding the evolution and adaptatiogenesis of one of the major eutherian branches.

The study of *Archaeomeryx* is very important not only for a better understanding of the early stages in the evolution of the Ruminantia and for studying the evolution of the infraorder Pecora, which are among the dominant groups of modern mammals, but also for the solution to a very difficult problem of the origin and early evolution of the order Artiodactyla. Moreover, the study of this animal is of great importance for resolving such problems of general biology as the main trends and patterns of evolutionary developments of living creatures.

Archaeomeryx represented by a series of almost complete skeletons attracted the attention of paleontologists from its first fossil records found by an expedition of the American Museum of Natural History in the 1920s in the Middle Eocene Ula Usu locality, northern China (Matthew and Granger, 1925a; Colbert, 1941; Webb and Taylor, 1980; etc.). From the very beginning, this genus has aroused exceptional interest because of its relatively early age, the superb fossil material, and as a probable ancestral type for higher ruminants (Pecora) (Matthew and Granger, 1925a).

Currently, the data on the morphology and ecology of *Archaeomeryx* and its role in the evolution of mammals are essentially enlarged due to the study of an extremely abundant collection stored at the Paleontological Institute of the Russian Academy of Sciences. These fossils were obtained by the Joint Soviet–Chinese Expedition during intensive excavations in the Ula Usu locality in 1959.

The finding of *Archaeomeryx*, extremely well preserved by nature and belonging to one of the main streams of mammal evolution, is a very rare event. Paleontologists usually deal with species that represent side branches, which became extinct during the course of evolution. The key species (such as *Archaeomeryx*), which occupy the basal position in large evolutionary branches and have their descendants in the Recent faunas, usually fall out of fossil record or are represented by rather fragmentary material. The study of such species is essential to the understanding of trends and the principal patterns of evolution.

Notwithstanding the fact that *Archaeomeryx* is usually involved in the consideration of the origin and relationships of ruminants, the evolutionary significance of this genus has been underestimated for a long time. Therefore, a detailed description of *Archaeomeryx* has not yet been performed. Today, almost 75 years after its first finding and more than 40 years after its second finding, we intend to improve this situation.

After the study performed by Colbert (1941), it was generally accepted that *Archaeomeryx* was rather similar in structure and ecology to Recent chevrotains, in particular, the mouse deer of the genus *Tragulus*. Chevrotains are usually regarded as living fossils (see, e.g., Janis, 1984). Even the first researchers recognized the primitive and unusual structure of chevrotains, the smallest extant ruminants, which are more similar in appearance to rodents than to deer or antelope. However, as compared to *Archaeomeryx*, the small and primitive living chevrotains look like the acme of perfection.

The main purposes of the present work are (1) to describe in detail the osteology and odontology of *Archaeomeryx*, (2) to perform morphofunctional analysis of the main structures of this animal, (3) and to clarify the role of *Archaeomeryx* in the evolution of the suborder Ruminantia and the order Artiodactyla.

We analyzed the adaptatiogenesis of the earliest ruminants, the relationships of archaeomerycids and other primitive members of the order Artiodactyla, the relationships of archaeomerycids with certain early

eutherians and the most primitive members of the grandorder Ungulata.

This study allowed us to recognize the evolutionary level of *Archaeomeryx* and the main trends and features of the evolution of the Ruminantia and to revise the opinions on the origin of the Tragulina, Pecora, and Artiodactyla.

In addition, new morphological data provide the possibility to introduce new reconstructions of the skeleton and appearance of this animal and give information on its ecology.

This study is based mainly on the collection of the Paleontological Institute of the Russian Academy of Sciences represented by 14 *Archaeomeryx* skeletons of those collected by the Joint Soviet-Chinese expedition during one field season in the Ula Usu locality in Inner Mongolia of China and prepared by Russian and Chinese workers. One of the authors took part in the excavations; the other had the possibility to examine the type collection from Ula Usu, housed at the American Museum of Natural History and previously studied by American researchers (Matthew and Granger, 1925a; Colbert, 1941; Webb and Taylor, 1980).

We also restudied the osteology of extinct and extant tragulines (Vislobokova, 2001), primitive pecorans, and the earliest ungulates and artiodactyls from collection of the Paleontological Institute of the Russian Academy of Sciences; American Museum of Natural History; Museum of Natural History, London; University of California, Berkeley; University of Kansas; and University of Montpellier.

The following abbreviation of the institutions and expeditions are used in the present study:

(AMNH) American Museum of Natural History;

(IVPP) Institute of Vertebrate Paleontology and Paleoanthropology, China;

(JSCPE) Joint Soviet–Chinese Paleontological Expedition;

(JSMPE) Joint Soviet–Mongolian Paleontological Expedition;

(PIN) Paleontological Institute of the Russian Academy of Sciences;

(UC) University of California, Berkeley.

CHAPTER 1

THE HISTORY OF STUDYING *ARCHAEOMERYX* AND THE MAIN PROBLEMS OF PHYLOGENY OF THE ARTIODACTYLA

Archaeomeryx is known by a series of skeletons from the Middle Eocene deposits of the Shara Murun Formation of the Ula Usu locality in Inner Mongolia of northern China and by isolated fragmentary fossil remains from the Middle and Late Eocene deposits of Kazakhstan and Mongolia (Matthew and Granger, 1925a; Gabunia, 1977; Tong and Wang, 1980) (Fig. 1).

In China, the first skeletons of *Archaeomeryx* were discovered by the Asiatic Expedition of the American Museum of Natural History in the 1920s and were originally described by Matthew and Granger (1925a) and, subsequently, by Colbert (1941) and Webb and Taylor (1980). The American paleontologists collected fossils of 52 individuals, including one complete articulated skeleton and two fragmentary skeletons with strongly deformed skulls (AMNH, nos. 20311–20318, 20320–20325).

In 1959, in Ula Usu, a joint Soviet–Chinese expedition found the remains of about 30 individuals, including 14 almost complete and fragmentary skeletons, 13 of which had skulls (collection PIN, no. 2198) (Fig. 2). The fossils were buried in an area of at most 100 m², in a bluish bed of lacustrine clay, with thin-layer seasonal bedding.

Thus, the two expeditions collected the most representative material on extinct ruminants and provided the basis for studying this animal and the early steps of the evolution of the Ruminantia.

Taxonomic Position of *Archaeomeryx*

The central problems of studying *Archaeomeryx* concern its position in the taxonomic system and the determination of taxonomic rank of the group, to which this genus belonged.

Matthew and Granger (1925a), who established the genus *Archaeomeryx*, and, subsequently, Colbert (1941) assigned it to the family Hypertragulidae (Table 1). Later, Simpson (1945) placed *Archaeomeryx* in a separate subfamily of the same family.

Scott (1940) was the first who put into doubt the close relationships of *Archaeomeryx* and hypertragulids in his classic monograph on the American artiodactyls from the White River Oligocene. Nevertheless, after the study performed by Colbert (1941), many paleontologists continued to refer this genus to the Hypertragulidae (e.g., Viret, 1961; Godina *et al.*, 1962) until Taylor and Webb (1976) proposed that *Archaeomeryx* was an early leptomerycid.

More than twenty years ago, Webb and Taylor (1980) undertook a detailed comparison of hornless ruminants to revise their interrelations and clarify the

origin of this group. Their reexamination of *Archaeomeryx* was based on additional preparation of old collections and produced new diagnostic characters. Webb and Taylor (1980) concluded that *Archaeomeryx* was more similar to the Leptomerycidae than to the Hypertragulidae. Based on certain structural details of the petrosal, epistropheus, and some dental and podial features, they referred *Archaeomeryx* to the former family. In this excellent work, the researchers revealed the actually existing *Archaeomeryx*–leptomerycid evolutionary lineage but mistakenly combined *Archaeomeryx* with leptomerycids in the same family. The viewpoint of Webb and Taylor (1980) was accepted by a number of researchers (e.g., Sudre, 1984; Janis and Scott, 1988; McKenna and Bell, 1997). However, some scientists continued to believe that *Archaeomeryx* was more primitive than the Leptomerycidae. This opinion was reflected in the lower position of *Archaeomeryx* than the Leptomerycidae in a number of cladograms developed during the 1980s and 1990s (Bouvrain and Geraads, 1985; Bouvrain *et al.*, 1986; Geraads *et al.*, 1987, text-fig. 45; Gentry and Hooker, 1988, text-figs. 9, 10; Scott and Janis, 1992, text-figs. 20.3, 20.5). These

Fig. 1. Main localities containing *Archaeomeryx* remains: (*1*) Ula Usu; (*2*) Irdin Manha; (*3*) Shinzhily; (*4*) Zaisan Basin; (*5*) Linbao; (*6*) Lushi; and (*7*) Eastern Gobi.

Fig. 2. Articulated skeleton of *Archaeomeryx*, PIN, no. 2198/200.

cladistic analyses were based mainly on the characters of dentition and limbs, such as the loss of the upper incisors and first premolars, the fusion of central metapodials, the extent to which the fibula and side metapodials were reduced, etc.

Geraads *et al.* (1987) in their classification excluded the genus *Archaeomeryx* from the composition of both the Hypertragulidae and the Leptomerycidae (and the Tragulina as a whole) and introduced it in a separate plesion within the infraorder Ruminantia.

Moyà-Solà (1988) considered *Archaeomeryx* to be a nonruminant and believed, as well as some other paleontologists (e.g., Webb and Taylor, 1980; Scott and Janis, 1992), that the most primitive ruminant was *Hypertragulus*.

Further study of fossil material housed at the American Museum of Natural History and the extensive additional fossils excavated by the Joint Soviet–Chinese Paleontological Expedition along with numerous specimens of early ruminants collected in Mongolia by the Joint Soviet–Mongolian Paleontological Expedition in the 1970s and 1980s allowed us to discover the key points in the evolution of a number of groups and introduce certain significant taxonomic changes (Vislobokova, 1998, 2001).

These data provided the possibility to reveal essential differences between *Archaeomeryx* and the Hypertragulidae, on the one hand, and between *Archaeomeryx* and the Leptomerycidae, on the other hand (Vislobokova, 1998, 2001; Vislobokova and Trofimov, 2000a).

It has been shown that *Archaeomeryx* and hypertragulids belong to two separate and early diverging lineages of the Tragulina and the differences between *Archaeomeryx* and leptomerycids are comparable to, or even greater than, the differences between leptomerycids and Recent tragulids, i.e., correspond to the family rank (Vislobokova, 2001).

The comparative morphological analysis corroborated the existence of a separate family, the Archaeomerycidae, comprising the genus *Archaeomeryx* along with three monotypic Asiatic genera, *Miomeryx, Xinjiangmeryx*, and *Notomeryx* (Vislobokova and Trofimov, 2000a). These animals were only known by the dental structure and, along with *Archaeomeryx*, assigned by most early researchers to the Hypertragulidae (Matthew and Granger, 1925b; Qiu, 1978; Zheng, 1978).

We paid much attention to the main characteristics of the skull and postcranial skeleton that permitted determination of the evolutionary level and taxonomic position of archaeomerycids (Vislobokova and Trofimov, 2000a). We also added new diagnostic characteristics, which were most important for a better understanding of the origin and evolution of the suborder Ruminantia, and showed that archaeomerycids were an archaic group of the Tragulina. Regarding the structural features, archaeomerycids combine very primitive characteristics, which make them close to the early Eutheria (placentates), and the main preadaptations of the Pecora.

Problems of Phylogeny

The morphology of *Archaeomeryx* is an important source of information on the key questions of the artiodactyl phylogeny, which concern the origin of the suborder Ruminantia, infraorder Pecora, and the order Artiodactyla as a whole.

The appearance of new fossil records, in particular, the complete skeletons of dichobunoids (Franzen, 1981, 1983), and their comparison with *Archaeomeryx* gives new evidence to answer some of these questions.

Origin of Artiodactyls. The order Artiodactyla comprises a great number of species assigned to three suborders: Ruminantia, Suiformes, and Tylopoda. The origin of artiodactyls is an important problem of the mammalian history. When solving this problem, one should reconstruct the pre-Eocene adaptatiogenesis of the group and reveal a suitable ancestor.

The actual early evolution of artiodactyls remains hidden in the darkness of geological history of the Mesozoic and Early Cenozoic (Paleocene). The first rather specialized artiodactyls are known from the Early Eocene. Nevertheless, *Archaeomeryx*, which is the most primitive ruminant with reference to many morphological characteristics, allows us to reconstruct the ancestor of ruminants and the entire artiodactyls (their archetypes) and reject a number of commonly accepted but erroneous concepts concerning the early evolution of these groups.

It is generally believed that artiodactyls are at a relatively high phylogenetic level of the evolution of the Ungulata and deviated rather late from the ungulate tree. However, the morphology of *Archaeomeryx* completely rejects this view and returns us to the earlier concepts proposed by the best researchers dealing with artiodactyls: Kowalevsky and Matthew.

Kowalevsky (1873–1874) was the first to propose a model of the pre-Eocene history of ungulates and hypothesize that early ungulates were divided into two groups (Paridigitata and Imparidigitata) as early as the Cretaceous.

Matthew (1929) showed that molars of ruminant artiodactyls lack hypocone, which is characteristic of many other ungulates, but preserve the metaconule, which is typical of the tribosphenic teeth of early eutherians.

Both these outstanding researchers divided artiodactyls into two early diverging branches. Kowalevsky (1873a, 1873b) named them the Paradigitata Selenodonta and Paradigitata Bunodonta. The first corresponds to the Ruminantia plus the Tylopoda, and the second is the same as the Suiformes. Some later

researchers also included the Tylopoda in the composition of the Ruminantia (Stirton, 1944; Romer, 1966). However, according to more natural classifications proposed by Flower (1883), Simpson (1945), and McKenna and Bell (1997), the Ruminantia and Tylopoda are separate suborders within the order Artiodactyla. The main classifications of artiodactyls are given in Table 1.

The assumption concerning a rather early divergence of the Selenodontia and Bunodontia, which was originally proposed by Kowalevsky (1873a, 1873b, 1873–1874), was corroborated in the 1970s by cytogenetic evidence. According to karyotypic data, the divergence between suiforms and ruminants is very deep (Todd, 1975). Following the most authoritative views of that time, Todd supposed that this divergence could be associated with the first adaptive radiation of the Palaeodonta (a partial synonym of the Suiformes).

The early appearance and early divergence of the Artiodactyla are corroborated by molecular evidence obtained at the end of the 20th century. A recent calibration of the molecular clocks suggests that the eutherian orders most likely diverged more than 100 Ma (Shimamura *et al.*, 1997). According to Shimamura and his coauthors, whales, ruminants, and hippopotamuses form a monophyletic group. Molecular data show that two families of short interspersed elements are present in the genomes of members of these groups and absent in those of camels and pigs.

Kowalevsky (1873–1874, 1875, 1877) divided artiodactyls into adaptive and inadaptive groups. He referred ruminants to the first group and dichobunids, along with *Hyopotamus, Anthracotherium*, and *Cainotherium*, to the second group. Certainly, Kowalevsky and Matthew were limited in the choice of the ancestor of artiodactyls, since the intensive study of Mesozoic mammals began only in the middle of the 20th century. Nevertheless, Kowalevsky (1873–1874) foresaw that the ancestor of artiodactyls should belong to the basal ungulate group. Matthew believed that the ancestors of artiodactyl were primitive creodonts resembling the Mesonichidae. Currently, the Mesonichidae are commonly referred to the order Cete rather than to the Creodonta (McKenna and Bell, 1997).

Cope (1887) proposed an original hypothesis that the origin of artiodactyls was associated with insectivores. Although fossil material on *Pantolestes*, which was indicated by Cope as an ancestral form, is currently assigned to *Diacodexis* (see Van Valen, 1971), his hypothesis is of great interest, since he emphasized the similarity between the orders Artiodactyla and Insectivora.

For a long period of time, most researchers believed that artiodactyls evolved from condylarths sensu lato. The latter were thought to give rise to different ungulate groups, including the Perissodactyla, Hyracoidea, Sirenia, Proboscidea, Cetacea, etc. A widely accepted view was that condylarths of the family Hyopsodontidae dominating the Paleocene faunas could be the ancestors of artiodactyls (see, e.g., Simpson, 1937; Schaeffer, 1947; Godina *et al.*, 1962). Currently, this concept has a small number of supporters.

To date, a more popular hypothesis is that proposed by Van Valen (1971) for the origin of artiodactyls from a small animal resembling *Metachriacus* (*Chriacus*), which is considered to be an arctocyonid (Van Valen, 1971; Rose, 1996; Szalay and Lucas, 1996) or an oxyclaenid member of the Procreodi (McKenna and Bell, 1997).

In recent years, the origin of the dichobunoid *Diacodexis*, one of the earliest Early Eocene artiodactyls, has usually been considered to be associated with an artiodactyl-like arctocyonid *"Chriacus truncatus"* (Rose, 1996). However, it is hardly probable that the specialized *Hyopsodus* and arboreal *Chriacus* (see Szalay and Lucas, 1996) could be an ancestor of artiodactyls.

The hypothesis of a *Chriacus*-like ancestor of artiodactyls (Van Valen, 1971) was based on the similarity in the dental structures between arctocyonids (oxyclaenids) and diacodexids. Subsequent findings allowed researchers to compare these groups with reference to the structure of postcranial skeletons and demonstrated essential differences in their morphology and adaptations (Rose, 1982, 1985, 1987). These data imply that either *Chriacus* is not ancestral to artiodactyls or *Diacodexis* should not be placed at the base of the artiodactyl tree (see Rose, 1982, 1987), or both statements are correct. The main argument against the basal position of *Diacodexis* in the Artiodactyla is its similarity to selenodont artiodactyls (tylopods, ruminants, etc.). This concept was developed by Gentry and Hooker (1988). They suggested to combine the Dichobunidae sensu stricto and Ruminantia in the Merycotheria, a new suborder of the Selenodontia. In addition to the Merycotheria, the latter included the suborder Tylopoda. We agree with Rose (1996) that *Diacodexis* approaches the primitive condition of the order Artiodactyla; however, we disagree with the idea that *Diacodexis* was a progenitor of ruminants.

Although diacodexids resemble early ungulates, such as *Protungulatum*, arctocyonids, etc., in a large number of characters (Schaffer, 1947; Van Valen, 1971; Rose, 1987, 1996), the origin of artiodactyls from the latter is not supported by all researchers. For example, based on a cladistic analysis, Prothero *et al.* (1988) have concluded that artiodactyls are at a lower evolutionary level than *Protungulatum*, a Late Cretaceous member of the Ungulata. Prothero *et al.* (1988) believe that artiodactyls are the most primitive group among ungulates. The data obtained by Wible (1987) based on a character analysis of the stapedial artery also testify to the early divergence of the Artiodactyla from the ungulate stem. Our data on the morphology of *Archaeomeryx* confirm this viewpoint. A comparison of *Archaeomeryx*, diacodexids, and arctocyonids (see Chapter 5) indicates that the origin of artiodactyls from arctocyonids is highly improbable.

Table 1. The main classifications of the Artiodactyla

Matthew, 1929	Colbert, 1941	Simpson, 1945
Palaeodonta	Suborder Ancodona	Suborder Ruminantia
Dichobunidae	Infrafamily Anthracotherioidea	Infraorder **Tragulina**
Entelodontidae	Infrafamily Oreodontoidea	Superfamily Amphimerycoidea
Hyodonta	Suborder Tylopoda	Superfamily Hypertraguloidea
Tayassuidae	Superfamily Camelidea	(including **Archaeomerycinae**)
Suidae	Family Xiphodontidae	Superfamily Traguloidea
Hyppopotamidae	Family Camelidae	Family Tragulidae
Ancodonta	Suborder **Tragulina**	Family Gelocidae
Anoplotheriidae	Superfamily Amphimerycoidea	Family Tragulidae
Caenotheriidae	Family Amphimerycidae	Infraorder Pecora
Oreodontidae	Superfamily Hypertraguloidea	Superfamily Cervoidea
Tylopoda	Family Hypertragulidae	Superfamily Giraffoidea
Xiphodontidae	(including *Archaeomeryx*)	Superfamily Bovoidea
Camelidae	Family Protoceratidae	
Pecora	Superfamily Traguloidea	
Amphimerycidae	Family Tragulidae	
Tragulidae	Suborder Pecora	
(including *Archaeomeryx*)	Superfamily Cervoidea	
Cervidae	Superfamily Giraffoidea	
Giraffidae	Superfamily Bovoidea	
Antilocapridae		
Bovidae		

Webb and Taylor, 1980	Gentry and Hooker, 1988	McKenna and Bell, 1997
Neoselenodontia	Selenodontia	Order Artiodactyla
Suborder Tylopoda	Suborder Tylopoda	Suborder Suiformes
(including Xiphodontidae	(including Oromerycidae,	Superfamily Suidea
and Amphimerycidae)	Xiphodontidae,	Superfamily Dichobunoidea
Suborder Ruminantia	Caenotheriidae, etc.)	Superfamily Anthracotheroidea
Infraorder Tragulina	Suborder Merycotheria	Superfamily Anoplotheroidea
Family Hypertragulidae	Dichobunidae sensu stricto	Superfamily Oreodontoidea
Family Tragulidae	Ruminantia	Superfamily Entelodontoidea
Family Leptomerycidae	(including Amphimerycidae,	Suborder Tylopoda
(including *Archaeomeryx*)	Hypertragulidae,	Suborder Ruminantia
Infraorder Pecora	Tragulidae,	Family Amphimerycidae
Division Moschina	Leptomerycidae, etc.)	Family Hypertragulidae
Family Gelocidae		Family Tragulidae
Family Moschidae		Family Leptomerycidae
Division Eupecora		(including **Archaeomerycinae**)
Superfamily Cervoidea		Family Bachitheriidae
Superfamily Giraffoidea		Family Lophiomerycidae
Superfamily Bovoidea		Family Gelocidae
		Superfamily Cervoidea
		Superfamily Giraffoidea
		Superfamily Bovoidea

Origin of Tragulines. The Tragulina is the basal group of the suborder Ruminantia (sensu Simpson, 1945). Colbert (1941) ranked it as a suborder within the Artiodactyla; however, the group is more often regarded as one of two infraorders of the Ruminantia. Tragulines comprise nine families referred to two superfamilies: the Traguloidea and Hypertraguloidea (Vislobokova, 2001).

The prevailing hypothesis is that tragulines and the entire ruminants evolved from certain primitive suiforms (or palaeodonts). Different suiform groups, including hyopotamids (Kowalevsky, 1873–1874) and oreodontids (Cope, 1887), were proposed as ancestors of the Ruminantia. Presently, hyopotamids are included in the Anthracotheriidae and oreodontids are included in the Oreodontoidea (McKenna and Bell, 1997). However, the majority of researchers traditionally regard dichobunids (or dichobunoids) as ancestors of the Ruminantia sensu stricto (Schlosser, 1886; Matthew, 1934; Pilgrim, 1941; Gentry and Hooker, 1988).

Simpson (1945) believed that tragulines originated from amphimerycids. This insufficiently studied group of selenodont artiodactyls displays clear resemblance to dichobunids, on the one hand, and to xiphodontids and cainotheriids, on the other. Many researchers considered amphimerycids to be closely related to the Xiphodontidae (Tylopoda) (Matthew, 1929; Sudre, 1978; Webb and Taylor, 1980). Some researchers believed that amphimerycids are closer to the Anoplotherioidea and, in particular, to the Dacrytheriidae within Bunoselenodontia (Viret, 1961). The others refer amphimerycids to the Ruminantia (Simpson, 1945; Gentry and Hooker, 1988; McKenna and Bell, 1997). A more correct determination of the taxonomic position of amphimerycids is the subject of future investigation; however, to date, it is obvious that amphimerycids and dichobunoids are more advanced than archaic tragulines. It is doubtful that they were the ancestors of the latter.

The hypotheses of the origin of tragulines from dichobunoids or amphimerycids presume the development of four-cusped molars of ruminants from five- or six-cusped molars of the ancestral groups, i.e., the case of reverse evolutionary development of molars in these groups. This assumption is in rather poor agreement with the general trends in the adaptatiogenesis of ruminants and considerably decreases the value of these hypotheses.

Origin of Higher Ruminants. The higher Ruminantia [infraorder Pecora sensu Colbert (1941) and Simpson (1945) or Eupecora sensu Webb and Taylor (1980)] comprise three superfamilies, the Cervoidea, Giraffoidea, and Bovoidea. According to Webb and Taylor (1980), the Pecora also contain the families Gelocidae and Moschidae combined in the division Moschina (Table 1). However, we support a better substantiated classification where the Pecora is divided into three superfamilies: the Cervoidea (Cervidae and Moschidae), Giraffoidea (Giraffidae and Palaeomerycidae), and Bovoidea (Bovidae and Antilocapridae).

The question of the origin of different groups of higher ruminants is widely discussed. The prevailing hypothesis is that the Pecora evolved from tragulines. According to an alternative and less popular point of view, tragulines and higher ruminants had a common ancestor (Pilgrim, 1941).

Even Kowalevsky (1873–1874, 1875, 1877) indicated that different ruminant groups originated from the same traguloid ancestor. At the base of higher ruminants, he placed the gelocid Gelocus aymardi from the Oligocene of France, which was the most appropriate pretender to this role among very few tragulines known at the time of Kowalevsky's work. Those scarce tragulines also included Lophiomeryx, Leptomeryx, and Dorcatherium.

Matthew and Granger (1925a) were the first to propose that Archaeomeryx was the ancestor of the Pecora. Mattew (1934) placed Archaeomeryx at the base of pecoran adaptive radiation resulting in the emergence of the Tragulidae, Gelocidae, Cervidae, Bovidae, and Antilocapridae. Matthew (1929) and Colbert (1935) placed this genus at the base of the Giraffidae and Palaeomerycidae as well. However, later, Colbert (1941) lessened the evolutionary role of Archaeomeryx and proposed that higher ruminants evolved from gelocids, which he regarded as a subfamily of the family Tragulidae. This concept was widely favored to the 1980s.

A number of later researchers considered different genera of the Gelocidae sensu lato to be ancestral to higher ruminants (Flerov, 1952; Trofimov, 1956; Hamilton, 1973; Webb and Taylor, 1980). As presumable ancestors of the Pecora were indicated Gelocus (Simpson, 1945; Trofimov, 1956; Viret, 1961; Webb and Taylor, 1980), Lophiomeryx (Flerov, 1952; Trofimov, 1956), and Prodremotherium (Bouvrain and Geraads, 1985).

The specialization of Lophiomeryx (rather high crowns of the lower cheek teeth and a peculiar eight-shaped configuration of the lingual portion of the lower molars) testify that this genus represents a separate lineage that differs from higher ruminants (Janis, 1987).

The morphology of Gelocus and Prodremotherium also indicate that they could not be the ancestors of higher ruminants. Each genus had strongly reduced side digits, whereas a number of Miocene cervids were still holometacarpal. The petrosal of Gelocus displays many advanced characters, which are similar to those of higher ruminants. Based on these features, Webb and Taylor (1980) placed gelocids in the infraorder Pecora. They believed that the phylogenetic progress developed from the Gelocidae to the Moschidae and, then, to the Eupecora. The conclusions of the researchers were based on the cladistic analysis. Although this was a case of especially efficient use of the cladistic analysis, the

insufficient morphological data and general demerits of the method resulted in the appearance of only a new artificial scheme; however, it was not representative of the actual history of ruminants. Nevertheless, the scheme created by Webb and Taylor (1980) correctly demonstrates the evolutionary level of almost all characters involved in the analysis of different ruminant groups.

The concept of Webb and Taylor (1980) concerning the taxonomic position of *Gelocus* and *Prodremotherium* was supported by some paleontologists (Scott and Janis, 1992). However, the traguline structural pattern (archetype) of these genera combined with certain advanced characters of dentition and distal limb segments, which are more advanced than those of some higher ruminants, give no way of taking these forms as the ancestors or members of higher ruminants (Vislobokova, 2001). Almost all gelocids are more advanced than archaic higher ruminants in the level of the development of selenodonty, crown height, elongation of the distal limb segments, the stage of the reduction of side metapodials, etc.

Janis and Scott (1987) presented a rather complete review of modern ideas concerning the origin of higher ruminants. In a number of studies, phylogenetic relationships of different groups of higher ruminants were analyzed from the standpoint of cladistics (Ginsburg, 1985; Janis and Scott, 1988; etc.). The most complete cladistic analysis was performed by Janis and Scott (1988). Such analyses are of significance, because they include a detailed examination of the evolutionary level of individual characters used for phylogenetic reconstruction. However, phylogenetic trees obtained by this method are far from the actual evolutionary development of ruminants, because the relationships between families are mainly analyzed on the basis of generic or species-specific characters rather than on the basis of fundamental characters distinguishing individual families.

In the light of modern data, the hypothesis of the monophyletic origin of higher ruminants, which was introduced by Kowalevsky and Matthew, appears well substantiated. This hypothesis is corroborated not only by paleontological data but also by the data on DNA (Miyamoto and Boyle, 1989; Miyamoto *et al.*, 1992).

Paleontological studies of the last decade corroborated that the most probable ancestor of the Pecora is *Archaeomeryx* (Vislobokova, 1990a, 1990b; Vislobokova and Trofimov, 2000a), as was proposed by the authors who described this genus.

CHAPTER 2

TAXONOMIC REVIEW OF THE ARCHAEOMERYCIDAE

Order Artiodactyla

Suborder Ruminantia

Infraorder Tragulina Flower, 1883

S u p e r f a m i l y Traguloidea Gill, 1872

Family Archaeomerycidae Simpson, 1945

Archaeomerycinae: Simpson, 1945, p. 151.

Archaeomerycidae: Vislobokova and Trofimov, 2000a, pp. 92–99; Vislobokova, 2001, pp. 134–135.

D i a g n o s i s. Skull with low and narrow cerebral region and relatively short facial region. Sagittal, temporal, and occipital crests well developed. Sagittal crest long. Temporal crests fused close to coronal suture and arched anteriorly. Occipital crest strongly projecting posteriorly. Orbits small, located low, in central position, and closed posteriorly. Parietal foramina small and located near sagittal crest. Mastoid exposure mainly lateral. Auditory bullae small, external acoustic meatus extremely short. Vagina of slyloid process weakly developed and widely open posteriorly. Petrosal small, short, broad, and closely adjoining basioccipital; ventral surface positioned almost horizontally. Anteroventral edge of petrosal located far from postglenoid process. Promontorium low, simple, occupying large part of ventral surface, and almost completely corresponding to main whorl of cochlea. Fenestra vestibuli (fenestra ovalis) small. Fossa for musculus tensor tympani small and located opposite to posterior region of promontorium. Fossa for musculus stapedius narrow and placed behind fenestra vestibuli. Recessus epitympanicus located on petrosal. Foramen ovale small, oval, and located close to posterior edge of alisphenoid. Facial and orbital surfaces of lacrimal small. Nasolacrimal fissure probably undeveloped. Nasals long and not projecting anteriorly between premaxillae. Jugal ventrally approaching tooth row and possessing short lacrimal process and long temporal process. Palate flat. Staphylion located behind M3. Upper jaw low and relatively short; buccal tubercle very weak. Infraorbital canal short and located low. Posterior opening of infraorbital canal located on orbital surface of maxilla. Premaxilla low and short, with short nasal process almost completely covering dorsally anterior opening of nasal cavity. Anterior opening of nasal cavity low and short, oval in dorsal view, and slightly narrowed posteriorly. Incisive foramina small. Body of mandible strongly curved; coronoid process low, well developed, and inclined posteriorly; angular process narrow and strongly projecting posteriorly. Upper incisors present. Upper canines small and procumbent. Lower canines incisiform but larger than first incisors. P1 undeveloped. Radius and ulna, fibula and tibia, and central metapodials separate. Trapezium and metacarpal I present.

Astragalus elongated, tripulley, with nonparallel trochleae. Manus pentadactyl. Pes probably tetradactyl.

G e n e r i c c o m p o s i t i o n. *Archaeomeryx* Matthew et Granger, 1925; *Miomeryx* Matthew et Granger, 1925; *Xinjiangmeryx* Zheng, 1978; and *Notomeryx* Qiu, 1978.

C o m p a r i s o n. The family Archaeomerycidae is distinguished from the other families of the superfamily Traguloidea by a primitive braincase, weakly elongated facial region of skull, and complete fibula. In addition, it is distinguished from the Leptomerycidae, Gelocidae, Bachitheriidae, and Tragulidae by the presence of the upper incisors, a more primitive structure of the astragalus, and separated metatarsals.

Genus *Archaeomeryx* Matthew et Granger, 1925

Archaeomeryx: Matthew and Granger, 1925a, pp. 9–11; Colbert, 1941, pp. 1–24; Webb and Taylor, 1980, pp. 121–153.

T y p e s p e c i e s. *Archaeomeryx optatus* Matthew et Granger, 1925.

D i a g n o s i s. Small-sized. Body of mandible low, ventral edge strongly curved under m3. Incisors procumbent, with almost symmetrical crowns; upper incisors small, reduced. Upper canines medium-sized, lower canines small, incisiform, but larger than incisors. P1 absent. C–P2 diastema short. Lower p1 small, caniniform, located approximately in middle between canine and p2. Premolar row relatively long. Lower premolars narrow with cutting edges, p4 with well developed metaconid and relatively small paraconid, entoconid, and hypoconid. Molars brachyodont and weakly crescentic with strongly developed paraslyle and mesostyle and strong cingulum. Pillar of metacone almost undeveloped. Valleys on m3 not deepened, heel short.

S p e c i e s c o m p o s i t i o n. Type species.

R e m a r k s. In addition to the type locality, fossil specimens of this genus determined as *Archaeomeryx* sp. are known from the Upper Eocene of China, Mongolia, and Kazakhstan (Gabounia, 1977; Savage and Russell, 1983).

O c c u r r e n c e. China, Mongolia, and Kazakhstan; Middle–Upper Eocene.

Archaeomeryx optatus **Matthew et Granger, 1925**

Archaeomeryx optatus: Matthew and Granger, 1925a, pp. 9–11; Colbert, 1941, pp. 1–24.

H o l o t y p e. AMNH, no. 20311, palate and lower jaws; China, Inner Mongolia; Middle Eocene, Shara

Murun Formation. For figures, see Matthew and Granger (1925a, text-fig. 10) and Colbert (1941, text-fig. 2).

M a t e r i a l. AMNH, no. 20320, articulated skeleton; AMNH, nos. 20312–20318 and 20321–20325, incomplete skeletons, jaws, and isolated bones; PIN, no. 2198/200, articulated skeleton; PIN, nos. 2198/148–2198/154, 156, 157, 162, 163, and 199, 12 incomplete skeletons; PIN, no. 2198/160, vertebral column and limb bones; PIN, nos. 2198/158 and 159, incomplete vertebral columns and limb bones; and PIN, collection no. 2198, jaws, isolated vertebra and limb bones.

M e a s u r e m e n t s, mm. Length: (P2–M3) 33; (P2–P4) 16.5; (M1–M3) 18; (p2–m3) 36.9; (p2–p4) 19; and (m1–m3) 22.5.

O c c u r r e n c e. China, Middle Eocene.

Genus *Miomeryx* Matthew et Granger, 1925

Miomeryx: Matthew and Granger, 1925b, pp. 10–11.

T y p e s p e c i e s. *Miomeryx altaicus* Matthew et Granger, 1925.

D i a g n o s i s. Small-sized. Body of mandible only slightly narrowed anteriorly, lower edge weakly curved under m2 and m3. Diastemata between C and P2 and between c and p1 weakly elongated. Lower p1 small, caniniform, and separated from p2 by short diastema. Premolar row slightly shortened. Lower premolars very narrow, with cutting edges. Lower p4 with well-developed metaconid and relatively smaller paraconid, entoconid, and hypoconid. Molars brachyodont and weakly crescentic, with strongly developed parastyle and mesostyle, distinct pillar of paracone, and stout cingulum. Crowns of M2 and M3 slightly extended labiolingually. Valleys on m3 deepened, heel slightly elongated. Cingulum well developed. Enamel rugose.

S p e c i e s c o m p o s i t i o n. Type species.

C o m p a r i s o n. *Miomeryx* is distinguished from *Archaeomeryx* by a larger size, more advanced structure of the mandible, elongated diastemata, narrower premolars, relatively narrow crowns of the posterior upper molars, higher cusps, weaker metastyle, stronger developed pillar of the paracone, and a longer heel on m3.

R e m a r k s. Similar to *Archaeomeryx*, *Miomeryx* was originally referred to the Hypertragulidae (Matthew and Granger, 1925b); subsequently, it was included in the Leptomerycidae (Sudre, 1984). Simpson (1945) assigned it to the Gelocidae. The morphology of *Miomeryx* became essentially better known due to the material collected by the JSMPE and JSCPE. Close similarity of *Miomeryx* to *Archaeomeryx* allows one to include it to the family Archaeomerycidae.

In addition to Mongolia and China, *Miomeryx* was recorded in the Upper Eocene of Kazakhstan.

O c c u r r e n c e. Central Asia; Upper Eocene–Lower Oligocene.

Miomeryx altaicus Matthew et Granger, 1925

Miomeryx altaicus: Matthew and Granger, 1925b, pp. 10–12.

H o l o t y p e. AMNH, no. 20383, upper jaw with P2–M3; Mongolia, Ardyn Obo (Ergiliin Dzo) locality; Lower Oligocene, Ergiliin Dzo Formation. For figure, see Matthew and Grange (1925b, text-fig. 13).

M a t e r i a l. In addition to the type, PIN, no. 3109, fragmentary jaws, Ergiliin Dzo, Mongolia; PIN, no. 3110-1225, lower jaw with dp2 and dp3; PIN, no. 3110-1226, lower jaw with p1–m3; PIN, no. 3110-1230, astragalus; and PIN, no. 3110-1227, astragalus with fibula and fragmentary tibia; Khoer Dzan, Mongolia; Ergiliin Dzo Formation, Lower Oligocene.

M e a s u r e m e n t s, mm. Length: (P2–M3) 37; (P2–P4) 19.3; (M1–M3) 19.7; (p2–m3) 40.5; (p2–p4) 17.0; and (m1–m3) 23.3.

O c c u r r e n c e. Mongolia, Lower Oligocene.

Genus *Xinjiangmeryx* Zheng, 1978

Xinjiangmeryx: Zheng, 1978, pp. 120–124; Qiu, 1978, pp. 11–12; Webb and Taylor, 1980. p. 154.

T y p e s p e c i e s. *Xinjiangmeryx parvus* Zheng, 1978.

D i a g n o s i s. Small-sized. Upper incisors possibly developed. Lower p1 absent. Molars brachyodont and weakly crescentic, with weakly deepened valleys.

S p e c i e s c o m p o s i t i o n. Type species.

C o m p a r i s o n. *Xinjiangmeryx* is distinguished from *Archaeomeryx* and *Miomeryx* by higher tooth crowns and by the absence of p1; it is also distinguished from Miomeryx by more extended lingual crescents.

R e m a r k s. Zheng (1978) originally included the genus along with *Archaeomeryx* in the family Hypertragulidae. Webb and Taylor (1980) assigned both genera to the family Leptomerycidae. In the morphology of cheek teeth, this genus is undoubtedly similar to *Archaeomeryx*.

O c c u r r e n c e. China, Middle Eocene.

Xinjiangmeryx parvus Zheng, 1978

Xinjiangmeryx parvus: Zheng, 1978, pp. 120–124.

H o l o t y p e. IVPP, no. V 4054, fragmentary skull with lower jaw; China, Turfan Depression, Sinkiang; Middle Eocene. For figure, see Zheng (1978, pl. II, fig. 4).

M a t e r i a l. Holotype.

M e a s u r e m e n t s, mm. Length: (P2–P4) 14.6; (M1–M3) 16.2; (p2–p4) 14.4; and (m1–m3) 18.3.

O c c u r r e n c e. China, Middle Eocene.

Genus *Notomeryx* Qiu, 1978

Indomeryx: Colbert, 1938, p. 394, text-fig. 55.
Notomeryx: Qiu, 1978, pp. 9–12.

Type species. *Notomeryx besensis* Qiu, 1978.

Diagnosis. Small-sized but larger than *Archaeomeryx*. Horizontal ramus of mandible thickened. Molars brachyodont with relatively well developed crescentic pattern and deepened valleys. Upper molars with strong pillar of paracone and well-developed pillar of metacone. Crowns of M2 and M3 almost not extended labiolingually; length almost equal to width. Lower m3 with elongated heel. Cingulum well developed. Enamel strongly rugose.

Species composition. Type species.

Comparison. *Notomeryx* is distinguished from the previous genera by a larger size, thickened mandible, higher and more crescentic molars with stronger developed pillars of the paracone and metacone, and by more rugose enamel. In addition, it is distinguished from *Archaeomeryx* by the proportions of the crowns of posterior upper molars.

Remarks. The genus *Notomeryx* was initially included in the family Hypertragulidae (Qiu, 1978). Sudre (1984) referred it to the Gelocidae, and Savage and Russell (1983) erroneously considered it to be a synonym of *Indomeryx*. The molars of *Notomeryx* have stronger developed lingual crescents than those of *Archaeomeryx* and resemble in some respects the teeth of gelocids; however, they are well distinguished from the teeth of *Indomeryx*.

Occurrence. China; Middle Eocene.

Notomeryx besensis Qiu, 1978

Indomeryx cotteri: Colbert, 1938, p. 394, text-fig. 55.
Notomeryx besensis: Qiu, 1978, p. 912, pl. I, figs. 1 and 2, pl. II, figs. 6 and 9.

Holotype. IVPP, no. 4957.1, fragmentary upper jaw with M1–M3, and IVPP, no. V 4957.2 (Qiu, 1978, pl. II, fig. 6), fragmentary lower jaw with m2 and m3. For figure, see Qiu (1978, pl. I, fig. 1); China, Baise Basin, Guangxi; Middle Eocene.

Material. IVPP, no. V 4957.3, M2; IVPP, no. V 4957.4, fragments of lower jaw with p3, m1, and m2; IVPP, no. V 4957.5, lower jaw with dp4 and m1; IVPP, no. V 4957.6, lower jaw with m1 and m2; AMNH, no. 73086; and AMNH, no. 73072.

Measurements, mm. Length of M1–M3, 24.

Occurrence. China; Middle Eocene.

CHAPTER 3

OSTEOLOGY AND ODONTOLOGY OF *ARCHAEOMERYX*

SKULL

Skull Shape and Proportions

Regarding the skull shape and proportion, *Archaeomeryx* represents a primitive stage of ruminant evolution and substantially differs from the majority of tragulines and all higher ruminants.

The skull of *Archaeomeryx* has a small braincase and a relatively short facial region (Figs. 3–5; Table 2). The facial region is approximately half as long as the basal length of skull (from the prosthion to the basion). Among the Tragulina, only juvenile *Hyemoschus* has a slightly shorter snout. The braincase is of almost the same length as the facial region. The index of the braincase length (ratio of the braincase length to the basal length of skull) is about 0.59–0.63. In all known traguline genera, the relative length of the braincase is somewhat less than in *Archaeomeryx*.

The braincase is primitively narrow. It is narrower than those of other ruminants, including *Lophiomeryx* and *Prodremotherium*, which have relatively narrow braincase. In the dorsal view, the braincase of *Archaeomeryx* is weakly expanded at the zygomatic processes of the squamosals and strongly narrowed behind these processes and behind the orbits. The temporal, sagittal, and occipital crests are well developed.

In lateral view, the skull roof is almost flat. The roof is weakly convex anteriorly and clear concave posteriorly. Among the Tragulina, a similar structure is only known in *Lophiomeryx*. The axis of the braincase base is raised anteriorly with reference to the skull roof and almost parallel to the axis of the tooth row. In *Archaeomeryx*, the angle between these axes is only several degrees. The angle between the axes of the facial and cranial regions is about 130°.

The bend of the cranial axis at the boundary between the facial and cranial regions increased in the course of ruminant evolution. The axes of the braincase base and the tooth row deviate from the parallel positions in advanced species.

The occiput is low and narrow. The plane of the occiput is mainly concave, with a strongly posteriorly projecting occipital crest. The angle between the occiput and the skull roof is approximately 100°. In the dorsal view, the occiput has a stout posteromedial projection formed by the occipital crest. A weaker projection is retained in *Prodremotherium* and *Hyemoschus*. In a strongly reduced state, this crest remains in some higher ruminants, in particular, in *Alces*.

The frontorbital skull region of *Archaeomeryx* is relatively short, the length of the frontals is almost equal to their interorbital width. The bent of the skull profile in the interorbital point extremely weak.

The facial region is primitively very low, short, and strongly anteriorly narrowed. The index of the snout length (relative to the basal length) is 0.55–0.59. In adults of other ruminants, this index is usually greater than 0.6. The nasolacrimal fissures are undeveloped, showing a primitive condition.

The snout virtually lacks expansion at the upper canines. In a number of tragulines with large canines, the snout is markedly expanded at this point.

Table 2. Measurements and indices of skull of *Archaeomeryx*

| No.	Measurements and indices	N	Min–Max	M	AMNH 20322 (Colbert, 1941)
1	Maximum length	20	80–105	88.1	–
2	Basal length	20	80–95	84.3	90e
3	Facial length	3	49–52	50.7	–
4	Braincase length	2	53.5–55	54.5	–
5	Occiput width	1	28.8	–	–
6	Preorbital length	19	25–46	36.4	37e
7	Postorbital length	19	30–52	36.8	52e
8	Occiput depth	7	25–35	31	–
9	Vertical orbital diameter	17	11.3–16.5	12	16.5
10	Horizontal orbital diameter	15	12–16	13	–
11	Index of facial length (3 : 2)	3	0.55–0.59	0.57	–
12	Index of braincase length (4 : 2)	2	0.59–0.63	0.61	–
13	Index of occiput height (8 : 2)	2	0.26	0.26	–
14	Index of the orbit position (6 : 2)	2	0.45–0.47	0.46	–

(1a)

(1b)
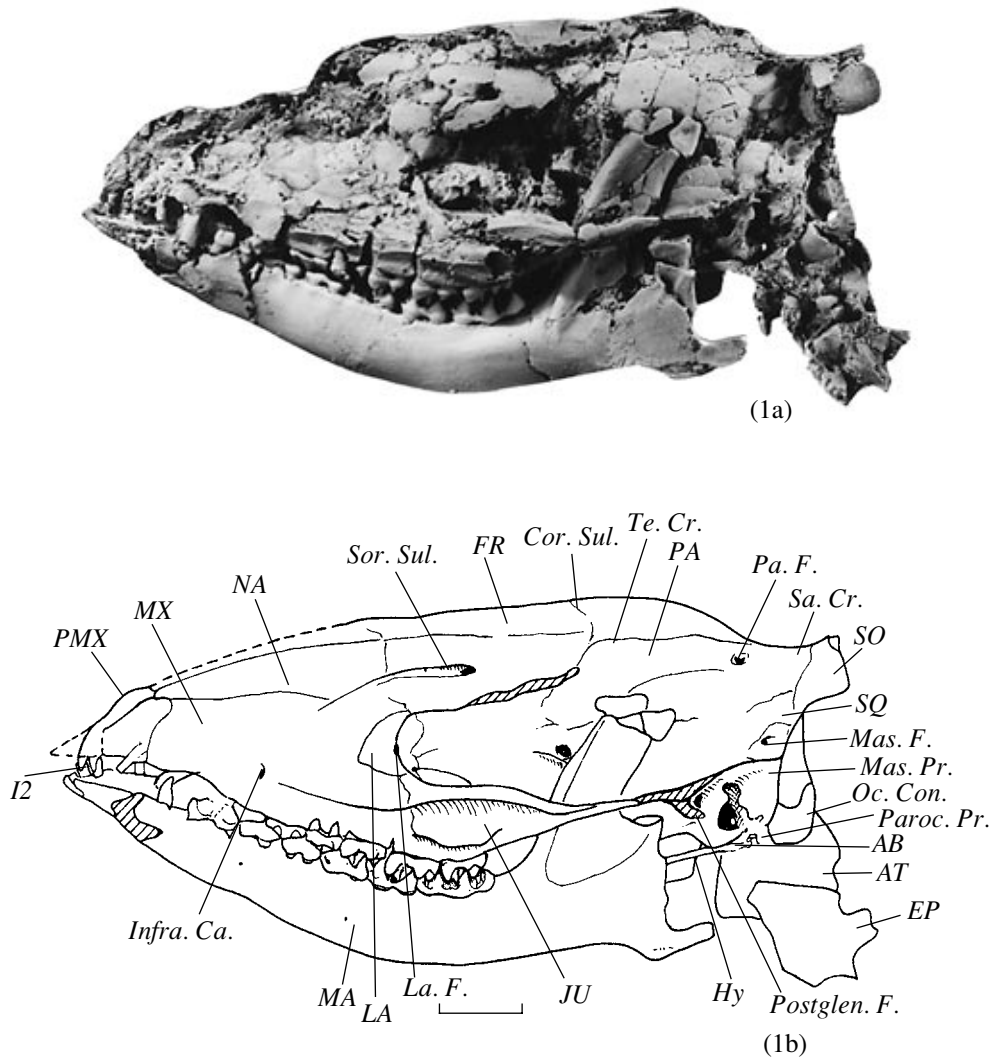
Fig. 3. Skull of *Archaeomeryx optatus*: (1) PIN, no. 2198/149, lateral views; (2) PIN, no. 2198/154: (a, b) dorsal and (c) ventral views. Designations: (*AB*) auditory bulla, (*Ant. Op. Nas. Cav.*) anterior opening of nasal cavity, (*AT*) atlas, (*C*) upper canine, (*Con. Pr.*) condylar process, (*Cor. Pr.*) coronoid process, (*Cor. Sut.*) coronal suture, (*EP*) epistropheus, (*Ethm. Fis.*) ethmoidal fissure, (*FR*) frontal, (*Hy*) hyoid, (*Infra. Ca.*) infraorbital canal, (*I1, I2, I3*) first, second, and third upper incisors, (*JU*) jugal, (*LA*) lacrimal, (*La. F.*) lacrimal foramen, (*Lamb. Sut.*) lamdoidal suture, (*MA*) mandible, (*Mas. F.*) mastoid foramen, (*Mas. Pr.*) mastoid process, (*MX*) maxilla, (*NA*) nasal, (*Oc. Con.*) occipital condyle, (*PA*) parietal, (*Pa. F.*) parietal foramen, (*Paroc. Pr.*) paroccipital process, (*PMX*) premaxilla, (*Post. Op. Infra. Ca.*) locus of posterior opening of infraorbital canal, (*Postglen. F.*) postglenoid foramen, (*Postglen. Pr.*) postglenoid process, (*Sa. Cr.*) sagittal crest, (*SO*) supraoccipital, (*Sor. F.*) supraorbital foramen, (*Sor. Sul.*) supraorbital sulcus, (*SQ*) squamosal, (*Te. Cr.*) temporal crest, and (*Zyg. Pr*) zygomatic process. Scale bar, 1 cm.

Skull Roof

The sagittal and temporal crests of *Archaeomeryx* remain most primitive among the Ruminantia. The sagittal crest is well developed and very long, as in creodonts and carnivores. The temporal crests are fused into the sagittal crest close to the bregma. They strongly curve anteriorly, and a large part of their extent is positioned almost perpendicular to the sagittal plane.

In other tragulines, including *Hypertragulus* and *Leptomeryx*, the sagittal crest is much shorter and the temporal crests fuse into the sagittal crest at a more posterior point. In higher ruminants and extant tragulids, the sagittal crest is weakly developed, and the temporal crests are transformed into the upper temporal line outlining the attachment area of the temporal muscle (musculus temporalis).

Braincase Base

In ventral view, the basicranium of *Archaeomeryx* has a relatively long posterior region behind the auditory bulla. The anterior region of the braincase in front of the external acoustic foramen is only slightly longer than the posterior region, as distinct from those of other ruminants.

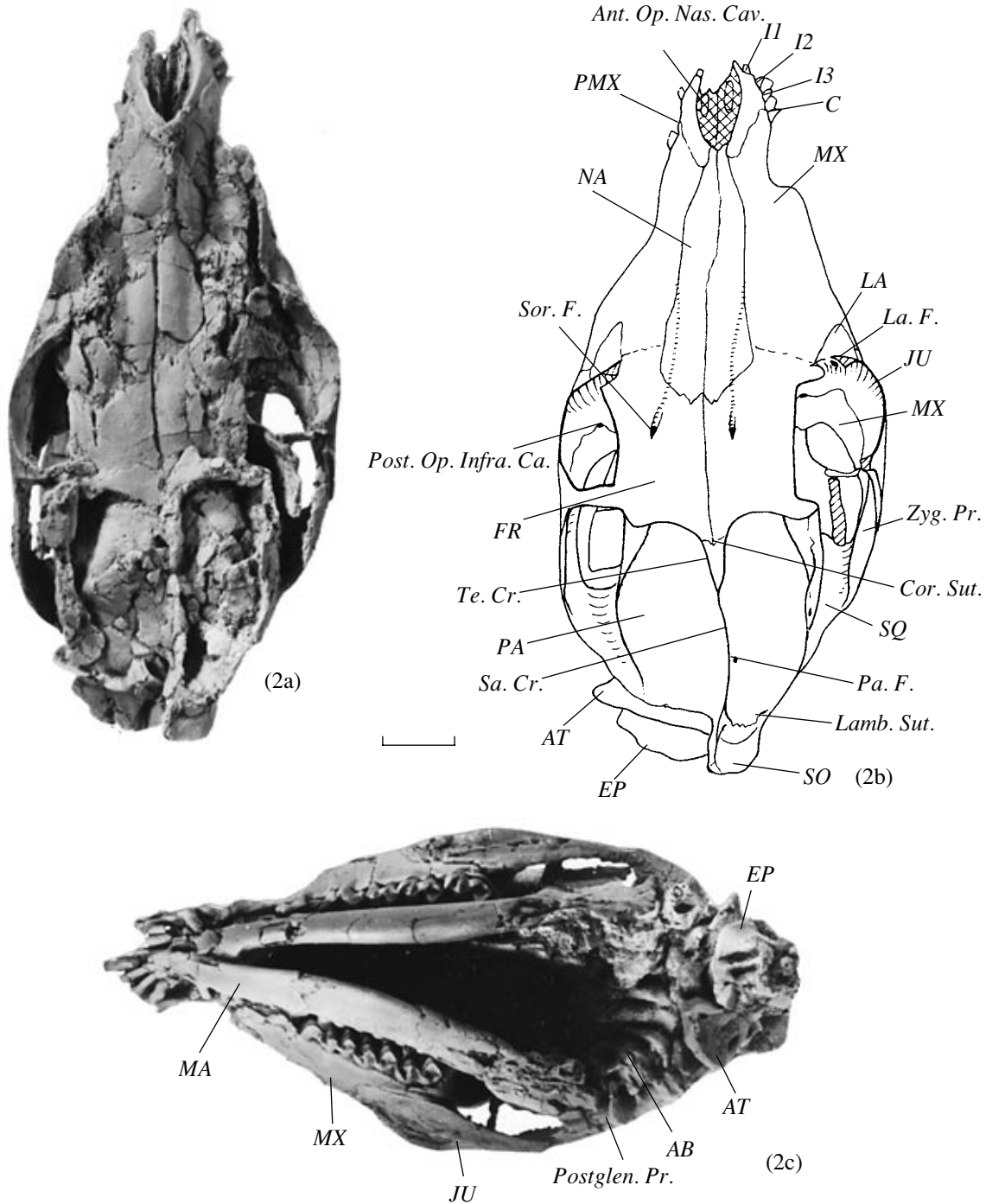The basicranium is rather narrow at the level of the mastoid processes, which are positioned anterior to the

Fig. 3. (Contd.)

Zygomatic Arch

Archaeomeryx markedly differs from the other Ruminantia in the structure of the zygomatic arch. The arch is long and low, being formed by a long zygomatic jugular processes of the occipital and posterior to the external acoustic meatus. The anterior edge of the mastoid is located somewhat anterior to the transverse tubercles.

process of the temporal and by the temporal process of the jugal. In lateral view, the suture between these processes is long, strongly oblique, and approximately parallel to the inferior orbital border. Anteriorly, the zygomatic process of the temporal almost reaches the zygomatic arch; the temporal process extends posteriorly to the base of the zygomatic process of the squamosal (Fig. 12). The zygomatic arch is slightly posteriorly raised and strongly curves dorsally at the midlength.
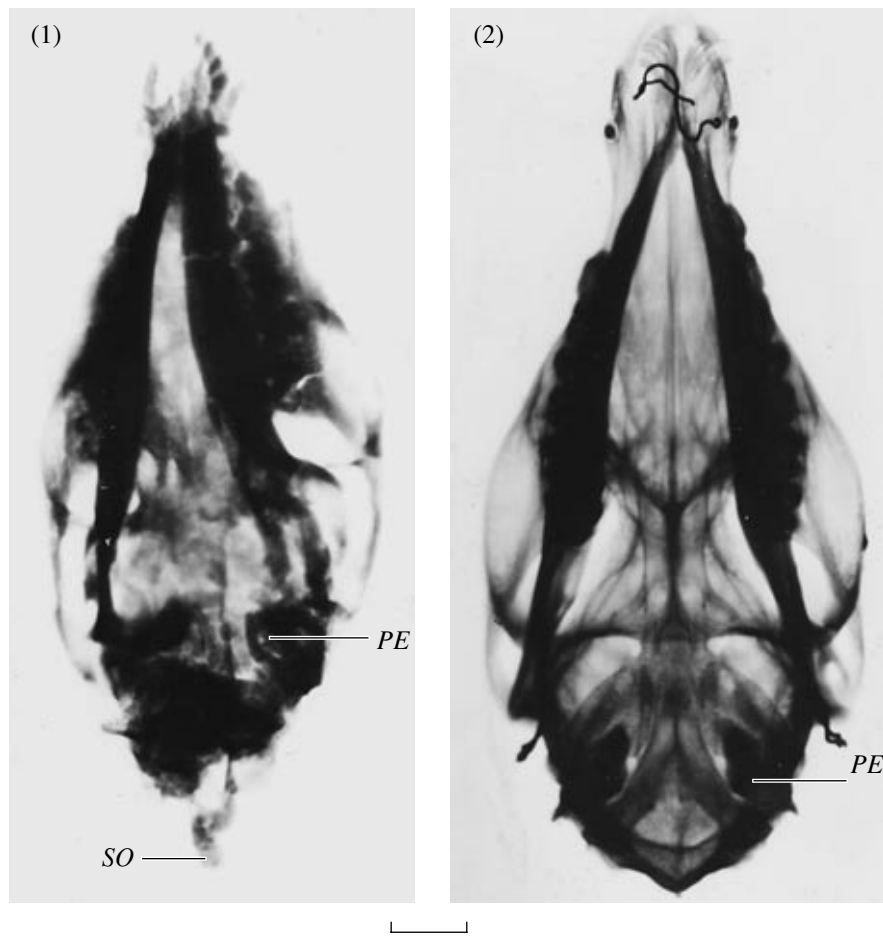
Fig. 4. Skulls examined by x-rays: (1) *Archaeomeryx*, PIN, no. 2198/154; (2) *Tragulus javanicus*, Recent. Designations: (*PE*) petrosal and (*SO*) supraoccipital. Scale bar, 1 cm.

In the dorsal view, the distance between the inferior orbital borders is somewhat larger than the distance between the dorsal borders of the zygomatic arches. The root of the zygomatic arch is narrow. Its posterior edge is strongly oblique and weakly convex.

The inner wall of the zygomatic arch is weakly concave and only slightly inclined laterally with reference to the sagittal plane.

Orbital Region

The orbit of *Archaeomeryx* is posteriorly closed, as in the majority of ruminants. This differs *Archaeomeryx* from the dichobunoid *Messelobunodon*, hypertraguloids *Hypertragulus* and, probably, *Praetragulus*, and from the lophiomerycid *Lophiomeryx*.

The postorbital bar is mostly formed by the jugal process of the frontal.

The orbits are small and nonprotruding. Their length does not exceed the length of M1–M3. The orbits retain a primitive low position (because of a small height of the maxilla and jugal) and virtually lacks backward displacement. The anterior rim of the orbit is located directly above M1. The distance from the anterior orbital rim to the prosthion is approximately equal to the distance from the posterior orbital rim to the basion, as in primitive eutherians.

The orbital mosaic pattern of *Archaeomeryx* is primitive, close to that of some insectivores, in particular, leptictids (see Novacek, 1986). This pattern is characterized by a relatively large orbital exposure of the frontal, almost equal sizes of the orbital exposures of the lacrimal and the maxilla, a very small orbital exposure of the jugal, the position of the posterior opening of the infraorbital canal (for the infraorbital nerve, artery, and vein) in the maxilla, and a higher position of this opening with reference to the sphenopalatine foramen.

The orbital exposure of the frontal in *Archaeomeryx* extends for nearly half the height of the orbital wall (Fig. 6) and contacts anteriorly with the lacrimal and palatine, inferiorly with the orbitosphenoid and alisphenoid, and posteriorly with the parietal.

Apparently, the orbital exposure of the frontal terminates short of reaching the sphenopalatine foramen. According to Novacek (1986), a large orbital wing of
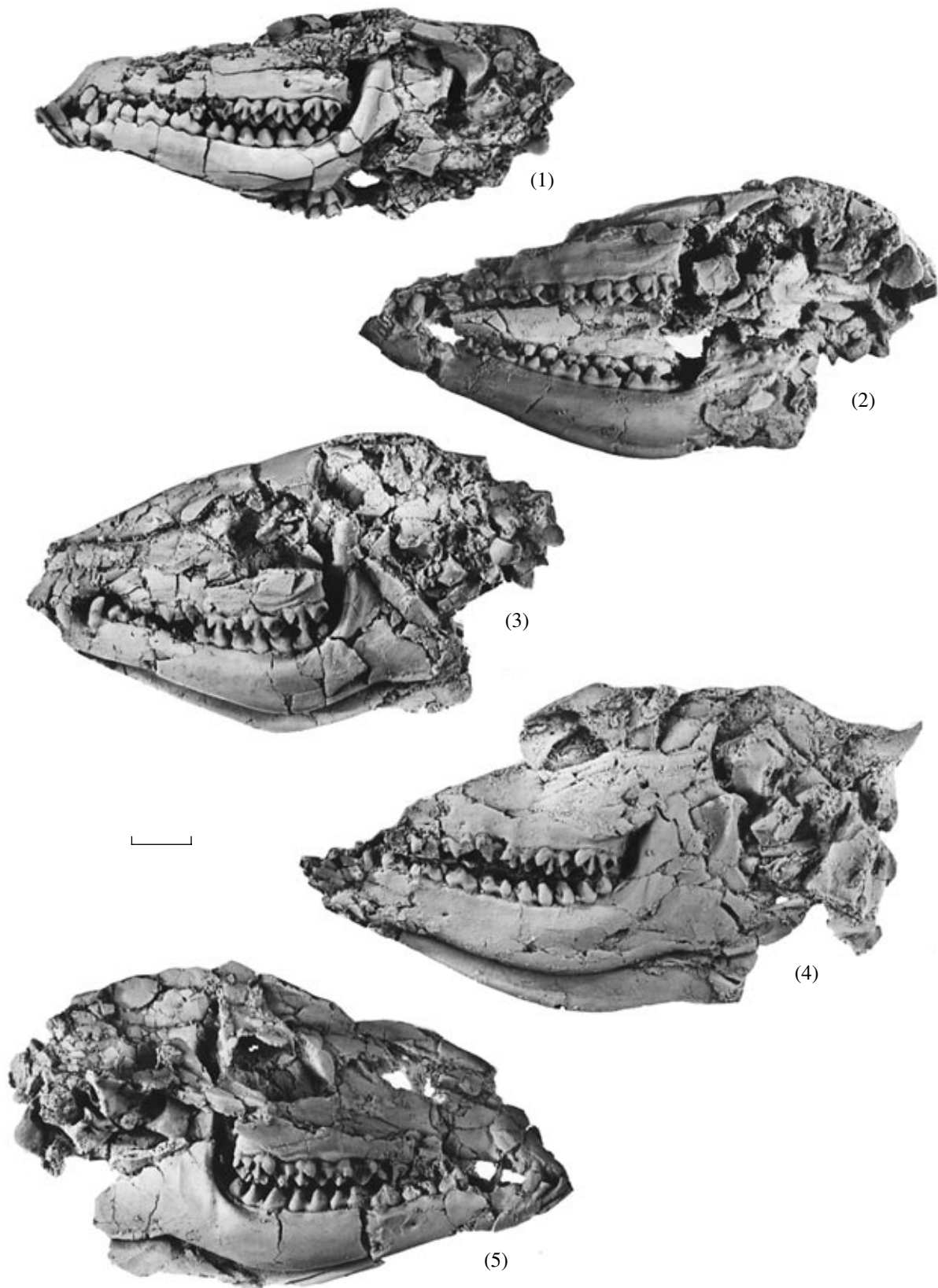
Fig. 5. Skulls of *Archaeomeryx optatus*, lateral view: (1) PIN, no. 2198/153; (2) PIN, no. 2198/152; (3) PIN, no. 2198/210; (4) PIN, no. 2198/156; and (5) PIN, no. 2198/151. Scale bar, 1 cm.
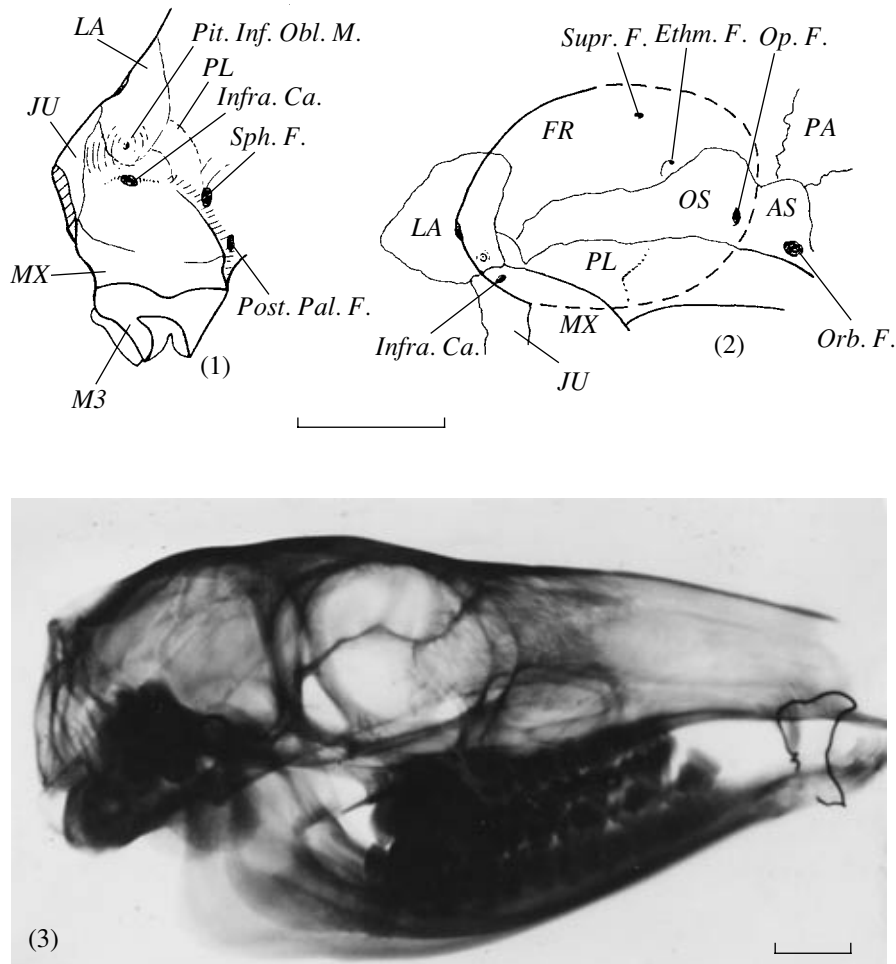
Fig. 6. Orbital region of *Archaeomeryx* and skull of *Tragulus* examined by x-rays: (1) *Archaeomeryx*, PIN, no. 2198/162, posterior view; (2) *Archaeomeryx*, PIN, no. 2198/149, lateral view; and (3) *Tragulus*, Recent. Designations: (*AS*) alisphenoid, (*Ethm. F.*) ethmoidal foramen, (*Infra. Ca.*) infraorbital canal, (*JU*) jugal, (*LA*) lacrimal, (*MX*) maxilla, (*M3*) third upper molars, (*Op. F.*) optic foramen, (*Orb. F.*) foramen orbitorotundum, (*OS*) orbitosphenoid, (*PA*) parietal, (*Pit. Inf. Obl. M.*) pit for inferior oblique muscle, (*PL*) palatine, (*Post. Pal. F.*) posterior palatine foramen, (*Sph. F.*) sphenopalatine foramen, (*Supr. F.*) supraorbital foramen, and (*FR*) frontal. Scale bar, 1 cm.

the frontal isolating the orbitosphenoid from the palatine is of a primitive eutherian character.

The orbital exposure of the frontal contains two openings; the dorsal opening is the supraorbital foramen for the supraorbital artery and vein; the second is the ethmoidal foramen providing passage for the ethmoidal artery and vein and located just above the orbitosphenoid and posterior to the orbital exposure of the palatine, as in primitive eutherians. In *Leptomeryx*, modern tragulids, and higher ruminants, the ethmoidal foramen is displaced anteriorly and lies above the palatine.

In *Archaeomeryx*, as in *Lophiomeryx, Prodremotherium*, and some insectivores and primates, most of the anterior orbital wall is formed by the lacrimal. The orbital exposure of the maxilla occupies the anteroinferior and inferior regions of the wall. The orbital portion of the jugal is very small and narrow. The posterior

opening of the infraorbital canal is located in a well-outlined fossa on the maxilla.

In a more advanced state characteristic of *Hypertragulus, Leptomeryx*, tragulids, and higher ruminants, the portion of the maxilla contributing to the orbital mosaic decreases because of the enlargement of the lacrimal and expansion of the jugal and palatine. The posterior opening of the infraorbital canal is displaced to the incisure in the inferior margin of the lacrimal.

The posterior opening of the infraorbital canal and the sphenopalatine foramen of *Archaeomeryx* are small and approximately equal in size. The posterior opening of the infraorbital canal lies at approximately half the height of the anterior orbital wall and slightly higher than the sphenopalatine foramen. In many tragulines and all higher ruminants, the sphenopalatine foramen is larger than the posterior opening of the infraorbital canal. In higher ruminants, the sphenopalatine foramen
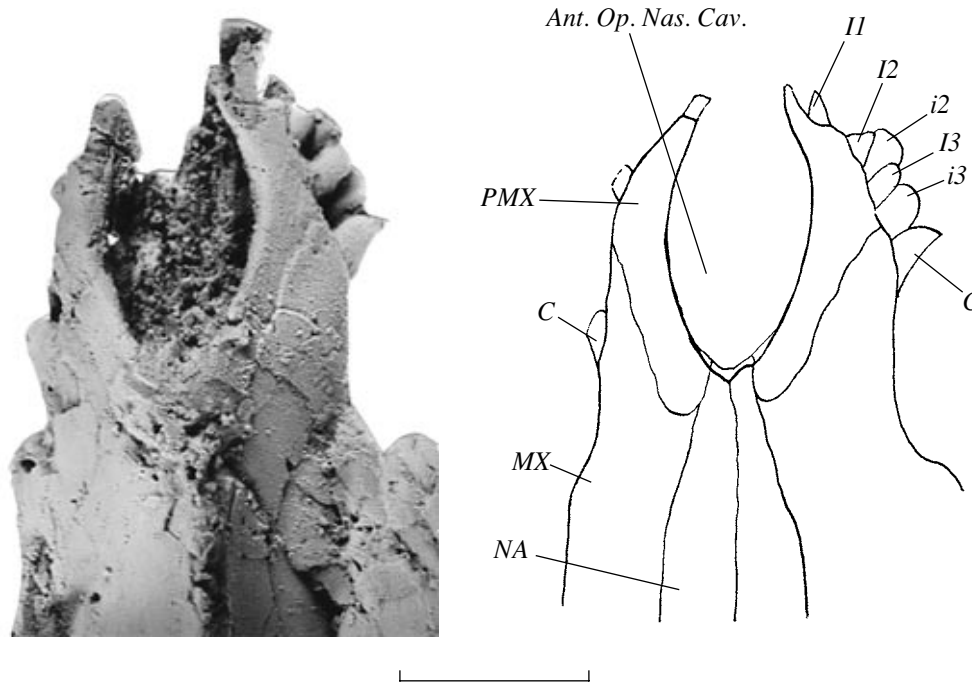
Fig. 7. Anterior region of skull of *Archaeomeryx*, PIN, no. 2198/154. Designations: (*Ant. Op. Nas. Cav.*) anterior opening of nasal cavity, (*C*) upper canine, (*I1, I2, I3*) first, second, and third upper incisors, (*i2, i3*) second and third lower incisors, (*MX*) maxilla, (*PMX*) premaxilla, and (*NA*) nasal. Scale bar, 1 cm.

occupies a higher position than the opening of the infraorbital canal.

In *Archaeomeryx*, the shape of the foramen orbitorotundum (= sphenorbital fissure + foramen rotundum) is typical of the Ruminantia. In true ruminants this foramen provides passage for the oculomotor (III), trochlear (IV), and abducens (VI); ophthalmic and maxillary rami of the trigeminal (V) nerve; and a venous trunk.

Anterior to the foramen orbitorotundum, at the base of the orbitosphenoid, there is the optic foramen, which is smaller than the foramen orbitorotundum. As in the majority of mammals, the optic foramina in *Archaeomeryx* are placed at a distance from each other and not confluent. In *Leptomeryx* and tragulids, they are located very close to each other.

Nasal Cavity

The nasal cavity (cavum nasi) opens anteriorly as the anterior opening of the nasal cavity (apertura nasi osseum). In *Archaeomeryx*, the structure of the latter considerably differs from those of other known artiodactyls. The low and short anterior opening of the nasal cavity is ovoid in outline and slightly narrows posteriorly (Fig. 7). The nasals do not protrude anteriorly above the opening, and the premaxillae virtually overlap the nasals dorsally. A similar structure of the anterior opening of the nasal cavity is typical of some insectivores, in particular, hedgehogs.

In the Artiodactyla, except for *Archaeomeryx* and *Hypertragulus*, the anterior processes of the nasals protrude anteriorly and cover the posterior region of the anterior opening of the nasal cavity.

The nasal cavity opens posteriorly as low, narrow, and oval choanae inferiorly isolated from each other by a low vomer. The inferior wall of the nasal cavity is formed by the hard palate (palatum osseum).

In *Archaeomeryx*, there are three long and narrow nasal passages: dorsal, medial, and ventral. The dorsal nasal passage (meatus nasi dorsalis) extends to the sphenopalatine foramen. The ventral nasal passage is the longest and widest of the three and extends dorsal to the palatum osseum.

Apparently, the ethmoidal complex was relatively simple. The basic pattern of the eutherian ethmoidal complex includes four endoturbinals and two or three ectoturbinals (Novacek, 1993). According to Novacek (1993), insectivores, chiropters, hyracoids, some primates, most rodents, and most carnivores share this pattern. The presence of two ectoturbinals is characteristic of didelphids, insectivoran leptictids, and some certain primitive mammals (Novacek, 1986).

Ungulates and, in particular, ruminants, usually have an increased number of ethmoturbinals. According to Carlsson (1926), Recent *Tragulus* has only seven ectoturbinals; *Cervus elaphus* and *Capreolus capreolus* have 20 and 23 ectoturbinals, respectively.

Palate

A primitive short and narrow palate has almost straight lateral sides, which only slightly diverge posteriorly (Fig. 4). The palate is almost flat and strongly narrowed anteriorly. The M3–M3 distance is almost 1.5 as wide as the P2–P2 distance.

The posterior palatal margin has a medium-sized median concavity, which is located posterior to the line connecting the posterior edges of M3, and two small lateral concavities, which reach the level of the posterior edges of M3.

The incisive foramina (for nerves and vessels passing to the incisive canals) are small, short, and very narrow (Fig. 13). According to a x-ray photograph, the incisive foramina are approximately 6 mm long and 1.5 mm wide. The foramina are incompletely isolated from each other and do not extend posteriorly beyond the canines. A small triangular posteromedial notch is well pronounced.

CRANIAL BONES

Occipitals

A primitive elongated and posteriorly expanded basioccipital (pars basilaris or basioccipitale) of *Archaeomeryx* has sharp and strongly laterally projecting posterior corner, a weak median sulcus, and very large and elongated muscular tubercles, tuberculi pharyngei (Figs. 8, 9). The pharyngeal tubercles are at least half as long as the basioccipital. Anteriorly, the pharyngeal tubercles spread onto the basisphenoid. The lateral edge of the basioccipital is weakly S-shaped. The ventral edge of the petrosal is strongly pressed to the latter. The petrooccipital fissure (fissura petrooccipitalis) located between them is very narrow. Anteriorly, it becomes a well-developed anterior lacerate foramen.

In the course of ruminant evolution, the relative length of the basioccipital decreased. However, some higher ruminants, in particular, dremotheriines, preserve many primitive characters of the basioccipital structure typical of *Archaeomeryx*.

The primitive low and narrow exoccipitals (exoccipitale) of *Archaeomeryx* form the lateral margins of the foramen magnum. The foramen is relatively wide and has a well-developed median notch in the upper border. The foramen magnum faces ventrally rather than posteriorly. In the course of ruminant evolution, the exoccipitals enlarged and became higher. In the advanced species, the foramen magnum usually faces posteriorly.

The primitive small and narrow occipital condyle (condylus occipitalis) has a small and only slightly convex dorsal lobe and a large and relatively convex ventral lobe. The lobes are positioned at an angle of about 42°–45°. The long axis of the dorsal lobe of the occipital condyle is inclined at an angle of about 25° with reference to the sagittal plane of skull. The ventral surface of the occipital condyle is inclined to the ventral surface of the basioccipital at an angle of about 125°. In all other ruminants, the dorsal surface of the occipital condyle is almost vertical, i.e., almost perpendicular to the ventral surface of the basioccipital; the lobes of the occipital condyle are positioned at almost a right angle.

The transverse tubercles of *Archaeomeryx* are rather strong and located anterior to the ventral condylar lobe.

The condylar foramen leading to the condylar canal (canalis condylaris) is medium-sized and located in a weakly outlined condylar fossa (fossa condylaris), which lies lateral to the occipital condyle.

The hypoglossal foramen for the nervus hypoglossus is larger than the condylar foramen and located just anteromedial to the latter.

The jugular notch (incisura jugularis) is small and forms a small foramen jugulare along with the jugular notch of the petrosal.

A primitive small and very short jugular or paraoccipital process (processus jugularis) of *Archaeomeryx* does not project ventrally beyond the transverse condylar tubercles.

A well-developed mastoid process anteroventrally adjoins the paraoccipital process. In all ruminants, except for *Lophiomeryx*, the paraoccipital process is longer and the suture between the paraoccipital and the mastoid processes is displaced to the lateral side of skull.

The supraoccipital or the upper region of the occipital (supraoccipitale) of *Archaeomeryx* is narrow and relatively high. A rather broad exposure of the supraoccipital contributes to the formation of the skull roof. The margo lambdoideus of the bone located on the skull roof is long, which is characteristic of the primitive state. The primitive broad exposure of the supraoccipital on the skull roof is preserved in extant tragulids. In lateral view, this region of the supraoccipital of *Archaeomeryx* is strongly inclined anteriorly and forms a stout occipital crest strongly projecting posteriorly. A similar structure appears is characteristic of *Lophiomeryx* and *Bachitherium*.

In other ruminants, this region is markedly reduced and usually inclined posteriorly; the occipital crest is strongly reduced. In addition, the occipital region of the supraoccipital is strongly widened in the majority of higher ruminants.

A well-developed occipital crest has a very large, relatively wide, and strongly posteriorly projecting occipital protrusion. Rudiments of this protrusion remain in such higher ruminants as dremotheriines, dromomerycids, and alcines.

The external occipital surface of the supraoccipitals is strongly concave in the upper segment. The external occipital crest (crista occipitalis externa) is very weak, narrow, and elongated. As in leptictids, it closely approaches the foramen magnum. The superior nuchal line (linea nuchae superiores) is prominent.
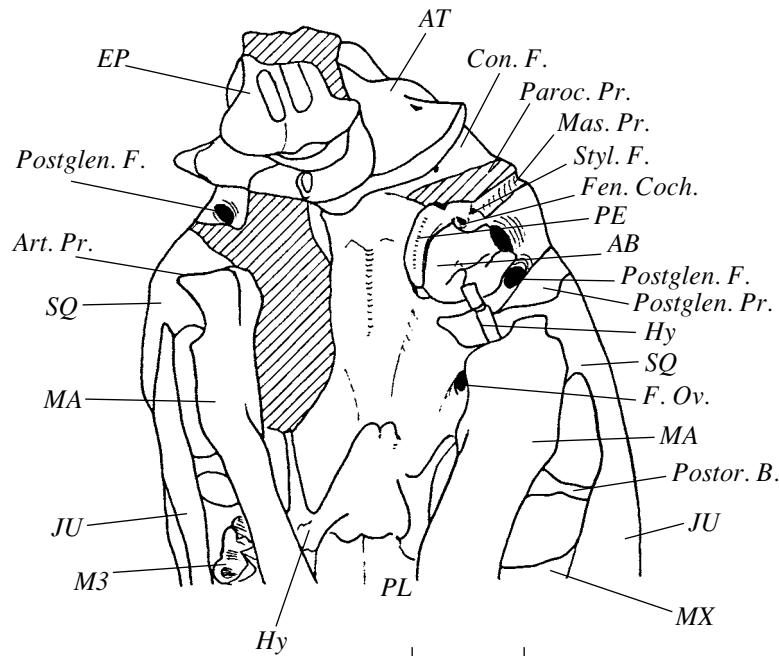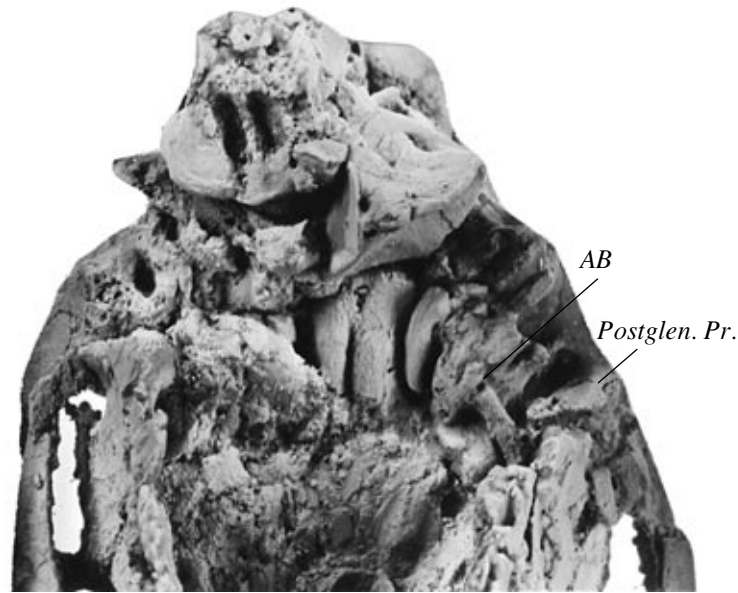
Fig. 8. Basicranium of *Archaeomeryx*, PIN, no. 2198/154. Designations: (*AB*) auditory bulla, (*Art. Pr.*) articular process, (*AS*) alisphenoid, (*AT*) atlas, (*BO*) basioccipital, (*BS*) basisphenoid, (*Con. F.*) condylar foramen, (*EP*) epistropheus, (*F. Ov.*) foramen ovale, (*Fen. Coch.*) fenestra cochlea, (*Hy*) hyoid, (*JU*) jugal, (*Jug. F.*) jugular foramen, (*MA*) mandible, (*Mas. Pr.*) mastoid process, (*MX*) maxilla, (*M3*) third upper molar, (*Paroc. Pr.*) paroccipital process, (*PE*) petrosal, (*PL*) palatine, (*Postglenoid. F.*) postglenoid foramen, (*Postglen. Pr.*) postglenoid process, (*Postor. B.*) postorbital bar, (*SQ*) squamosal, and (*Styl. F.*) stylomastoid foramen. Scale bar, 1 cm.

Basisphenoid and Alisphenoid

Archaeomeryx has a primitive narrow and elongated basisphenoid (basisphenoidale or basisphenoideum), which is strongly expanded posteriorly. The ventral surface of the basisphenoid is strongly ventrally convex, especially in the posterior third of the bone extent where the muscular tubercles and the median sulcus between them are well pronounced. In *Leptomeryx* and modern tragulids, the ventral surface of the basisphenoid is markedly flattened, as in many higher ruminants.

The alisphenoid (alisphenoideum) of *Archaeomeryx* deviates from the basisphenoid in the plane of the basisphenoid. Posteriorly, the base of the alisphenoid
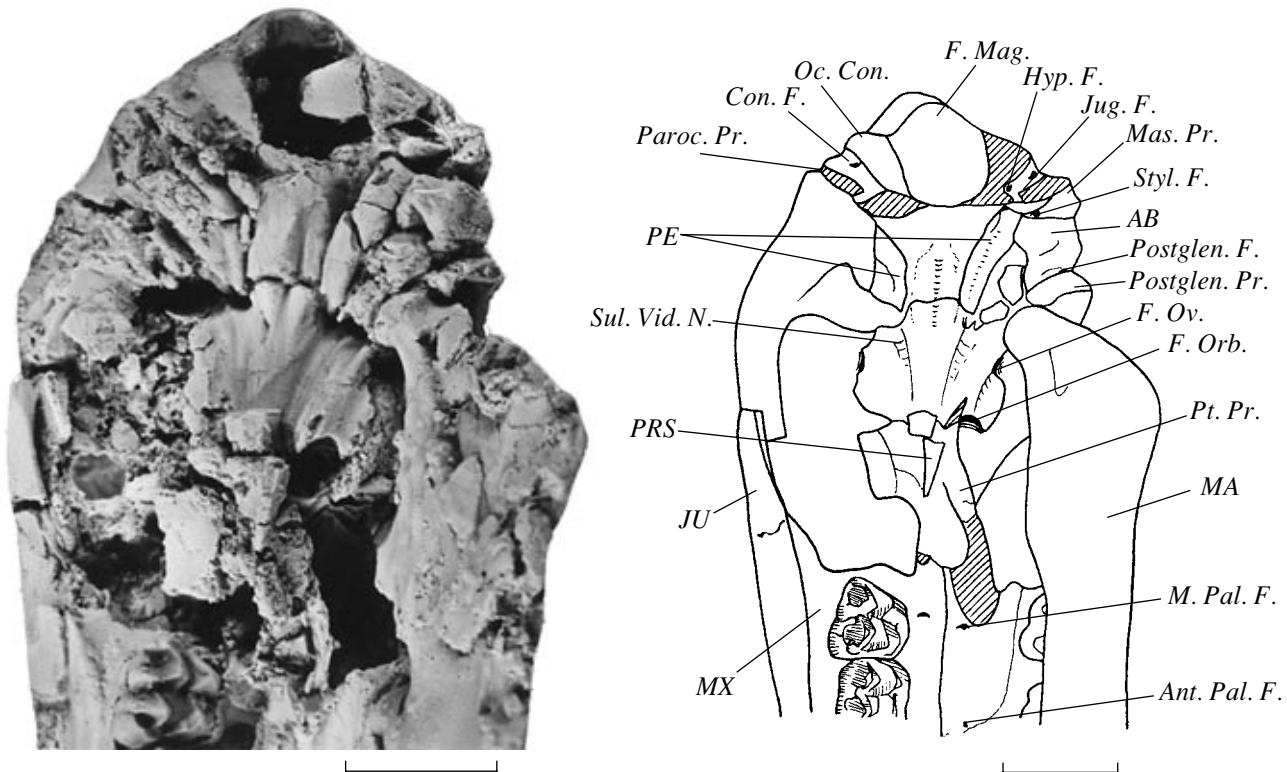
Fig. 9. Basicranium of *Archaeomeryx*, PIN, no. 2198/152. Designations: (*AB*) auditory bulla, (*Ant. Pal. F.*) anterior palatine foramen, (*AS*) alisphenoid, (*AT*) atlas, (*BS*) basisphenoid, (*Con. F.*) condylar foramen, (*F. Mag.*) foramen magnum, (*F. Orb.*) foramen orbitorotundum, (*F. Ov.*) foramen ovale, (*Hyp. F.*) hypoglossal foramen, (*JU*) jugal, (*Jug. F.*) jugular foramen, (*MA*) mandible, (*Mas. Pr.*) mastoid process, (*MX*) maxilla, (*M. Pal. F.*) middle palatine foramen, (*Paroc. Pr.*) paroccipital process, (*PE*) petrosal, (*PL*) palatine, (*Postglen. F.*) postglenoid foramen, (*Postglen. Pr.*) postglenoid process, (*PRS*) presphenoid, (*Pt. Pr.*) pterygoid process, (*SQ*) squamosal, (*Styl. F.*) stylomastoid foramen, and (*Sul. Vid. N.*) sulcus for the Vidian nerve. Scale bar, 1 cm.

markedly deviates upward above the ventral surface of the basisphenoid. The frontal–alisphenoid contact is rather broad and positioned relatively high. In the majority of ruminants, the alisphenoids dorsolaterally diverge from the basisphenoid; the frontal–alisphenoid contact is narrow and positioned lower or absent.

There are two foramina at the base of the alisphenoid in *Archaeomeryx*.

(1) The oval foramen (foramen ovale) is small and ovoid. The long axis of the foramen is almost parallel to the lateral side of the basisphenoid. The foramen is positioned close to the posterior edge of the alisphenoid. The medial side of the foramen adjoins a crest extending to the base of the pterygoid process. Because of the crest, the base of the alisphenoid is divided into two parts; the region located medial to the crest is almost horizontal and the lateral region is slightly elevated.

(2) A large foramen orbitorotundum is located at the base of the alisphenoid anterior to this crest.

The alisphenoid of *Archaeomeryx* lacks openings of the alisphenoid and pterygoid canals. By analogy with *Leptomeryx*, Webb and Taylor (1980) proposed the presence of the pterygoid foramen in *Archaeomeryx*; however, the examination of fossil material did not corroborate this assumption.

The groove for the Vidian nerve at the base of the alisphenoid is well developed and broad. A crest located lateral to the Eustachian canal is rather prominent.

The pterygoid crest (crista pterygoidea) at the boundary of the basicranial and orbital exposures of the alisphenoid is well developed in *Archaeomeryx*.

The primitive low pterygoid processes of *Archaeomeryx* have strongly oblique posterior edges.

Presphenoid

The presphenoid (os praesphenoidale) lies anterior to the basisphenoid. In *Archaeomeryx*, the body of the presphenoid is narrow and almost round in section. Anteriorly, it wedges in between the palatines. The ala or orbitosphenoid (orbitosphenoideum) is low and contacts posteriorly with the alisphenoid, superiorly and anteriorly with the frontal, anteriorly with the palatine, and inferiorly with the palatine and alisphenoid.

At the base of the orbitosphenoid, there is a round optic foramen (foramen opticum) leading into the optic canal and providing passage for the optic nerve and artery. In *Archaeomeryx*, this foramen is smaller than in *Leptomeryx* and Recent tragulids. This foramen remains small in higher ruminants.
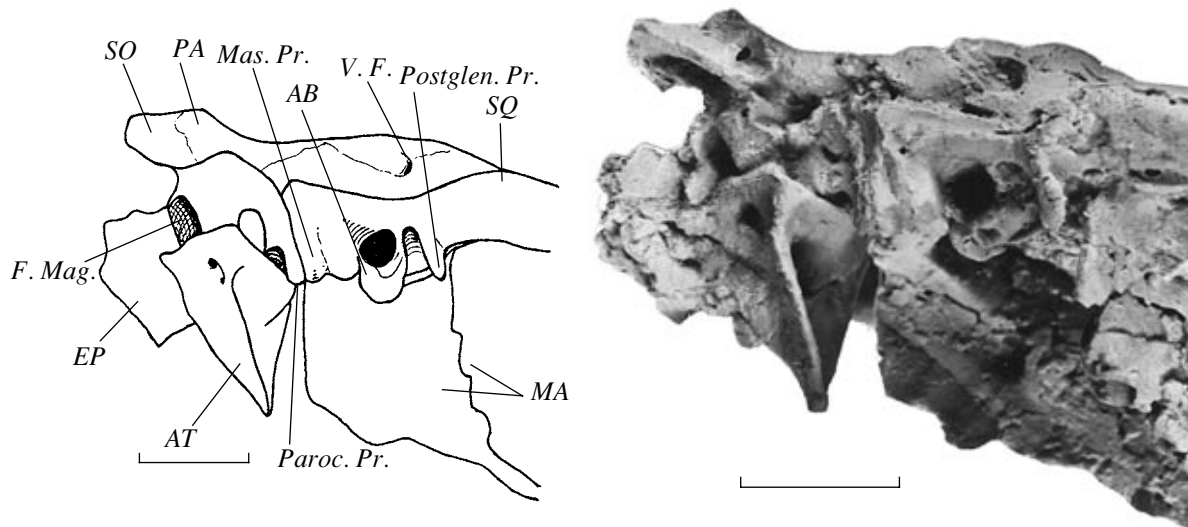
Fig. 10. Braincase of *Archaeomeryx*, PIN, no. 2198/154, lateral view. Designations: (*AB*) auditory bulla, (*AT*) atlas, (*EP*) epistropheus, (*F. Mag.*) foramen magnum, (*MA*) mandible, (*Mas. Pr.*) mastoid process, (*PA*) parietal, (*Paroc. Pr.*) paroccipital process, (*Postglen. Pr.*) postglenoid process, (*SO*) supraoccipital, (*SQ*) squamosal, and (*V. F.*) vascular foramen. Scale bar, 1 cm.

Temporal

The temporal (os temporale) is composed of a well-developed squamosal (pars squamosa), well-developed petrosal (pars petrosa or petrosum), and a small tympanic region (pars tympanica) (Fig. 10).

The squamosal provides support for the masticatory apparatus and is ventrally articulated with the lower jaw. A broad base of the zygomatic process (processus zygomaticus) is located ventrolateral to the external acoustic pore (porus acusticus externus). In *Archaeomeryx*, the medial region of the base of the zygomatic process is almost horizontal and has a weak, superficial, transversely elongated, and beanlike mandibular fossa (fossa mandibularis) for the mandibular condyle. A well-pronounced, long, and low postglenoid process extends along the posterior edge of the base of the zygomatic process. It slightly curves anteriorly and is oblique posteriorly. Its long axis is positioned at an angle of approximately 60° to the sagittal plane of skull.

The articular tubercle (tuberculum articulare) is located anterior to the glenoid fossa and low. The postglenoid foramen (foramen retroarticulare) is medium-sized and clearly visible posterior to the postglenoid process somewhat anterolateral to the external acoustic meatus (meatus acusticus externus). A similar postglenoid foramen, nonoverlapped by the tympanic region, is present in *Lophiomeryx* and *Leptomeryx*. In the majority of ruminants, the tympanic region completely covers the postglenoid foramen, so that it is invisible inferiorly.

In *Archaeomeryx*, the lateral region of the zygomatic process base is elevated. Anteriorly, its upper margin weakly curves medially. The anterior end of the zygomatic process is pointed and connected to the temporal process (processus temporalis) of the jugal to form the zygomatic arch. The anterior region of the zygomatic process is long, directed anteriorly, and closely approaches the postorbital bar; it is strongly pressed to the braincase and positioned in an almost parasagittal plane. The medial surface of the anterior region of the zygomatic process is weakly convex and the lateral surface is concave. Laterally, the superior and inferior edges of the zygomatic process are gently arched.

The petrosal of *Archaeomeryx* lies very close to the basioccipital and exoccipitals. Its long axis is anteromedially directed at an angle of about 35°–40° to the sagittal plane of skull.

The petrosal of *Archaeomeryx* displays a number of primitive features, which resemble a primitive trisulcate petrosal pattern described by MacIntyre (1972). This type is characteristic of primitive placentate mammals. The petrosal of *Archaeomeryx* is similar in structure to the ferungulate variant of the trisulcate petrosal, which was found, in particular, in *Protungulatum* from the Late Cretaceous of Montana and creodonts (MacIntyre, 1972, text-figs. 4, 5). The position of the sulci and the pattern of the internal carotid artery were probably similar to those of a hypothetical eutherian ancestor reconstructed by Wible (1987, text-fig. 3).

On the surface of the *Archaeomeryx* petrosal, there are three well-pronounced main sulci (for the facial nerve, stapedial artery, and for the inferior petrosal sinus vein) typical of the trisulcate type (Fig. 11).

The sulcus of the facial nerve extends from the apertura externa canalis facialis to the fossa musculus stapedialis. The petrosal of *Archaeomeryx* is characterized by the relatively straight course of the facial nerve between the foramen of the facial canal and the stylomastoid foramen. The same direction is observed in *Lophiomeryx* and *Leptomeryx*. In Recent tragulids and in the genus *Hypertragulus*, the canalis facialis curves
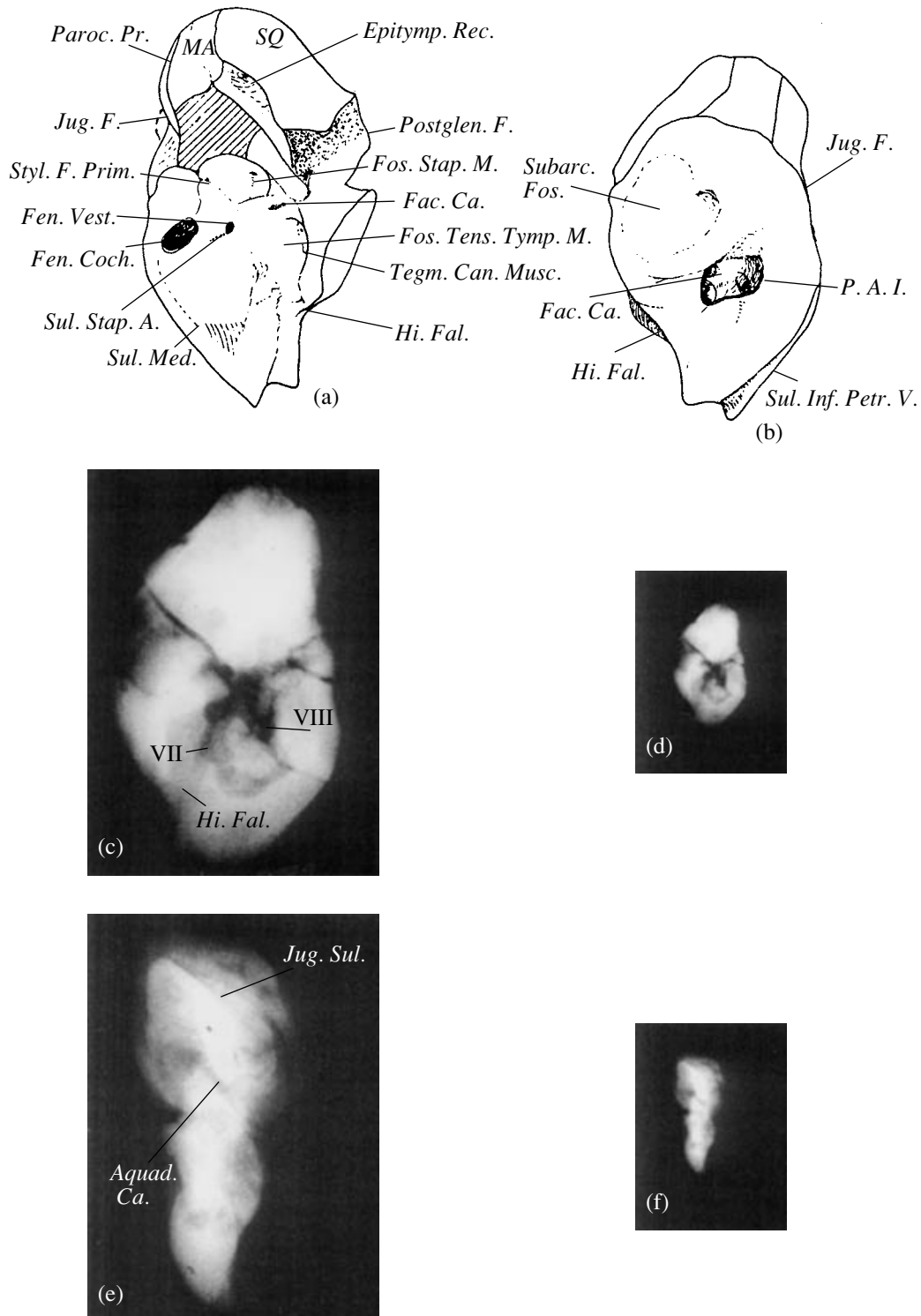
Fig. 11. Petrosal of *Archaeomeryx*, PIN, no. 2198: (a) ventral and (b–d) dorsal views, ×3; (e, f) medial views, ×1; (c–f) x-ray photographs. Designations: (*Aquad. Ca.*) aquaduct canal, (*Epitim. Rec.*) epitympanic recess, (*Fac. Ca.*) facial canal, (*Fen. Coch.*) fenestra cochlea, (*Fen. Vest.*) fenestra vestibuli, (*Fos. Stap. M.*) fossa for stapedial muscle, (*Fos. Tens. Tymp. M.*) fossa for tensor tympani muscles, (*Hi. Fal.*) hiatus Falloppii, (*Jug. F.*) jugular foramen, (*Jug. Sul.*) jugular sulcus, (*MA*) mastoid, (*P. A. I.*) porus acousticus internus, (*Paroc. Pr.*) paroccipital process, (*Postglen. F.*) postglenoid foramen, (*SQ*) squamosal, (*Styl. F. Prim.*) foramen stylomastoid primitivum, (*Subarc. Fos.*) subarcuate fossa, (*Sul. Med.*) sulcus medialis, (*Sul. Stap. A.*) sulcus for stapedial artery, (*Tegm. Ca. Musc.*) tegmen canalis musculotubarius, (*Sul. Prom. A.*) sulcus for promontory artery; (VII) foramen for facial nerve; and (VIII) foramen for acoustic nerve. Scale bar, 1 cm.

dorsally and posteriorly around the posttympanic neck (Webb and Taylor, 1980). The apertura externa canalis facialis leads to a straight passage that opens anterior to the hiatus Fallopii. In *Archaeomeryx*, the latter occupies a primitive position on the ventral side of the petrosal.

A weak but distinct sulcus for the stapedial artery is on the promontorium, extending in a medial direction from the medial edge of the fenestra vestibuli where the footplate of the stapes lies. The stapedial artery sensu MacIntyre (1972) is the same as the proximal stapedial artery sensu Wible (1987). It diverges lateral to the internal carotid artery. In nearly all forms possessing the proximal stapedial artery, the latter crosses the foramen vestibuli through the stapes and, then, turns anteriorly. Anteriorly, the proximal stapedial artery is divided into the inferior and superior rami. The first bifurcates anteriorly into the arteries passing into the infraorbital and mandibular regions. The second passes into the braincase and branches to form the arteria diploetica magna, ramus temporalis, and the meningeal rami. Wible (1987) proposed that, in the hypothetical eutherian ancestor, the supraorbital ramus could diverge from the superior ramus in the anterior region.

In *Archaeomeryx*, the proximal stapedial artery most likely deviated from the internal carotid artery posterior to the auditory bulla but not in the tympanic cavity, as observed in nearly all eutherians (see Wible, 1987). In the skull of specimen PIN, no. 2198/154, the auditory bulla does not cover the fenestra cochleae and the stapedial muscle fossa. The stapes is visible posterior to the auditory bulla. The proximal stapedial artery leaves the internal carotid artery posterior to the auditory bulla in the monotreme *Ornithorhynchus* and some muroid rodents (Wible, 1987).

In contrast to the model proposed by Wible (1987) for primitive eutherians, in *Archaeomeryx*, the sulcus for the internal carotid artery occupies the medial position. On the ventral side under the crista promontorii medioventralis, there is the sulcus medialis, probably, for this artery. According to MacIntyre (1972), the sulcus medialis provides passage for the medial ramus of the internal carotid artery. The sulcus medialis is reported in some primitive placentates and known in species with the trisulcate variety of the petrosal (MacIntyre, 1972). The medial position of the internal carotid artery is probably the primitive condition for mammals (Presley, 1979; Novacek, 1986). Such a position is observed in monotremes, marsupials, and some eutherians, including *Kennalestes* and *Asioryctes* (Novacek, 1992). Wible (1987) proposed that, in the primitive state, the internal carotid artery occupies an intermediate (indifferent) position on the promontorium and, in the advanced state, it is shifted either laterally or medially.

The sulcus of the inferior petrosal sinus vein (sulcus sini petrosi inferior) extends from the sulcus jugularis (foramen lacerum posterior) to the apex along the medial edge of the petrosal above the crista promontorii medioventralis.

The sulcus for the promontory artery is not observed on the surface of the promontorium. According to MacIntyre (1972), the promontory artery is the promontory ramus of the internal carotid artery (other than the internal carotid artery sensu Wible, 1987). Presley (1979) proposed that the promontory artery could be a laterally displaced internal carotid artery. The promontory sulcus is typical of many eutherians and observed in the ferungulate and unguiculate petrosal varieties from the Late Cretaceous Bug Creek, Montana. It is undeveloped in the marsupials *Didelphodon* and *Didelphis* (see MacIntyre, 1972; Cifelli, 1982) and some early placentates. *Lophiomeryx* lacks this sulcus, whereas in *Hypertragulus, Leptomeryx, Gelocus*, and Recent tragulids, it is present.

The anterior end of the petrosal (apex partis petrosae) of *Archaeomeryx* is two-pointed, with two projections and a shallow notch between them.

A primitively simple and low promontorium on the petrosal of *Archaeomeryx* almost entirely corresponds to the main whorl of the cochlea and occupies a considerable part of the ventral surface of the petrosal.

The fenestra cochleae (or fenestra rotundum) for the membrane tympanica secunda is medium-sized. It faces posterolaterally and is widely exposed ventrally. In the majority of tragulines, it is larger and exposed ventrally to a lesser extent.

Archaeomeryx has a primitive small and oval fenestra vestibuli (or fenestra ovalis). In *Protungulatum* and the majority of other tragulines, it is larger (Webb and Taylor, 1980, text-fig. 4).

The stapedial muscle fossa (fossa muscularis minor) is narrow. In *Archaeomeryx*, it occupies a primitive position behind the fenestrae vestibuli and cochleae, whereas in the majority of tragulines, including *Leptomeryx*, this fossa is displaced anteriorly. In *Protungulatum*, the stapedial muscle fossa lies behind the fenestra vestibuli.

The musculus tensor tympani fossa (fossa muscularis major) of *Archaeomeryx* is relatively small and rounded, with a weakly overhanging lateral wall. The fossa is located approximately opposite the middle of the promontorium somewhat anterior to the fenestra vestibuli, as in the petrosal from the Late Cretaceous of Montana. This position of the tensor tympani fossa is typical of *Gelocus*, although in this genus, the fossa is broader. In tragulids, the fossa is pocketed in the medial wall and placed more anteriorly. The increase in breadth and depth and anterior displacement of the fossa are among common trends in progressive mammalian evolution.

The medial edge of the petrosal of *Archaeomeryx* is primitively thick, as in *Lophiomeryx* and *Leptomeryx*. It has two crests: a relatively sharp ventromedial crest and a weak dorsomedial crest.

In other tragulines, the medial edge of the petrosal is thinner. Some higher ruminants retain a rather thick medial edge of the petrosal; in particular, this concerns the cervid *Pavlodaria*.

A primitive deep and broad subarcuate fossa (fossa subarcuata) for the flocculus of the cerebellum is observed in *Archaeomeryx* and most tragulines, except for *Gelocus*, in which the fossa is shallow. In extant tragulids, the posterior wall of this fossa has a pocketlike depression.

Archaeomeryx has a separate carotid foramen (foramen caroticum), which is not confluent with the posterior lacerate foramen (foramen jugulare). In the more advanced *Hypertragulus* and *Leptomeryx*, these foramina are confluent. In Recent tragulids, a separate median carotid foramen notches the wall of the bulla.

A well-pronounced fossa cerebellaris is typical of the petrosal of *Archaeomeryx*. It is placed above the meatus acusticus internus. The fossa is well developed in *Gelocus* (Webb and Taylor, 1980, text-fig. 5E). This fossa has not been found in the petrosal from the Late Cretaceous of Montana.

Another primitive feature of *Archaeomeryx* is the presence of the foramen stylomastoideum primitivum. Among tragulines, this foramen is preserved in *Lophiomeryx*. In addition, this foramen is reportedly present in *Prodremotherium* (Jehenne, 1977).

In the petrosal of *Archaeomeryx*, the tympanic process and the tympanohyal are unfused, as in primitive trisulcate pattern (MacIntyre, 1972). They form an almost complete ring around the foramen stylomastoideum primitivum.

The epitympanic recess (recessus epitympanicus) in the petrosal of *Archaeomeryx* lies lateral to the foramen of the canalis facialis, as in the petrosal from Montana. The same position of the epitympanic recess is observed in *Hypertragulus* and *Praetragulus*. In the majority of ruminants, the lateral wall of the epitympanic recess is formed by the squamosal (Van Kampen, 1904).

The canalis musculotubarius of *Archaeomeryx* is partially formed by the petrosal. In true ruminants, it is formed by the tympanicum and the basisphenoid. In ruminants, this canal contains the tensor of the velum palatini (musculus tensor veli palatini). The tendon of this muscle accompanies the auditory tube.

The mastoid process (processus mastoideus) of *Archaeomeryx* occupies a primitive lateral position rather than the occipital position, which is typical of the majority of ruminants; an exception is provided by hypertraguloids, tragulids, and *Lophiomeryx*. According to MacIntyre (1972), the lateral exposure of the mastoid is observed in the Cretaceous arctocyonids showing a primitive trisulcate variant of the petrosal. Among early ungulates, dichobunids and *Cainotherium* have their mastoids in the lateral position.

In the ontogeny of living tragulids, the mastoid is gradually narrowed and displaced posteriorly because of the posterior expansion of the squamosal. In juvenile *Tragulus* and *Hyemoschus*, the mastoid is relatively broader and occupies a more lateral position than in adults. In some adult *Hyemoschus aquaticus* (BMNH, no. 48.1314), the mastoid is rather broad and located in an intermediate position between the lateral and occipital ones (Vislobokova, 2001).

The mastoid process of *Archaeomeryx* expands ventrally and has a well-pronounced mastoid notch (incisura mastoidea) from which the digastric muscle (musculus digastricus) originates. Posteriorly, the base of the mastoid process meets the paraoccipital process of the occipital. A similar structure is typical of the genus *Lophiomeryx*. Novacek (1986) indicated that the deep sulcus for the digastric muscle on the mastoid process is a primitive eutherian state. In particular, this position remains in humans. In the majority of ruminants, the mastoid becomes the attachment area for the muscles moving the head and neck; therefore, it is displaced to the occipital surface.

The mastoid foramen (foramen mastoideum) is large. It is placed on the external surface of the mastoid close to the mastoid–squamosal suture but not in the occipitomastoid suture, which is observed in *Leptomeryx, Prodremotherium*, and higher ruminants.

Archaeomeryx has a primitive small tympanic region (pars tympanica). The long axis of the tympanic region is strongly oblique relative to the sagittal plane of skull and positioned at an angle of approximately 40° to the latter.

The auditory bulla (bulla tympanica) of *Archaeomeryx* is small, rugose, and noninflated. It projects ventrally only slightly lower than the postglenoid process does. In the ventral view, the auditory bulla covers only two-thirds of the lower surface of the petrosal; the latter is well seen between the basioccipital and the tympanic region.

The external acoustic meatus of *Archaeomeryx* is very short and only weakly developed. The external acoustic foramen (porus acusticus externus) is large, about 3 mm in diameter. It is approximately on the level with the epitympanic recess and the middle of the postglenoid process.

The stylohyoid vagina (vagina processus styloidei) is very shallow and extremely weakly developed. It is located on the posterolateral side of the auditory bulla and broadly open posteriorly. Among tragulids, approximately the same structure of the tympanic region is typical of *Lophiomeryx*. In all other ruminants, the tympanic region is more developed, the external acoustic meatus is longer and weaker inclined posteriorly, the axes of the auditory bulla and external auditory tube are usually noncoincident, and the stylohyoid vagina is deeper and, in the majority of advanced species, enclosed posteriorly. At the same time, in a number of species, including *Hypertragulus* and *Leptomeryx*, the auditory bulla remains relatively small and is not pressed to the basioccipital.

Parietal

The parietal (os parietale) forms the upper and lateral sides of the skull roof. It lies between the frontal, occipital, squamosal, and alisphenoid. The parietals very early fused with the interparietal.

Short temporal crests (cristae temporalis), which continue the frontal crests (cristae frontalis), are fused at the parietal tuber near the coronal suture to form the sagittal crest. A long sagittal crest (crista sagittalis) extends along the sagittal edge of the bone and is elevated over the entire length; in the posterior third, it is especially high. The temporal and sagittal crests serve for the attachment of the temporal fascicles (fascea temporalis) of a strong temporal muscle.

The parietal foramina are medium-sized. They lie lateral to the sagittal crest, close to the latter, at approximately two-thirds of the parietal length. In leptomerycids, the parietal foramina remain at a short distance from the sagittal crest. In the majority of other ruminants, they are placed at a larger distance from the sagittal crest, owing to the enlargement of the skull and an decrease in the attachment area for the temporal muscle.

The anterior (frontal) edge (margo frontalis) of the parietal forms a posteriorly curved coronal suture (sutura coronoidea) with the temporal edge of the frontal.

The posterior (occipital) edge (margo occipitalis) contacts with the occipital by the lambdoid suture (sutura lambdoidea). This suture is weakly posteriorly convex at the sagittal crest.

The inferior (squamosal) edge (margo squamosus) is arched and has a narrow notch at a level of the mastoid process.

Frontal

The frontal (os frontale) is relatively short. The coronal suture lies just posterior to the posterior orbital margin. The suture weakly posteriorly curves. The posterior edge of the nasofrontal suture (sutura nasofrontalis) closely approaches the midlength of the orbit. The nasofrontal suture is serrated. At the sagittal suture, it forms a V-shaped projection between the nasals. In lateral view, it is strongly oblique and directed anterolaterally to adjoin a short frontomaxillary suture (sutura frontomaxillaris).

The external surface (facies externa) of the frontal is weakly concaved, almost flat. The frontal tuber (tuber frontale) is undeveloped. The frontal suture (sutura frontalis) is not elevated.

The supraorbital foramen occupies a primitive posterior position behind the line connecting the orbital centers. The foramen is placed at the posterior end of the supraoccipital sulcus.

The supraorbital sulci are lyriform and approach each other toward the nasal edge (margo nasalis). They cross the nasofrontal suture and extend onto the external surface of the nasals, as in *Hyemoschus* and *Sus*.

The zygomatic process (processus zygomaticus) of the frontal contacts the frontal process of the jugal.

The orbital surface (facies orbitalis) is separated from the temporal region by the orbitotemporal crest (crista orbitotemporalis). The orbital surface has a small ethmoidal notch (incisura ethmoidalis).

The inferior and posterior edges of the orbital region of the frontal contacts with the orbitosphenoid and alisphenoid, respectively. Anteriorly, the orbital region of the frontal adjoins the lacrimal.

The frontal surface of the frontals is separated from the temporal surface (facies temporalis) by a well-developed temporal crest (crista temporalis). Anteriorly, the temporal crests weakly curve and closely approach the posterior orbital margin. Posteriorly, they converge to the sagittal crest. Behind the supraorbital edge, the temporal crests have a small arched projection, which is directed backwards.

Vomer

The vomer is very low. It forms the posterior region of the nasal plate. Posteroinferiorly, the vomer isolates the openings of the nasal cavities (choanae). The wings of the vomer are small and adjoin the presphenoid.

FACIAL BONES

Lacrimal

The lacrimal (os lacrimale) of *Archaeomeryx* has a primitive short facial process and a small orbital process. The lacrimal foramen (foramen lacrimale) is single and lies inside the orbit at the anterior orbital rim close to the lacrimozygomatic suture (sutura lacrimozygomatica).

The facial process of the lacrimal of *Archaeomeryx* is triangular, short, and low. The anterior edge of the lacrimal only slightly projects anteriorly beyond the anterior orbital rim. The frontolacrimal suture (sutura frontolacrimalis) is placed inferior to the supraorbital rim. The lacrimomaxillary suture (sutura lacrimomaxillaris) located on the facial process is very short. In the course of ruminant evolution, the facial process of the lacrimal was substantially elongated. In hypertraguloids, in addition to this, the posterior region of the frontolacrimal suture, which reaches the orbit, is markedly displaced toward the skull roof.

In posterior view, the orbital face of the lacrimal is irregularly rhomboid in shape. It only slightly expands inferiorly and has a small pit for the inferior oblique muscle of the eye at the inferior corner near the lacrimomaxillary suture just above the posterior opening of the infraorbital canal (canalis infraorbitalis).

The orbital process of the lacrimal and the alveolar process of the maxilla lack contacts with one another. With respect to this feature, *Archaeomeryx* is similar to *Lophiomeryx, Prodremotherium*, and *Tragulus* and differs from all other ruminants.

Within tragulines, the same structural pattern of the lacrimal is characteristic of *Lophiomeryx*. This lacrimal pattern resembles that of leptictids and probably shows the primitive eutherian state (Novacek, 1986).
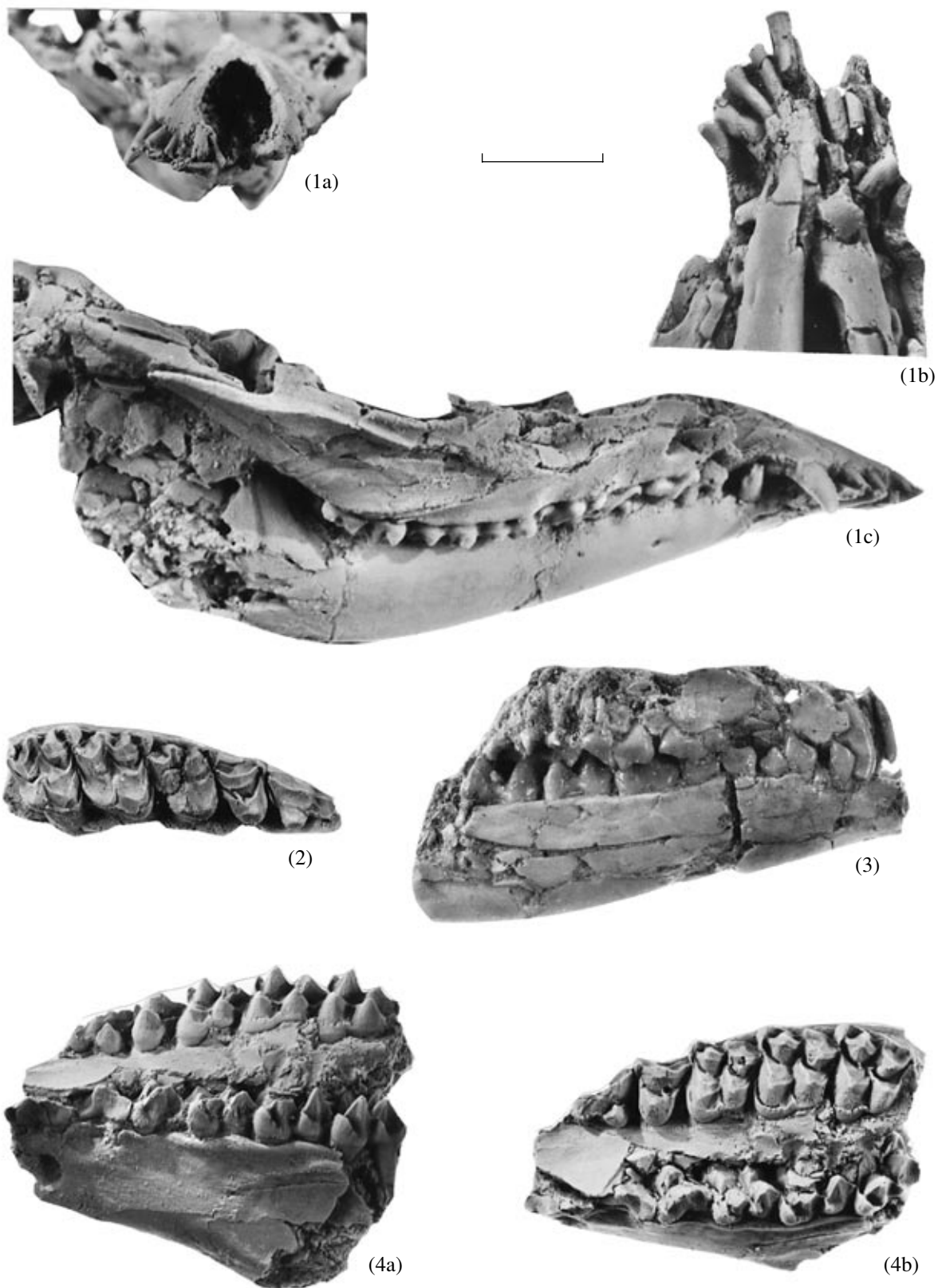
(1a)

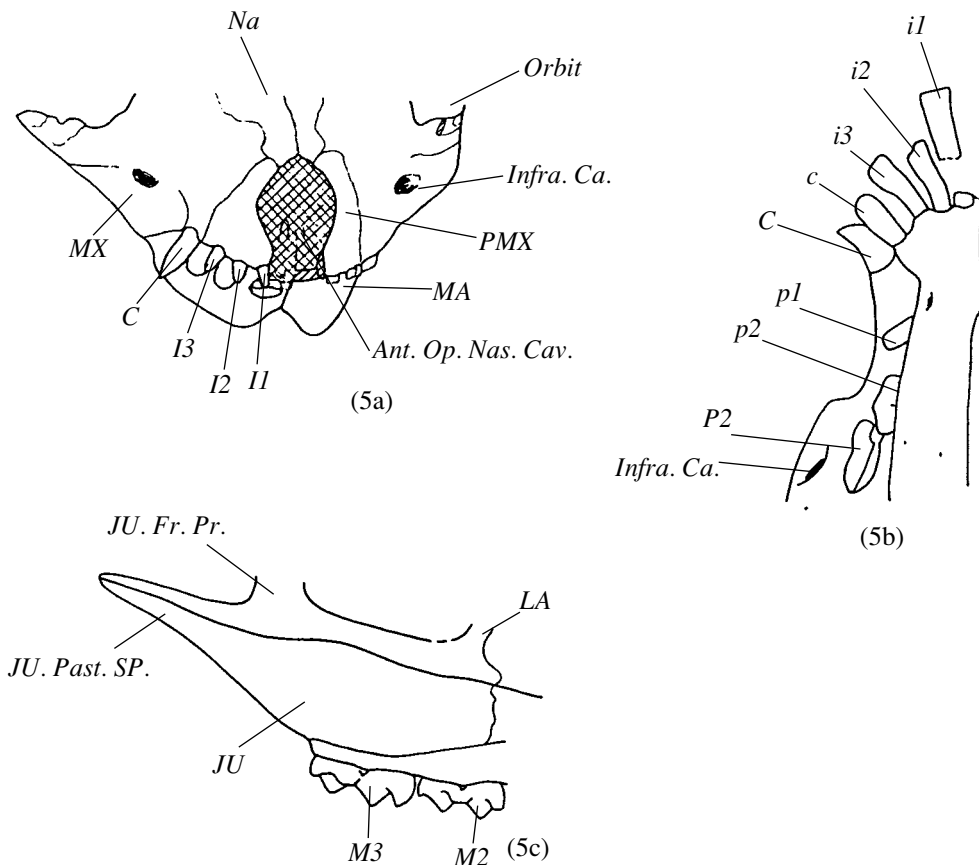(1b)

(1c)

(2)

(3)

(4a)

(4b)

Fig. 12. (Top)

Fig. 12. Complete and fragmentary skulls of *Archaeomeryx*: (1) PIN, no. 2198/154: (a) anterior, (b) ventral, and (c) lateral views; (2) fragmentary facial region with P3–M3, PIN, no. 2198/163, ventral view; (3) fragmentary facial region, PIN, no. 2198/155, lateral view; and (4) fragmentary facial region with P3–M3, PIN, no. 2198/168: (a) lateral and (b) ventral views. Designations: (*Ant. Op. Nas. Cav.*) anterior opening of nasal cavity; (*C*) upper canine; (*c*) lower canine; (*I1, I2, I3*) first, second, and third upper incisors; (*i1, i2, i3*) first, second, and third lower incisors; (*Infra. Ca.*) infraorbital canal; (*JU*) jugal; (*JU. Fr. Pr.*) frontal process of jugal; (*JU. Post. Sp.*) posterior spine of jugal; (*LA*) lacrimal; (*MA*) mandible; (*MX*) maxilla; (*PMX*) premaxilla; (*NA*) nasal; (*M2, M3*) second and third upper molars; (*P2*) second upper premolar; and (*p1, p2*) second and third lower premolars. Scale bar, 1 cm.

Nasal

The nasal (os nasale) of *Archaeomeryx* is primitively long, dorsally convex, and relatively narrow; it is narrowed posteriorly and anteriorly and weakly widened at the contact between the maxilla and the frontal. A similar structure of the nasal is preserved in *Hypertragulus*; however, in this genus, it is somewhat more advanced. In the course of ruminant evolution, the nasal decreased in length and became wider in the posterior region and narrower in the anterior region.

The tapering posterior end of the nasal closely approaches the line connecting the orbital centers. The anterior edges of the nasal border the anterior opening of the nasal cavity and do not protrude above this opening.

In all other ruminants (including *Hypertragulus*) and in *Cainotherium*, the posterior edges of the nasals are displaced orally and the anterior edges project to a greater or lesser extent.

The anterior edge of the nasals of *Archaeomeryx* has a medial concavity, which is also present in *Hypertragulus*. In *Archaeomeryx*, the anterior edge of the nasal and the medial edge of the premaxilla form a weakly concave lateral wall of the anterior opening of the nasal cavity. In the dorsal view, the opening is ovoid in outline, with the top directed backwards.

On the facial surface of the nasal, there is a clear sulcus, which is an extension of the supraorbital sulcus located on the frontal, as in *Sus*.

Maxilla

Archaeomeryx has a primitive low and short maxilla; the ventral edge of the bone is almost straight, only slightly curves dorsally between the canine and the premolars, and is ventrally inclined in the anterior region.

The facial tuber (tuber faciale) is very weak. It is placed ahead of the anterior border of the jugal above P4 and M1 and serves for the attachment of the profound longitudinal portion of the buccal muscle (pars bucallis m. bucinator) and for the tendon of the superficial portion of the masseteric muscle (pars superficialis m. masseter). In the course of ruminant evolution, the tuber substantially increased in size.
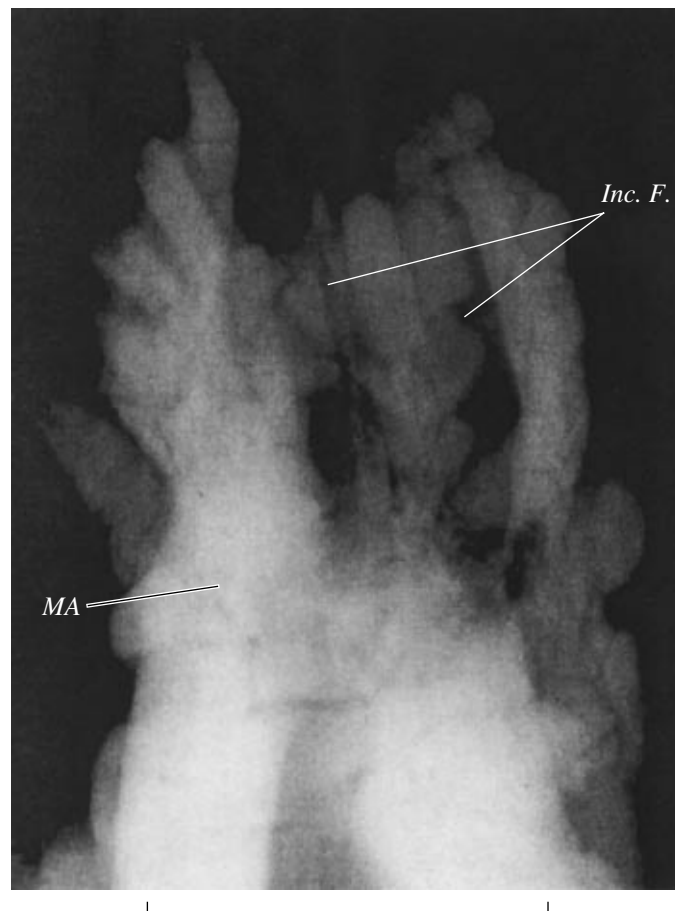
Fig. 13. Facial region of skull of *Archaeomeryx*, PIN, no. 2198/154, examined by x-rays. Designations: (*Inc. F.*) incisive foramen and (*MA*) mandible. Scale bar, 1 cm.

The anterior opening of the infraorbital canal is in a primitive low position. It is medium-sized and lies on a level with the posterior part of P2. The infraorbital canal is very long and, judging from an x-ray photograph, very weakly curved.

Premaxilla

Archaeomeryx has a primitive low and short premaxilla (os praemaxilla or incisivum) with a long and narrow posterodorsal (nasal) process; posteriorly, the latter overlaps the anterior opening of the nasal cavity (Figs. 3, 7, 12). The contact with the nasal is short.

This premaxillary pattern could be inherited from primitive eutherians. In almost all ruminants, the posterodorsal processes of the premaxillae are displaced aside, because the anterior opening of the nasal cavity is enlarged and the nasals become longer and protrude anteriorly between the premaxillae.

In addition to *Archaeomeryx*, only *Hypertragulus* has a premaxillary pattern that resembles the primitive state. However, in the latter genus, the posterodorsal processes of the maxillae are positioned at a greater distance than in *Archaeomeryx*.

In the course of ruminant evolution, the posterodorsal process of the maxilla changed in shape; it elongated and decreased in transverse measurements. The contact between the premaxilla and the nasal became longer. The posterior corner of the posterodorsal processes gradually became wedged in between the nasal and the maxilla. In some ruminants (e.g., in *Hyemoschus* and *Alces alces*), the premaxilla and the nasal have lost their contact.

The anterior edge of the premaxilla is slightly inclined posteriorly in *Archaeomeryx*. In other ruminants, the inclination becomes greater, because both the alveolar process of the premaxilla and the anterior opening of the nasal cavity are elongated.

The alveolar process (processus alveolaris) of *Archaeomeryx* has an arched anterior edge. Medially, it strongly anteriorly projects. The interalveolar plates are almost equal in width to the dental alveoli. The incisor alveoli are almost equal in width to each other; the first alveolus opens anteriorly, the second faces anterolaterally, and the third faces laterally. The third alveolus is located close to the premaxillary–maxillary suture. Among ruminants, the presence of the upper incisor alveoli is also recorded in *Hypertragulus* and *Leptom-*

eryx (Scott, 1940); however, it remains uncertain whether or not the upper incisors actually present in these genera, as in *Archaeomeryx*.

The palatine process (facies palatina) of the premaxilla has small and elongated incisor foramina, which are also observed on the palatine (Fig. 13).

Palatine

The palatine (os palatinum) of *Archaeomeryx* forms a large part of the base and the lateral wall of the nasal cavity.

The horizontal plate (lamina horizontalis) of the palatine of *Archaeomeryx* is flat and spreads anteriorly to the P4 level, as in many tragulines, excluding the most advanced in this character *Leptomeryx* and *Hyemoschus*, in which this plate terminates on a level with M1. Within tragulines, the greatest anterior extension of the horizontal plate is probably observed in *Simimeryx*, the anterior palatine foramina of which are placed between P3.

In *Archaeomeryx*, the horizontal plates of the palatines lack anterior expansion; i.e., they are primitive in this respect. They form a narrow and rounded anterior projection between the maxillae. In a more derived state, in particular, characteristic of *Leptomeryx* and *Hyemoschus*, the anterior palatine projection expands; the anterior edges of the horizontal plates of the palatine form an almost straight transverse suture (sutura palatina transversa), which is perpendicular to the sagittal plane of skull.

The horizontal plates of the palatines of *Archaeomeryx* have small palatine foramina at the anterior edge of the palatine between M1 and large foramina on a level with M2. They lead to the grater palatine canal (canalis palatinus major). *Lophiomeryx* and *Tragulus*, as with the majority of mammals, have two pairs of the palatine foramina. The small and large palatine foramina (foramina palatina minor et majus) occupy anterior (between M1) and middle (between M2) positions, respectively. However, a large number of tragulines, including *Hypertragulus, Leptomeryx, Prodremotherium*, and *Hyemoschus*, have only the middle palatine foramen located between M2.

The perpendicular plate (lamina perpendicularis) of the palatine of *Archaeomeryx*, which is bordered by the pterygoid process (processus pterygoideus) and the maxilla, contains the opening of the major palatine canal.

The upper margin of the perpendicular plate of the palatine has the orbital and sphenoid processed (pr. orbitalis et sphenoidalis), which are isolated from each other by the sphenopalatine notch (incisure sphenopalatina). This notch borders the sphenopalatine foramen. The orbital process adjoins the orbital portion of the maxilla.

Jugal

Archaeomeryx has a primitive low and lowly positioned jugal (os zygomaticum). The lateral surface (facies lateralis) of the bone is not widened. The jugal virtually does not extend anteriorly to the anterior orbital rim and has a long posterior spine. Under the infraorbital rim, the jugal almost reaches M3. The temporal process originating from the posterior corner of the jugal is long. It is connected to the zygomatic process of the squamosal by a diagonal suture, which obliquely extends from almost the anteriormost point of the dorsal edge of the zygomatic arch near the frontal process of the jugal to the ventral edge of the zygomatic arch near the base of the zygomatic process of the squamosal.

In all other tragulines (including *Leptomeryx, Hypertragulus, Prodremotherium*, and *Lophiomeryx*) and in tragulids, the inferior border of the jugal under the infraorbital rim is located much higher; the jugal and the maxilla are almost equal in height at this point. In the course of the evolution of higher ruminants, the jugal and maxilla increased in height; at the same time, the infraorbital portions of these bones remained approximately equal in height (Vislobokova, 2001).

In lateral view, the zygomaticomaxillary suture is anterosuperiorly inclined approximately to the level of the anterior half of M2; at this point, it abruptly curves, extends almost vertically, and anteroinferiorly outlines the dorsal process of the jugal. The anterior dorsal process of the jugal of *Archaeomeryx* is primitively short and narrow. The process terminates at the infraorbital rim short of reaching the vertical line, which descends from the anterior point of the orbit. Superiorly, the process adjoins the lacrimal. In almost all ruminants, except for *Lophiomeryx* and *Prodremotherium*, the anterior edge of the dorsal process of the jugal extends ahead of the anterior point of the orbit. In higher ruminants, this process often reaches the anterior edge of the lacrimal.

The frontal process of the jugal of *Archaeomeryx* is relatively short, as in many ruminants. It is connected to the jugal process of the frontal by the zygomaticofrontal suture (sutura frontozygomatica), which is placed at approximately the midlength of the postorbital bar. Only Recent tragulids and the genus *Bachitherium* have relatively long frontal processes.

In *Archaeomeryx*, the facial ridge for the masseter (musculus massetericus) is prominent but short. The area of its origin is restricted to a narrow lateral surface of a weakly expanded jugal. In the course of ruminant evolution, the facial ridge gradually became larger and longer.

The orbital face of the jugal of *Archaeomeryx* is strongly inclined inferiomedially.

The temporal surface of the jugal is narrow and divided into two facets. The first facet is located on the posterior side of the frontal process, and the second is on the inner side of the anteroinferior part of the zygomatic arch.
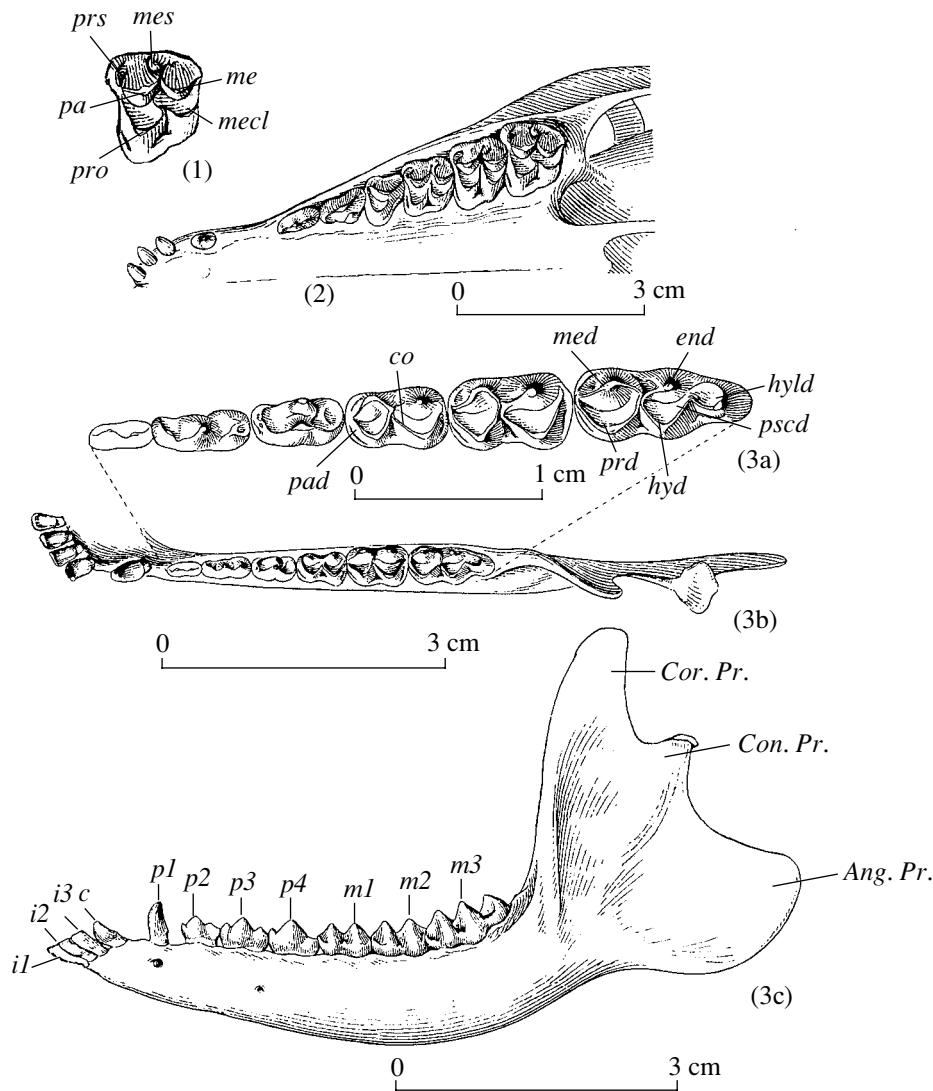
Fig. 14. Dentition of *Archaeomeryx*: (1) third upper molar; (2) upper dentition; (3) lower jaw: (a) dentition and (b) occlusal and (c) lateral views. Designations: (*Ang. Pr.*) angular process; (*Ant. Ment. F.*) anterior mental foramen; (*Con. Pr.*) condylar process; (*Cor. Pr.*) coronoid process; (*i1, i2, i3*) first, second, and third lower incisors; (*m1, m2, m3*) first, second, and third lower molars; (*p1, p2, p3, p4*) first, second, third, and fourth lower premolars; upper molar elements: (*me*) metacone, (*mecl*) metaconule, (*mes*) mesostyle, (*pa*) paracone, (*prs*) parastyle, and (*pro*) protocone; lower molar elements: (*co*) cristid oblique, (*end*) entoconid, (*hyd*) hypoconid, (*hyld*) hypoconulid, (*med*) metaconid, (*pad*) paracristid, (*prd*) protoconid, and (*pscd*) postcristid. Scale bar, 1 cm.

Mandible

The lower jaw (mandibula) of *Archaeomeryx* preserves many primitive structural characteristics resembling those of *Protungulatum*.

The body of the mandible (corpus mandibulae) is low and weakly narrows anteriorly, the alveolar edge gently curves, and the inferior edge is strongly convex (Figs. 12, 14, 15; Table 3). The alveolar edge is weakly concave in the cheek region and anteroinferiorly inclined in the incisor region. The most concaved part of the inferior edge of the mandible lies under m3. The diastemata between p1 and p2 and the canine are very short, usually not longer than the width of a very small

p1. In all other ruminants, the diastemata are longer owing to the elongation of the facial region of skull and reduction of p1.

The mental foramina (foramina mentalia) occupy the posterior position. A small anterior mental foramen is under p1, and a very small posterior mental foramen is under p3. As the diastemata become longer in ruminants, the anterior mental foramen is displaced in a more anterior position.

The symphysis of *Archaeomeryx* is relatively short and extends to p1. In all other ruminants, it terminates short of reaching p2.

The inner surface of the mandibular body has small fossae for the digastric muscle (fossa digastrica).

Table 3. Measurements of mandible of *Archaeomeryx*

No.	Measurements	N	Min–Max	M	AMNH 20322 (Colbert, 1941)
1	Length	22	68–82	74	70
2	Body height under p2	23	7–9	8.1	9
3	Body height under m3	25	9.5–12	–	11

The mandibular ramus (ramus mandibulae) is short and low.

The angular process (processus angularis) is narrow, rounded, and strongly posteroinferiorly projects. It resembles in structure the angular process of *Protungulatum*. A similar structure is observed in *Lophiomeryx* and some hypertraguloids. In other ruminants, the angular process is wider and more rounded and the mandibular angle (angulus mandibulae) projects posteriorly to a lesser extent.

The lateral surface of the angular process bears a shallow masseteric fossa (fossa masseterica) for the pars profunda m. masseter and the masseteric tuberosity for the pars superficialis m. masseter.

On the medial side of the angular process, there is a distinct pterygoid fossa (fossa pterygoidea) for the lateral pterygoid muscle and the tuberosity for the sternomandibular muscle (tuberositas m. sternomandibularis).

The coronoid process (processus coronoideus) is high, strongly dorsally narrowed, and possesses a convex anterior edge. The latter is weakly inclined relative to the tooth row axis. A deep fossa for the temporal muscle is present on the lateral surface of the coronoid process. Somewhat below the fossa, there is a large mandibular foramen with a small inside projection. The foramen leads to the mandibular canal (canalis mandibularis) for nerves and vessels and opens by the mental foramina on the surface of the mandibular body. In ruminants, as the temporal muscle decreases in size, the coronoid process becomes shorter and the anterior border of the coronoid process becomes less posteriorly inclined.

The condylar process (processus condylaris) is positioned not very high with reference to the tooth row, as those of the most primitive tragulines (*Lophiomeryx, Simimeryx,* and *Hypertragulus*). In all other ruminants, the condylar process is positioned higher because of the development of rumination. Among tragulines, the highest position of the condylar process is observed in Recent tragulids. The condylar process of *Archaeomeryx* is placed far from m3. The distance from the posterior edge of m3 to the posterior edge of the condylar process is greater than the m1–m3 length, composing about 26% of the mandibular length. In other ruminants, this distance is shorter than the m1–m3 length and the mean value of the index is lower.

The mandibular head (caput mandibulae) is narrow, weakly convex, and beanlike in outline. The articular surface is weakly oblique with reference to the mandibular ramus and inclined somewhat posteroinferiorly.

The mandibular neck (collum mandibulae) is weakly developed. The mandibular notch (incisura mandibulae) is shallow. Its inferior edge extends directly upwards from the mandibular head; however, in several specimens (e.g., PIN, no. 2198/149), it is weakly concave just anterior to the head.

DENTITION

In the youngest individuals of *Archaeomeryx* from the Ula Usu locality, all deciduous teeth are already replaced. Different stages of tooth wear are present.

Incisors

In contrast to other ruminants, *Archaeomeryx* has a complete set of incisors (Figs. 5, 7, 12, 14, 16).

The upper incisors are reduced and do not form a closed row. They are small, thin, pointed, and positioned at a short distance from each other (Fig. 7). The incisors are strongly procumbent. Their crowns are labially convex and weakly flattened lingually.

The lower incisors are larger than the upper incisors. They are also strongly procumbent but spatulate and have almost symmetrical crowns. The incisors are arranged in a fan-shaped pattern and do not form a closed row, which is typical of other ruminants. The first lower incisors are almost straight. The outer edges of the second and third lower incisors are weakly pulled outward. The incisors decrease in size from the central to the external teeth. The lingual surfaces of the incisors have a weak central elevation, thin grooves along the crown sides, and a weak heel at the base.

Canines

The upper canines are small and anterolaterally procumbent. The anterior edge of the canines are rounded, and the posterior edges are sharp (Fig. 12). As the jaws are closed, the upper canine fits in between the lower canine and the first lower premolar.

The lower canines are incisiform; however, they are larger than the incisors (Fig. 14). The lower canine is anterolaterally directed. Its labial surface is convex, and the lingual surface is weakly concave. The anterior
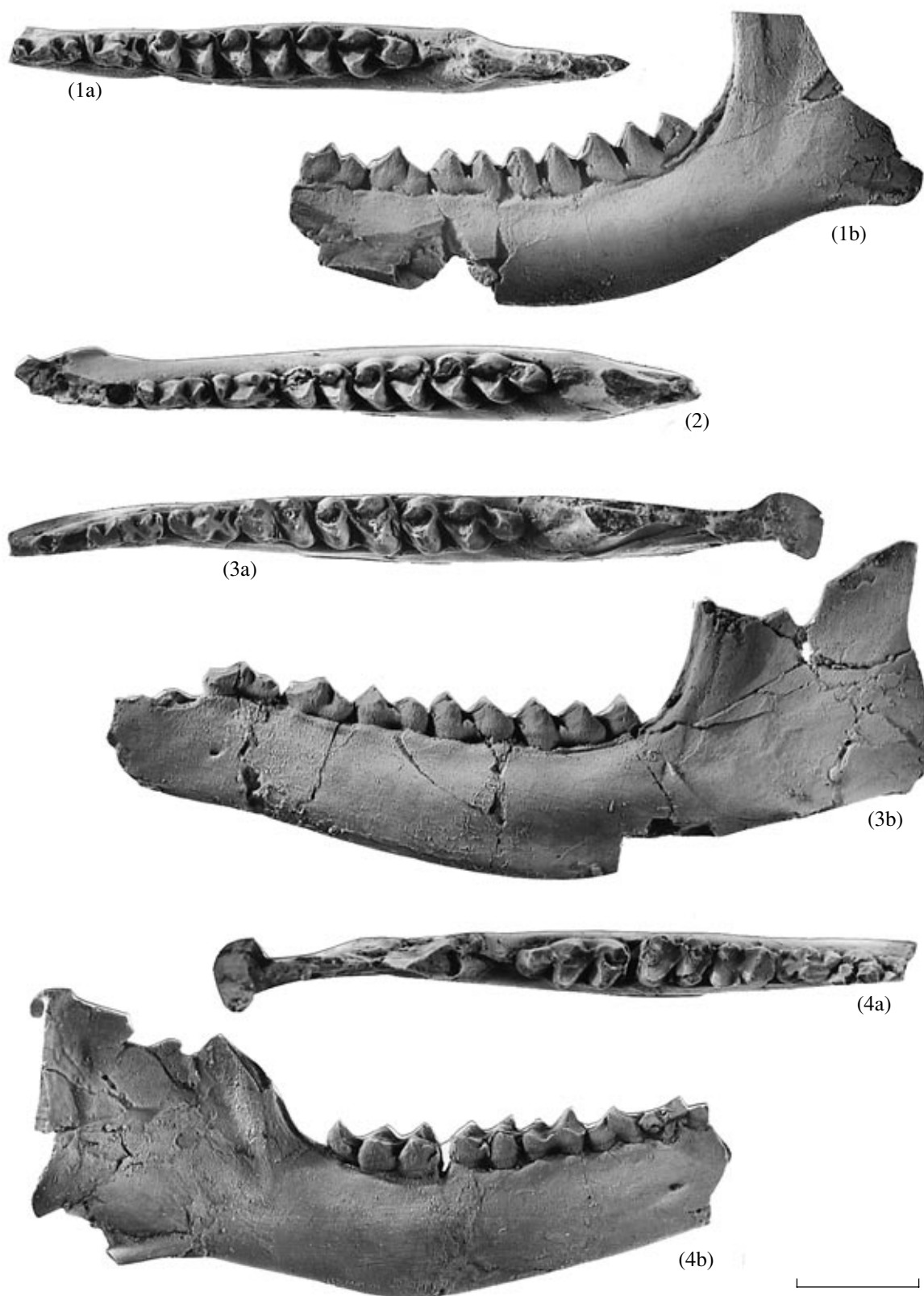
Fig. 15. Mandibles of *Archaeomeryx*: (1) PIN, no. 2198/162; (2) PIN, no. 2198/167; (3) PIN, no. 2198/152; and (4) PIN, no. 2198/163: (a) occlusal surface and (b) lateral view. Scale bar, 1 cm.

Table 4. Measurements and indices of the upper dentition of *Archaeomeryx*

No.	Measurements and indices	N	Min–Max	M	AMNH 20322 (Colbert, 1941)
1	Length of I–M3	19	43–56	50.1	–
2	Length of P2–M3	22	33–37.5	43.1	–
3	Length of P2–P4	22	14–18	15.9	16.5
4	Length of M1–M3	27	17–20	18.3	18
5	Index P2–P4/M1–M3	22	0.74–0.95	0.86	0.86
6	Width of I1	4	0.5–1.2	0.8	–
7	Width of I2	7	0.8–1.5	1.1	1.1
8	Width of I3	8	1.0–1.5	1.2	1.3
9	Length of C	13	2.2–2.5	2.2	2.2
10	Length of P2	23	4.0–6.5	5.3	5.9
11	Width of P2	4	2.0–2.9	2.5	2.9
12	Length of P3	28	5.0–6.3	5.6	6.3
13	Width of P3	10	2.5–4.0	3.4	3.5
14	Length of P4	29	4.0–6.5	4.4	4.5
15	Width of P4	8	4.5–5.1	5.0	5.1
16	Length of M1	29	4.5–5.5	5.4	5.0
17	Width of M1	8	4.5–6.2	6.0	6.0
18	Length of M2	22	5.0–6.0	5.7	5.5
19	Width of M2	8	6.0–7.0	7.0	7.0
20	Length of M3	29	6.0–7.5	6.7	6.0
21	Width of M3	8	6.5–7.1	7.0	7.1

edge of the crown is convex, and the posterior edge is concave with the posterosuperior angle pulled outward. As the jaws are closed, the lower canine is placed between the upper canine and the third incisor.

In *Archaeomeryx*, the first lower premolar functioned as the lower canine. In many tragulines and all higher ruminants, the lower canines are functionally included in the incisor row.

Premolars

Archaeomeryx lacks the first upper premolar (P1), as the majority of tragulines and all higher ruminants.

The premolar crowns are brachyodont and inflated at the base. The length of the premolar row (P2–P4) widely varies relative to the length of the molar row (M1–M3). The index of the relative length of the upper premolar row is 0.74–0.95 and that of the lower premolar row is 0.87–0.97 (Tables 4, 5).

P2 is double-rooted, triangular in outline, and non-molarized. The tooth is simple and has three labial cusps. The paracone is a prominent but low cusp located close to the anterior edge of the crown. The anterior and posterior cusps are approximately equal in height. The inferior margin of the tooth is trenchant.

P3 and P4 have three roots and a lingual cusp (protocone) in addition to tree labial cusps. The structure of the outer cusps is similar to a simple tritubercular pattern, as in P2. In unworn P3, the paracone is prominent and pointed, the parastyle is very strong, and the metastyle is strongly pulled outward and backward. The protocone lies on a perpendicular to the middle of the long axis of the tooth. This axis is inclined with reference to the tooth row; therefore, the protocone seems to be displaced backward to the posterolingual angle of the crown. In unworn teeth, the protocone is pointed. The protocone base is semicircular in outline. The protocone is not connected to the paracone by crests. The anterior edge of the protocone does not project anteriorly beyond the middle of the crown. The posterior surface of the crown between the protocone and the metastyle is concave.

P4 is molarized and has well-developed labial and lingual crescents, as those of all ruminants. The P4 crown is almost symmetrical with the metastyle weakly pulled backward and outward. The parastyle is enlarged. The posterior wing of the protocone has a spur (small fold). The anterior wing of the protocone and the parastyle are confluent. The posterior wing of the protocone and the metastyle remain unfused even in worn teeth. The cingulum is well developed.

Table 5. Measurements and indices of the lower dentition of *Archaeomeryx*

No.	Measurements and indices	N	Min–Max	M	AMNH 20322 (Colbert, 1941)
1	Length of p1–m3	19	34.0–43.0	–	–
2	Length of p1–p4	21	14.0–21.0	19.0	19.0
3	Length of p2–p4	6	15.3–16.8	–	–
4	Length of m1–m3	27	19.0–22.5	21.1	22.5
5	Index p1–p4/m1–m3	6	0.87–0.97	0.91	–
6	Index p2–p4/m1–m3	6	0.71–0.81	0.75	–
7	Width of i1	15	1.5–2	1.9	2
8	Width of i2	17	1.0–2.5	1.6	1.8
9	Width of i3	16	1.5–2	1.7	1.8
10	Length of c	17	2.0–2.5	2.2	2.1
11	Length of p1	17	2.0–2.8	2.3	2.3
12	Width of p1	2	1.2–1.5	1.3	–
13	Length of p2	26	4.0–5.5	4.6	5
14	Width of p2	5	2	2	–
15	Length of p3	27	4.5–6.2	5.1	6.2
16	Width of p3	9	2.2–2.5	2.3	–
17	Length of p4	27	4.0–5.5	5.5	5.6
18	Width of p4	9	2.5–3	2.7	–
19	Length of m1	29	5.0–6.0	5.3	5.8
20	Width of m1	11	3.0–4.0	3.5	–
21	Length of m2	29	5.2–6.2	5.9	6.1
22	Width of m2	11	3.5–4.5	4.3	–
23	Length of m3	29	7.0–10	9.3	10.0
24	Width of m3	11	4.0–4.2	4	–
25	Length of heel of m3	17	2.5–3.0	2.7	–

The first lower premolar (p1) is small, unicusped, and single-rooted. It is high but lower than those of hypertraguloids. In some individuals, the occlusion of the upper canine and the first lower premolar is complete (PIN, no. 2198). As the jaws occlude, the posterior edge of the upper canine closely adjoins the anterior edge of the first lower premolar. The conical protocone of the first lower premolar rests posteriorly against the upper canine base. Such an occlusion forms a secant pattern typical of many mammals.

The other lower premolars are double-rooted and elongated. The second lower premolar is approximately three-fourths as long as p3 and p4 and two-thirds as wide as p4. The third lower premolar is equal in length to the fourth premolar or slightly shorter than the latter. The second and third lower premolars are extremely weakly molarized and remain similar in structure to the tritubercular pattern. The protoconid is closer to the anterior edge of the crown than to the posterior edge. The paraconid is higher than the hypoconid. The second lower premolar is tree-cusped with a relatively large protoconid and smaller paraconid and hypoconid.

The third lower premolar consists of four cusps. The entoconid is added to the three main cusps.

The fourth lower premolar is five-cusped. The metaconid is located lingual to the protoconid; it is lower than the protoconid, conical, and weakly buccolingually flattened. As the tooth is worn, the base of the metaconid weakly expands in anteroposterior direction; however, it remains unfused with the anterior and posterior cusps. The wings of the entoconid and hypoconid are almost perpendicular to the long axis of the crown, being only slightly turned backward. They do not form a lingually enclosed valley. The paraconid is strongly enlarged.

Molars

The molars are brachyodont. The upper molars are obliquely oriented and increase in size from M1 to M3. A complete set of four principal cusps (paracone, metacone, protocone, and metaconule) is present; the protocone and metacone are positioned anterior to the para-

cone and metaconule (Figs. 12, 14). On worn teeth, the cusps form weak crescents. On unworn teeth, the cusps are low, pointed, and the anterior cusps are higher than the posteriors cusps. The protocone is developed to a greater extent than the metaconule, especially in M3. In a worn tooth, the outer crescents are higher and narrower than the inner crescents, the anterior crescents are higher than the posterior crescents, the valleys are very shallow, and the crescent of the protocone is most developed.

The crowns of the upper molars are narrowed posteriorly, expanded labially, and have strongly projecting styles. The crown of M3 is especially strongly narrowed posteriorly. The parastyle is very strong and shaped into a posteriorly curving fold. The mesostyle is present but developed to a much lesser extent than the parastyle. The parastyle and mesostyle are low and strongly widened at the crown base. On the occlusal surface of weakly worn teeth, the mesostyle is almost indistinguishable; on strongly worn teeth, it clearly projects buccally. The pillar of the paracone is enlarged, whereas the pillar of the metacone is poorly pronounced and very thin. The fold of the protocone is developed. This fold is preserved in early cervoids and giraffids. In *Archaeomeryx*, the lingual side of the crowns bears a strong cingulum, which is particularly well developed at the base of the protocone.

The lower molars increase in size from m1 to m3 (Figs. 14, 15). The tooth crowns are inflated at the base and become much narrower toward the occlusal surface. The crowns of m1 and m2 are posteriorly widened, and the buccolingual diameter of the posterior lobe of the tooth is slightly larger than that of the anterior lobe. The m3 crown gradually narrows posteriorly. The first and second lower molars are four-cusped. The third lower molar is five-cusped and has a well-developed hypoconulid. The conids of unworn teeth are pointed. On worn teeth, they form weak crescents. The metaconid and protoconid are higher than the hypoconid. The outer crescents are better developed than the inner crescents. The anterior wing of the metaconid and the posterior wing of the entoconid are short. The anterior wing of the metaconid is weakly inclined outward. On weakly worn teeth, the anterior valley is open anteriorly; the posterior valley is open anteriorly, and, on the lingual side, it is open posteriorly. The ectostylid between the protoconid and hypoconid is low and pillarlike or flattened. The hypoconulid is long, only slightly shorter than one-third of the tooth length. The anterior wing of the hypoconid (cristid oblique) is short. It is directed toward the valley between the metaconid and the protoconid. On weakly and moderately worn teeth, the cristid oblique is not confluent with the wings of the protoconid and entoconid and does not close anteriorly the posterior (second) valley. On unworn m1 and m2, the posterior wing of the protoconid (protocristid) virtually lacks posterior inclination and positioned almost perpendicular to the long (anteroposterior) tooth axis. The anterior wing of the protoconid

(paracristid) and the anterior wing of the hypoconid retain clear anterior inclination. On the buccal side of the lower molars, the cingulum is well developed.

DIASTEMATA

Archaeomeryx differs from all known ruminants by the primitive weakly developed diastemata. It has three diastemata: one in the maxilla and two in the mandible.

The longest diastemata, between C and P2, is shorter than the sum of P2 and P3 lengths. The C–P2 diastema is only slightly longer (by 1 or 2 mm) than the space required for the placement of the first premolar in this area. The C–P2 diastema is as long as p1 plus a piece of p2, which is placed at a very short distance from p1. As the jaws occlude, the protocone of p2 rests on the posterior edge of the maxillary diastema and p1 fits into the area a little posterior to the upper canine (Fig. 12).

The p1–c diastema corresponds in length to the transverse diameter of a small upper canine, which fits into this space as the jaws occlude.

The diastema between p1 and p2 is shorter than the other two diastemata and shorter than the width of the p1 root.

ENAMEL ULTRASTRUCTURE

The enamel ultrastructure of molars of *Archaeomeryx* is primitive and apparently similar to the initial type, which is presumed in a hypothetical basal group of the earliest ruminants.

Archaeomeryx has a simple radial enamel, which covers rather low tooth crowns (Fig. 16). The wear surface of molars coincides very closely with the transverse section of the prisms. In this plane, the enamel of *Archaeomeryx* consists of large arcade-shaped prisms, which lie at equal distances from each other and do not form chains. The density of prisms is approximately 32000 per 1 mm^2, i.e., comparable to those of some insectivores of the family Ptilodontidae (Carlson and Krause, 1985). In the longitudinal section, the prisms are rather short, radially oriented, positioned almost parallel to each other, and surrounded by well-developed interprismatic crystallites. The prisms are approximately perpendicular to the occlusal surface and the enamel–dentine junction. In all other traguline and early ruminants, the enamel ultrastructure is more advanced and more complex.

In the course of evolution, the enamel structure became complicated through an increase in the enamel durability and thickness, a more effective arrangement and orientation of crystallites, and a more compact arrangement of the interprismatic crystallites. In tragulines, the enamel structure gradually transformed from a simple radial pattern to a more complex structure composed of simple parallel chains, simple bands, or decussate structure known as Hunter-Schreger
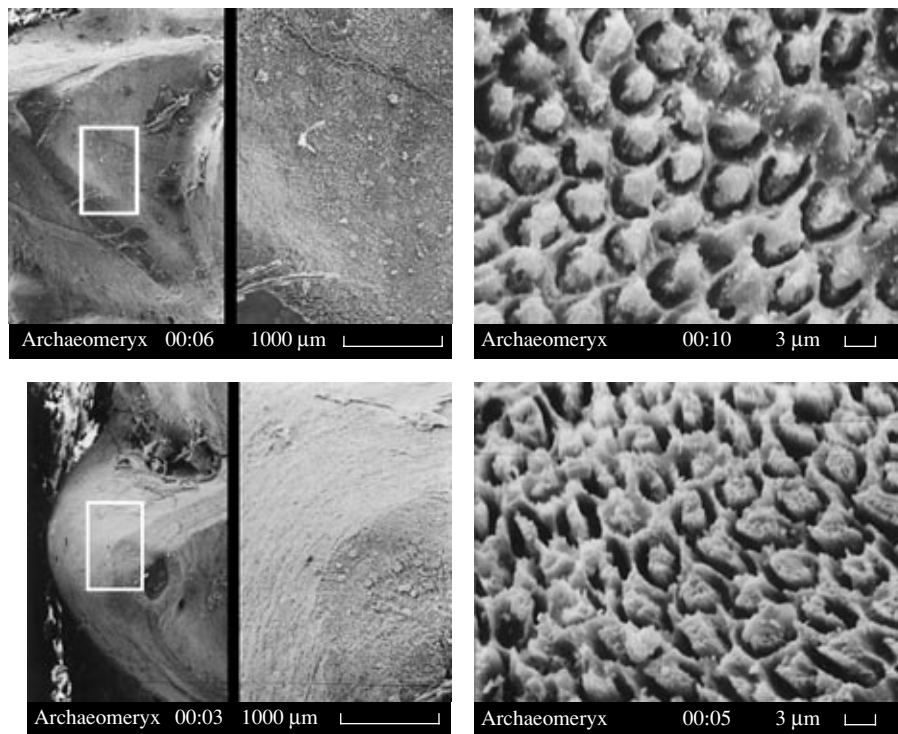
Fig. 16. Enamel ultrastructure in molars of *Archaeomeryx*.

bands. In addition, even in some Late Eocene tragulines, the arcade-shaped prisms transformed into the circular prisms by their enclosing, i.e., complete development of organic sheaths by which the prisms are isolated from the interprismatic crystallites (Vislobokova and Dmitrieva, 2000).

Higher ruminants differ from tragulines by a denser and thicker enamel and by a more advanced (perfected) enamel structure. In particular, this structure is characterized by well-developed Hunter-Schreger bands, which decussate at an angle of about 90° and form a complex network structure composed of a repetitive wavy pattern designated by Koenigswald *et al.* (1992) as Schmelzmuster.

Higher ruminants usually have a complex multi-layer enamel, which consists of the main layer of multiserial Hunter-Schreger bands underlain by a layer of uniserial Hunter-Schreger bands and overlain by a layer of radial enamel (Koenigswald *et al.*, 1992).

Similar to a number of other morphological features, the enamel structure of *Archaeomeryx* (which is most primitive among ruminants) appears to be inherited from primitive eutherians. Regarding the shape and simple (i.e., almost parallel) position of prisms, the enamel of *Archaeomeryx* resembles those of multituberculates and Late Cretaceous eutherians (including the earliest ungulate *Protungulatum donnae*) (see Carlson and Krause, 1985; Koenigswald *et al.*, 1987). It is more primitive than the enamel of the majority of arctocyonids and hyopsodontids.

VERTEBRAL COLUMN

The vertebral column (columna vertebralis) of *Archaeomeryx* consists of seven cervical vertebrae (vertebrae cervicales), 13 thoracic vertebrae (vertebrae thoracicae), six lumbar vertebrae (vertebrae lumbales), four sacral vertebrae (vertebrae sacrales), and more than 20 caudal vertebrae (vertebrae caudales).

Cervical region (pars cervicalis). The cervical region of *Archaeomeryx* is long (Figs. 17, 18, and 22; Table 6). All but the first cervical vertebrae have the spinous process, in contrast to those of the majority of ungulates.

The first cervical vertebra (atlas) has wide transverse processes usually called wings (ala atlantis) with arched lateral edges and pointed caudal angles, which are strongly pulled backward. The cranial articular fossa (fovea articularis atlantis) for the articulation with the occipital condyles is strongly concave, low, and narrow. The caudal articular fossa (fovea articularis caudalis) for the articulation with the second cervical vertebra is weakly concave. The dorsal margin of this fossa reaches the ventral edge of the dorsal arch (arcus dorsalis). The ventral side of the atlas has the pterygoid fossa and the pterygoid foramen. The dorsal side has an intervertebral foramen, which is located cranial to the pterygoid foramen. A small vascular groove extends in the caudal direction from the pterygoid foramen. The ventral tubercle (tuberculum ventrale) is well pronounced.
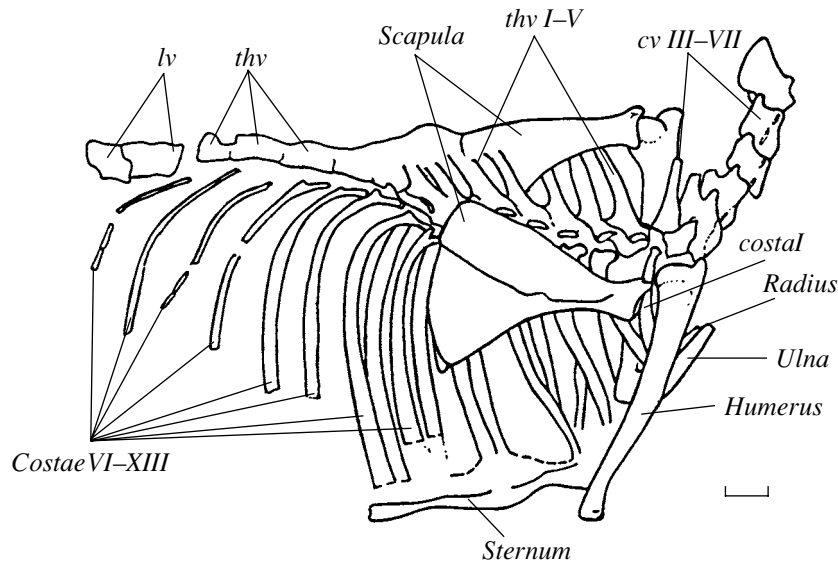
Fig. 17. A fragment of articulated skeleton of *Archaeomeryx*, PIN, no. 2198/ 151. Designations: (*cv III–cv VII*) cervical vertebrae 3–7, (*thv I–thv V*) thoracic vertebrae 1–5, (*thv*) thoracic vertebrae, and (*lv*) lumbar vertebrae. Scale bar, 1 cm.

The crests originating from the outer edges of the caudal articular fossae converge at this point.

The second cervical vertebra (axis or epistropheus) is relatively short. The odontoid process (dens) is short and conical. The cranial articular surfaces are relatively low and terminate short of reaching the superior edge of the vertebral foramen. The spinous process or neural spine (processus spinosus) is stout. The transverse process is weakly developed and pulled backward.

Cervical vertebrae 3 and 4 are somewhat shorter than the epistropheus. Cervical vertebrae 5 and 6 are slightly shorter than vertebrae 3 and 4. Vertebra 7 is the shortest cervical vertebrae; its centrum (corpus vertebrae) is almost as long as those of the thoracic verte-

Table 6. Measurements of the regions of the vertebral column, limb segments, and limb bones of *Archaeomeryx*

No.	Measurements	N	Min–Max	M	Colbert, 1941
1	Body length (excluding tail)	2	450–750	600	–
2	Length of cervical region	16	65–72	68.5	69e
3	Length of thoracic region	22	125–150	141	150
4	Length of lumbar region	18	100–110	108	108
5	Length of sacral region	14	32–40	36.5	35
6	Length of tail	12	140–304	177	304e
7	Length of scapula	18	52–60	57.9	65e
8	Length of humerus	23	70–79	73	–
9	Length of radius	18	52–70	62	65
10	Length of ulna	13	70–78	64.8	–
11	Length of manus	11	55–70	64.2	76e
12	Length of metacarpal II	8	27–30	28.3	29
13	Length of metacarpal III	8	29–35	32.3	35e
14	Length of metacarpal IV	7	30–35	32.3	35
15	Length of metacarpal V	7	24–29	26	–
16	Length of pelvis	21	76–108	89	96
17	Length of femur	26	82–100	96.4	90
18	Length of tibia	25	90–107	97.7	101
19	Length of pes	18	100–120	118.3	113
20	Length of metatarsal II	17	42–50	42.3	45
21	Length of metatarsal III	19	45–55	52	54e
22	Length of metatarsal IV	21	46–56	52.5	55
23	Length of metatarsal V	15	40–51	31	–

brae. The spinous processes are rather broad and gradually increase in height from the third to the seventh cervical vertebrae. The transverse thoracic processes (processus costotransversarius) of cervical vertebrae 3 and 4 look like broad plates. In cervical vertebra 5, these processes are divided into the cranioventral or costal process (processus costarius) and the laterocaudal or transverse process (processus transversus). In cervical vertebra 6, the transverse process is directed laterally and the costal process resembles a broad and long ventral plate (lamina ventralis). Cervical vertebra 7 has only the transverse process, whereas the costal process is most likely undeveloped. Two small caudal costal fossae for the heads of the first pair of ribs are well pronounced at the caudal end of the centrum of cervical vertebra 7. The ventral crests are developed in all cervical vertebrae. In cervical vertebrae 2–4, they have stout caudal expansions.
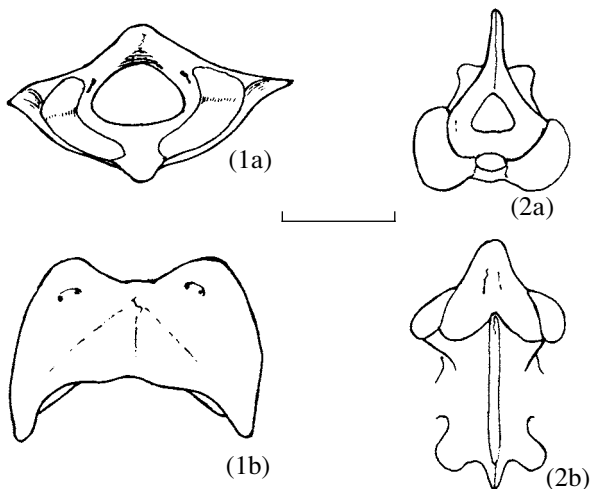
Thoracic region (pars thoracica). The vertebrae of the thoracic region have very low centra, long spinous processes, one pair of weak transverse processes, and three pairs of costal fossae (fovea costalis) (Figs, 17, 19, 23). The first thoracic vertebra is the most massive and has especially strongly developed transverse processes compared to the other thoracic vertebrae. The transverse process bears a strongly concave facet for the head of the first rib. The cranial and caudal costal fossae (fovea costalis cranialis et caudalis) for the heads of other ribs are located on the vertebral centra,
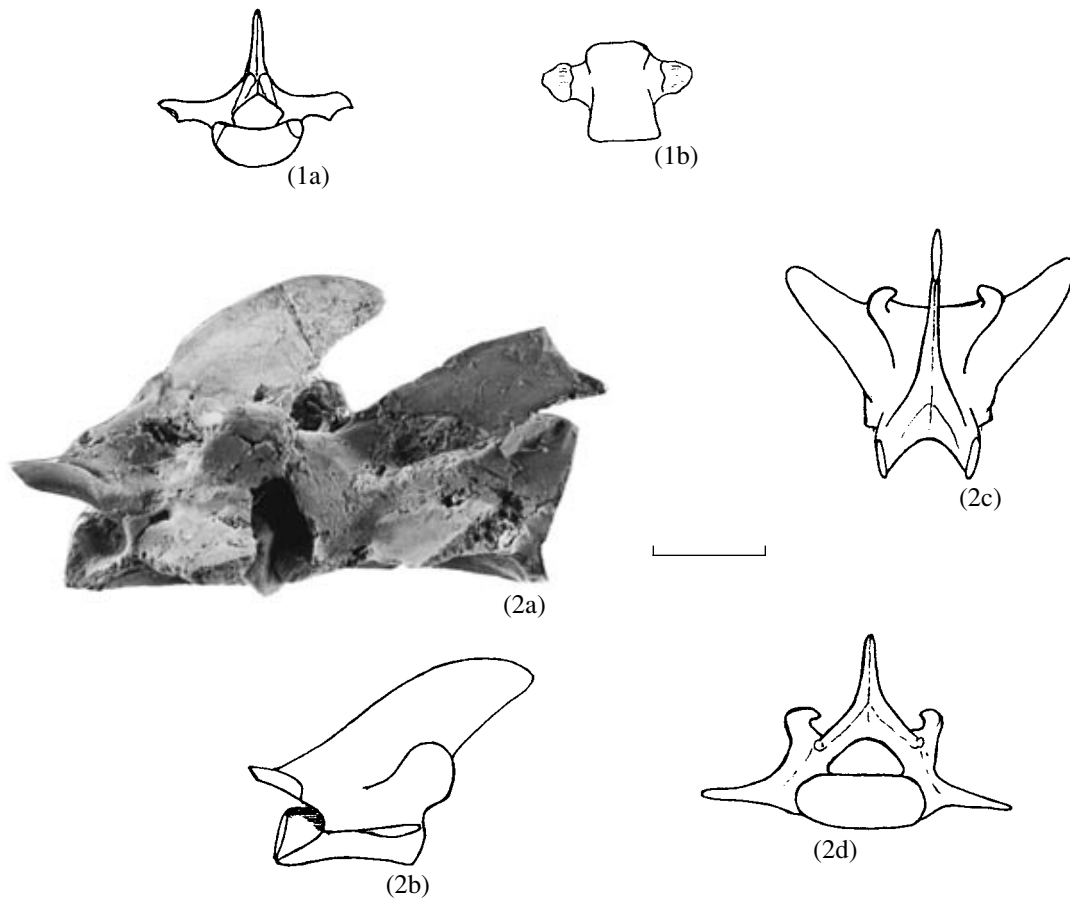

Fig. 18. Cervical vertebrae of *Archaeomeryx*: (1) atlas and (2) epistropheus: (a) anterior and (b) dorsal views. Scale bar, 1 cm.

Fig. 19. Thoracic and lumbar vertebrae of *Archaeomeryx*: (1) PIN, no. 2198/148, thoracic vertebra 8: (a) posterior and (b) ventral views; (2) PIN, no. 2198/156, lumbar vertebrae 5 and 6: (a, b) lateral, (c) dorsal, and (d) posterior views. Scale bar, 1 cm.

whereas the transverse costal fossa for the tubercle of the rib (fovea costalis transversalis) is placed on the transverse process.

The spinous processes somewhat increase in length from the first to the third thoracic vertebrae; in the succeeding vertebrae, they gradually decrease in length to the posteriormost thoracic vertebra. The spinous process of each thoracic vertebra (except for vertebra 6 and, possibly, vertebra 5) gradually narrows to the apex. The apex of the spinous process of vertebra 6 is flat and expanded. The spinous processes of the two anterior and three posterior thoracic vertebrae are almost vertical, and those of vertebrae 3–10 are weakly inclined posteriorly. The distance between the tips of the spinous processes of cervical vertebra 7 and thoracic vertebra 1 is greater than between those of other vertebrae. In the thoracic region, the distances between vertebrae 3 and 4, 4 and 5, and 5 and 6 are relatively large.

The ventral crests are developed in only five anterior thoracic vertebrae.

Lumbar region (pars lumbalis). In the lumbar region, the vertebral centra are long and gradually decrease in length from the anterior to the posterior lumbar vertebrae. The posterior lumbar vertebra has the shortest centrum (Figs. 19, 20). The latter is broad, flattened, and oval in cross section. The head of the vertebra (caput vertebrae) is weakly convex. The fossa of the vertebra (fossa vertebrae) is weakly concave. The vertebral canal (canalis vertebralis) is low. The vertebral arch is low.

The spinous processes of the lumbar vertebrae are relatively narrow and almost equal in length to each other. They are strongly anteriorly inclined, expanded at the base, and narrowed in the distal region, as in carnivores. The spinous processes of two posterior lumbar vertebrae are slightly more anteroposteriorly expanded than those of the other lumbar vertebrae.

The transverse costal processes of the lumbar vertebrae are relatively short. They are inclined backward. The inclination decreases from the first to the last lumbar vertebrae.

The articular processes (zygapophyses or processi articularis cranialis et caudalis) of all but posterior lumbar vertebrae do not form locks. Very narrow and anteroposteriorly elongated locks are present between lumbar vertebrae 5 and 6 and between lumbar vertebra 6 and sacral vertebra 1.
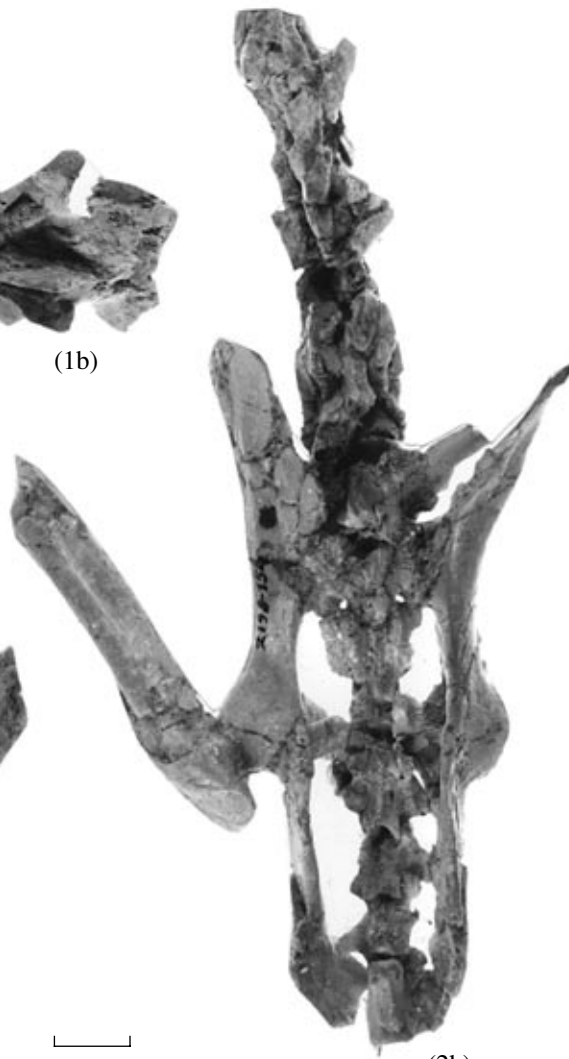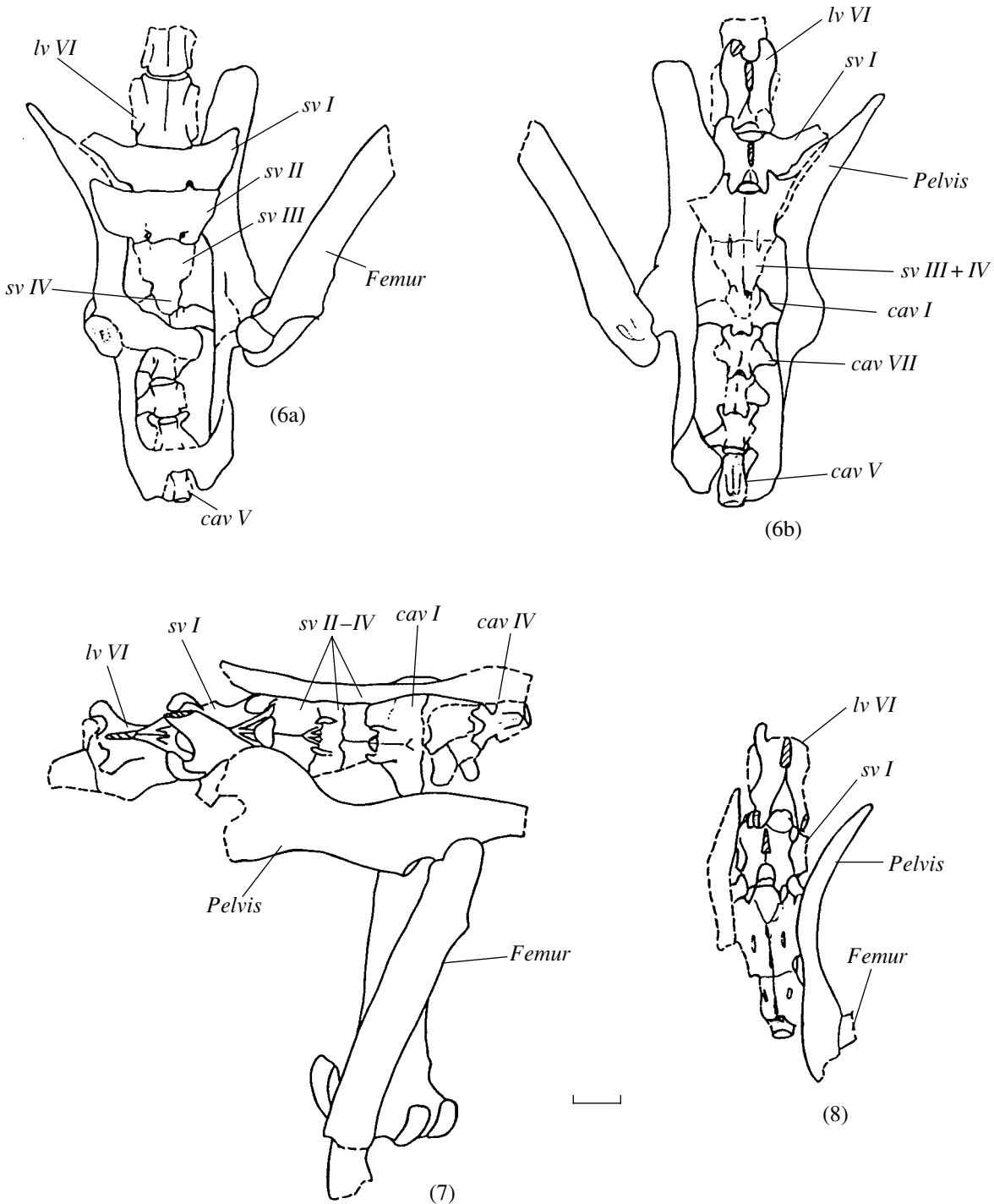
Fig. 20. Fragments of vertebral column and limb bones: (1) PIN, no. 2198/156, lumbar vertebrae: (a) lateral and (b) dorsal views; (2, 6) PIN, no. 2198/154, fragment of vertebral column with pelvis and incomplete femur: (a) ventral and (b) dorsal views; (3) PIN, no. 2198/165, fragments of vertebral column and pelvis, lateral view; (4) PIN, no. 2198/210, fragment of vertebral column and pelvis, ventral view; (5, 8) PIN, no. 2198/148, vertebral column and fragment of pelvis, dorsal view; and (7) PIN, no. 2198/159, fragment of vertebral column with pelvis and femurs, dorsolateral view. Designations: (*cav*) caudal vertebrae, (*lv*) lumbar vertebrae, and (*sv*) sacral vertebrae. Scale bar, 1 cm.

The ventral crest (crista ventralis) is well developed on each lumbar vertebra.

Sacral region (pars sacralis). The spinous process of the first sacral vertebra is stout and inclined cranially to a lesser extent than the spinous process of the posterior lumbar vertebra. The transverse processes of the first and second sacral vertebrae are well developed and form wings. In some specimens (e.g., PIN, no. 2198/154), the wings are underdeveloped. Two first sacral vertebrae are connected to the iliac bone by their
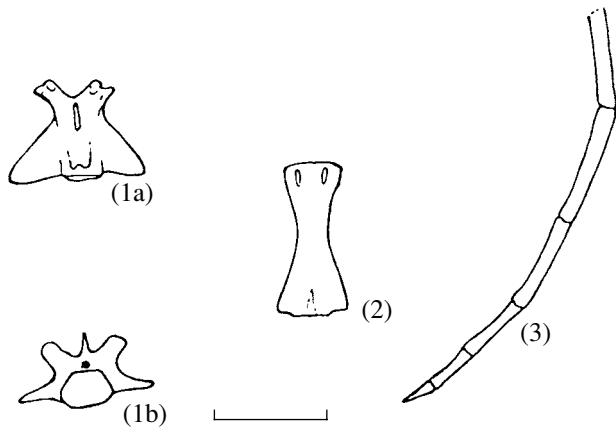
Fig. 21. Caudal vertebrae of *Archaeomeryx:* (1) PIN, no. 2198/159, caudal vertebra 4: (a) dorsal and (b) posterior views; (2) PIN, no. 2198/152, caudal vertebra; and (3) PIN, no. 2198, six posterior caudal vertebrae. Scale bar, 1 cm.

wings. Sacral vertebrae 3 and 4, fused in only some individuals (PIN, nos. 2198/154 and 2198/160). Colbert (1941), indicated that these vertebrae fused in only one specimen from the AMNH. The ventral sacral foramina are present between the transverse processes of each sacral vertebra.

Caudal region (pars caudalis). *Archaeomeryx* differs from most artiodactyls and all ruminants (including *Hypertragulus, Hypisodus*, and living tragulids) by a very long and relatively strong tail (Fig. 21).

Five anterior caudal vertebrae, combined with the sacral vertebrae, form the dorsal wall of the pelvic cavity. The first four caudal vertebrae have a vertebral arch, weak spinous processes, well-developed transverse processes, and small articular processes. The transverse processes are also well developed on caudal vertebrae 5 and 6.

The transverse processes are laterocaudally inclined and abruptly decrease in size from caudal vertebrae 1 to 6. The transverse processes of caudal vertebra 1 are most developed and least caudally inclined. Caudal vertebra 1 is located on a level of the acetabulum.

The ventral surface of the transverse processes is the attachment area for the elevator of the tails (musculus levator caudi). Rudimentary transverse processes are well pronounced to vertebra 14 inclusive.

Well-developed fossae for the depressors of the tail are present on the ventral surface of caudal vertebra 2 at the boundary between the centrum and the transverse process.

Beginning with vertebra 5, the vertebral arches are gradually reduced; thus, the vertebral centra retain only a groove, which replaces the vertebral canal.

Four anterior vertebral centra are relatively short. Vertebrae 5–7 are somewhat longer. Beginning with caudal vertebra 7, the vertebrae gradually decrease is massiveness; however, they remain approximately the same length to vertebra 16. Beginning with vertebra 12, the centra become quadrangular in section with the well-developed dorsal, ventral, and lateral crests.

From the 16th to 24th vertebrae, the vertebral centra gradually decrease in length; caudal vertebra 24 is almost half as long as vertebra 16. The vertebral centra of the posterior vertebrae are very thin.

The cranial articular processes of caudal vertebrae 1–5 are large. Posteriorly, they gradually decrease in size over the entire tail extent and are replaced by the mammilaris processes. The caudal articular processes of caudal vertebrae 1–3 are stout; they are clearly reduced in vertebrae 4 and 5; and, in the posterior vertebrae, they are lost. The centrum of the posteriormost vertebra substantially narrows caudally.

The vertebral centra lack ventral crests.

RIBS

The first rib (costa) is thin and weakly curved (Fig. 22). Its head has two convex articular facets isolated from each other by a crest and articulated with the transverse process of the first thoracic vertebra. The other ribs have a flattened body (corpus costae), which is strongly widened in thoracic vertebrae 3–8 (Figs. 17, 22, 23).

The costal heads (caput costae) have two convex articular facets for the vertebrae. The costal necks (collum costae) gradually increase in length beginning with the second rib. The tubercle of ribs (tuberculum costae) has a saddle-shaped articular surface (facies articularis tuberculi costae) for the transverse process of the vertebrae.

In the first rib, the angle of the rib (angulus costae) is located close to the costal tubercle. In the other ribs, it is located at certain distance from the tubercle; this distance gradually increases from the second to posterior ribs. On the cranial edge of the first rib, there is an eminence for the attachment of the scalene muscle (tuberculum m. scaleni medii and scaleni medii muscle, respectively). The second and succeeding ribs have a pronounced tuberosity for the anterior serrate muscle (tuberositas m. serrati anterioris and musculus serratus anterior, respectively). A groove extends along the lateral surface of the cranial costal edge. Another groove (sulcus costae) for vessels and nerves extends along the medial surface of the caudal costal edge.

FORELIMB BONES

Scapula

The scapula (Figs. 22, 23, 24) is relatively broad and has a long neck (collum scapulae), broad rounded cranial angle, and a less rounded caudal angle (anguli cranialis et caudalis).

The spine of the scapula (spina scapulae) is high and long. It provides the attachment area for a stout deltoid muscle (muscle deltoideus). The scapular spine divides the scapula into two almost equal parts; a larger posterior part is the infraspinous fossa (fossa infraspinata) for a strong abductor of the humeral articulation and the
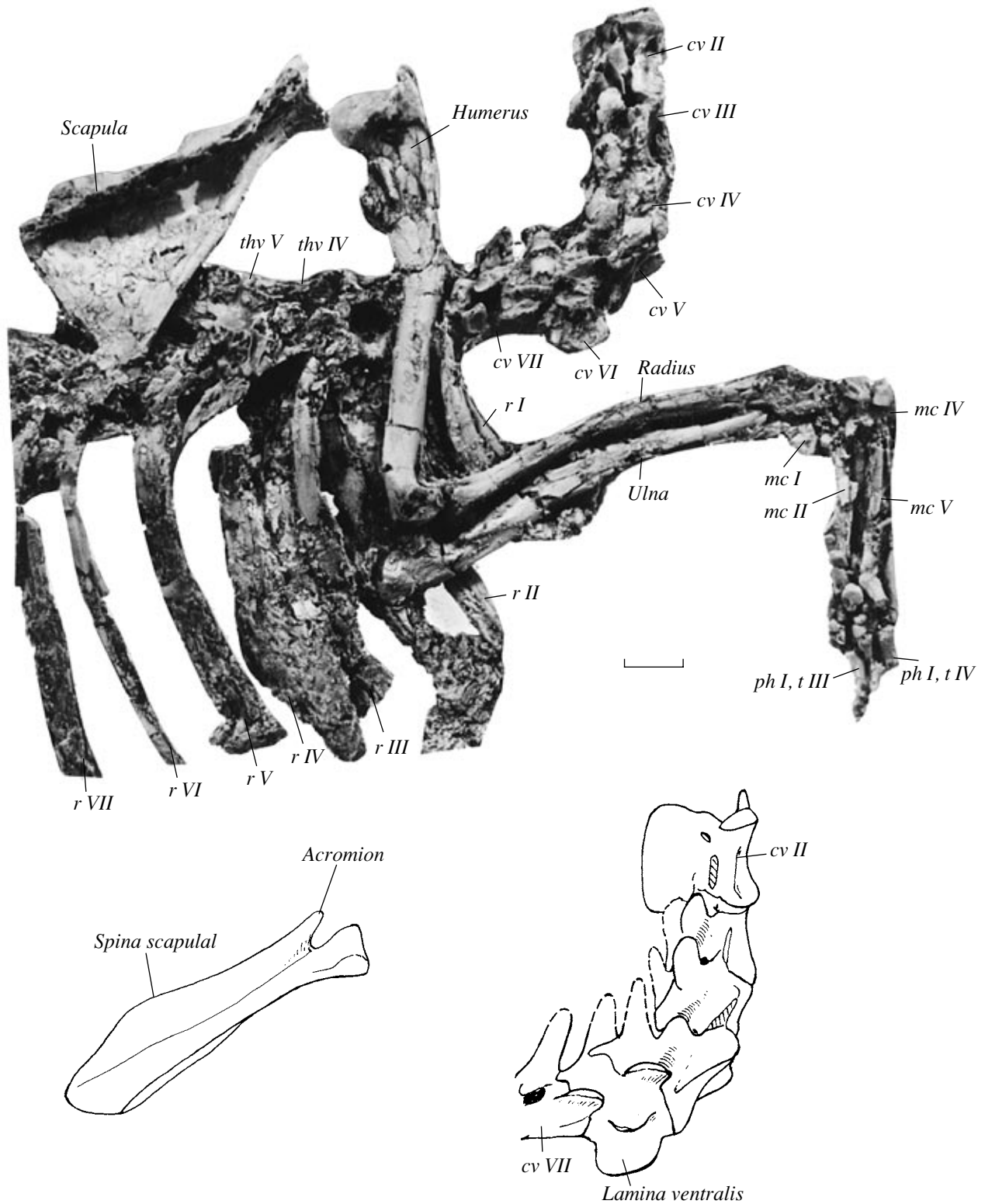
Fig. 22. Fragment of articulated skeleton of *Archaeomeryx*, PIN, no. 2198/150. Designations: (*cv II–cv VII*) cervical vertebra 2–7; (*t III, t IV, t V*) digits 3, 4, and 5; (*mc I, mc II, mc IV, mc V*) metacarpals I, II, IV, and V; (*ph I*) phalanx 1; (*r I–r VII*) ribs 1–7; and (*thv IV, thv V*) thoracic vertebrae 4 and 5. Scale bar, 1 cm.
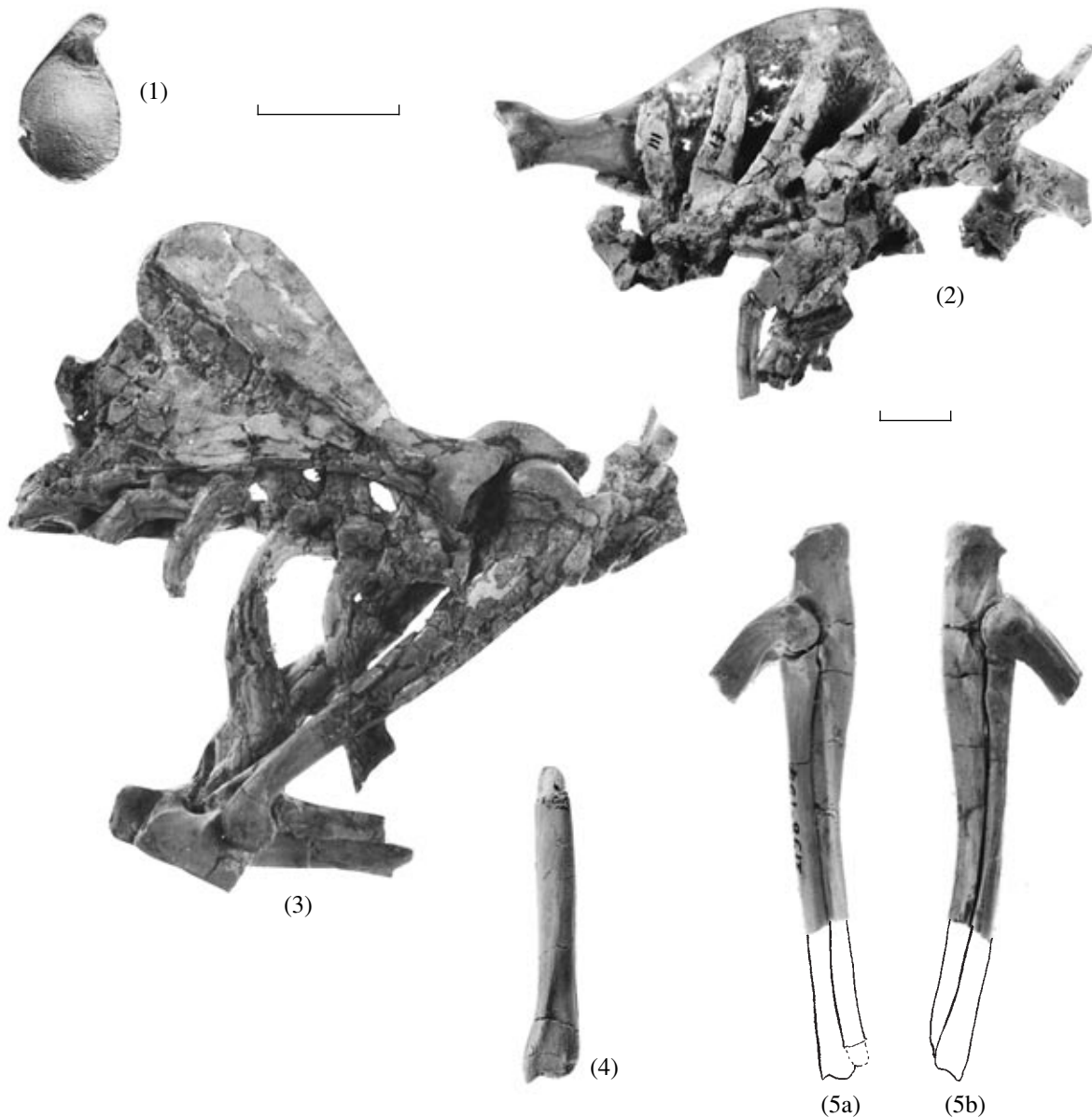
Fig. 23. Fragment of vertebral columns and forelimb bones: (1) PIN, no. 2198, scapula, glenoid cavity; (2, 7) PIN, no. 2198/148, fragment of skeleton; (3, 6) PIN, no. 2198/156, fragment of skeleton; (4) PIN, no. 2198/162, distal half of the radius, anterior view; and (5) PIN, no. 2198/154, elbow joint: (a) lateral and (b) medial views. Designations: (*thv II, thv III–thv VIII*) thoracic vertebrae 2 and 3–8. Scale bar, 1 cm.

rotator of the humerus and a smaller anterior part is the supraspinous fossa (fossa supraspinata) for the extensor and abductor of the humeral articulation. The dorsal edge of the scapula (margo dorsalis) is weakly convex.

A well-developed acromion is located at the end of the scapular spine. Close to the base, it curves distally and cranially. In many higher ruminants, the acromion remains rather large.

The glenoid cavity (cavitas glenoidalis) is weakly ovoid.

The scapular tuber (tuber scapulae) has a well-developed coracoid process (processus coracoideus) for the tendon of the coracobrachial muscle, which is the an extensor and abductor of the humeral joint.

In the course of ruminant evolution, the scapula became narrower and more elongated; the scapular spine displaced toward the cranial edge of the scapula; the supraspinous fossa narrowed; the coracoid process and the scapular neck decreased in size; the articular fossa of the scapula changed its shape from nearly circular to oval; and the caudal and ventral angles of the scapula became more angular.

Humerus

The humerus is slender and relatively short, with a relatively broad proximal end, epiphysis, a short shaft,
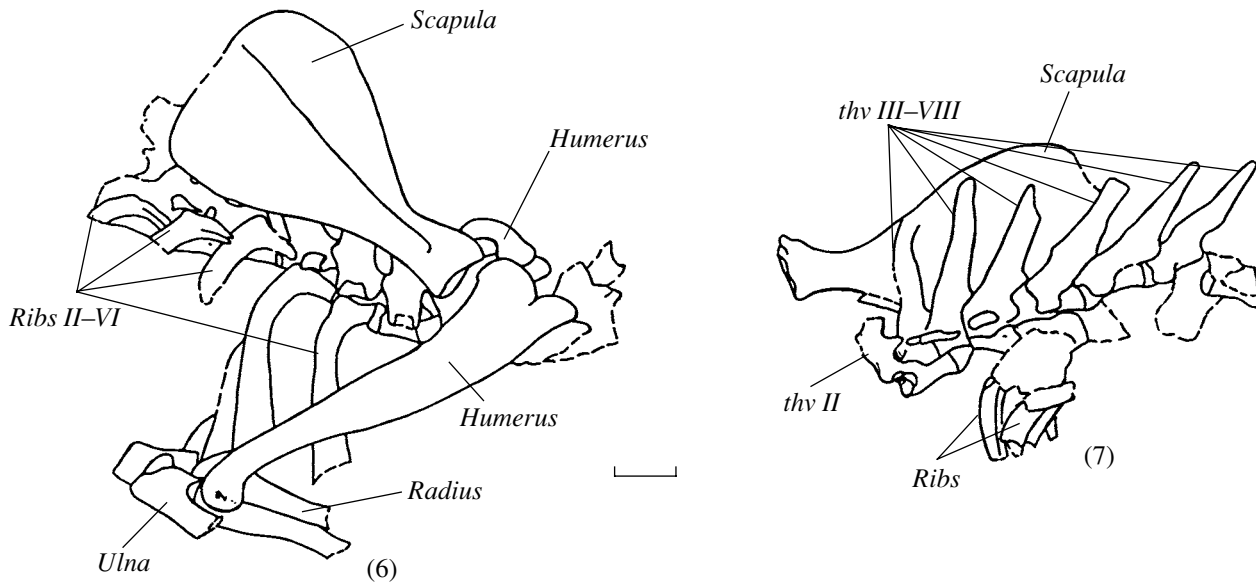
Fig. 23. (Contd.)

diaphysis, and a narrow distal end (Figs. 22, 23, 24). The long axes of the epiphyses are almost perpendicular to each other.

The head of the humerus (caput humeri) is almost hemispherical in shape and directed posteriorly. The neck of the humerus (collum humeri) is more pronounced than those of extant tragulids.

The greater tubercle of the humerus (tuberculum majus humeri) for the supraspinous and infraspinous muscles is relatively low and broad. It weakly projects above the humeral head. The smaller tubercle (tuberculum minus humeri) is small and low. The intertubercular groove (sulcus intertubercularis) is broad and shallow. It lies between weak crests of the greater and smaller tubercles (cristae tuberculi majoris et tuberculi minoris), which extend distally. The intertubercular groove serves for the attachment of the tendon of the brachial biceps muscle (m. biceps brachii), which is the extensor of the humeral articulation and the flexor of the elbow joint. The tendon originates from the scapular tuber.

Distally, at the boundary between the proximal and middle third of the bone, the crest of the minor tubercle becomes the tuberosity for the teres minor muscle (musculus teres minor and tuberositas teres minor).

On the anterolateral surface of the diaphysis, the crest of the greater tubercle is thickened to form the deltoid tuberosity (tuberositas deltoidea) for the deltoideus muscle.

The distal trochlea of the humerus (trochlea humeri) is narrow and weakly tapers laterally. The medial region of the humeral trochlea is only slightly inflated. The medial epicondyle (epicondylus medialis) is well developed. The ulnar and radial flexors of the carpus (musculus flexor ulnaris medialis et musculus flexor carpi radialis) are attached to it. The extensors of the

metacarpus and digits originated from the smaller lateral epicondyle (epicondylus lateralis).

Both the olecranal fossa (fossa olecrani) located on the posterior surface of the bone above the trochlea and the coronoid fossa (fossa coronoidea) located on the anterior surface of the bone above the trochlea are rather high and deep. The supratrochlear foramen (foramen supratrochleare) is most likely developed in some individuals, in contrast to those of *Gelocus* and higher ruminants.

In the course of evolution, the humerus of ruminants became thicker and longer. The humeral head became more trochlear (more pulleylike). It increased in transverse diameter and became anteroposteriorly flattened. The long axis of the head had an oblique position relative to the long axis of the distal trochlea in *Leptomeryx* and became almost perpendicular to it (in *Hypertragulus*). The greater tubercle became higher, and the intertubercular groove increased in breadth. The distal trochlea also became broader and its medial region expanded.

Tragulines display various combinations of primitive and advanced features. In *Hyemoschus*, a short and massive humerus is combined with well developed epiphyses; in *Hypertragulus* and *Hypisodus*, elongated and slender humeri are combined with strongly narrowed humeral head (Vislobokova, 2001).

Ulna and Radius

In *Archaeomeryx*, the diaphyses of the ulna and radius are of approximately the same size, in contrast to those of almost all known ruminants (Figs. 22, 23, 24).

A relatively slender radius is only slightly shorter than the humerus. The shaft of the radius (corpus radii) is thin and only slightly expanded at the epiphyses. The
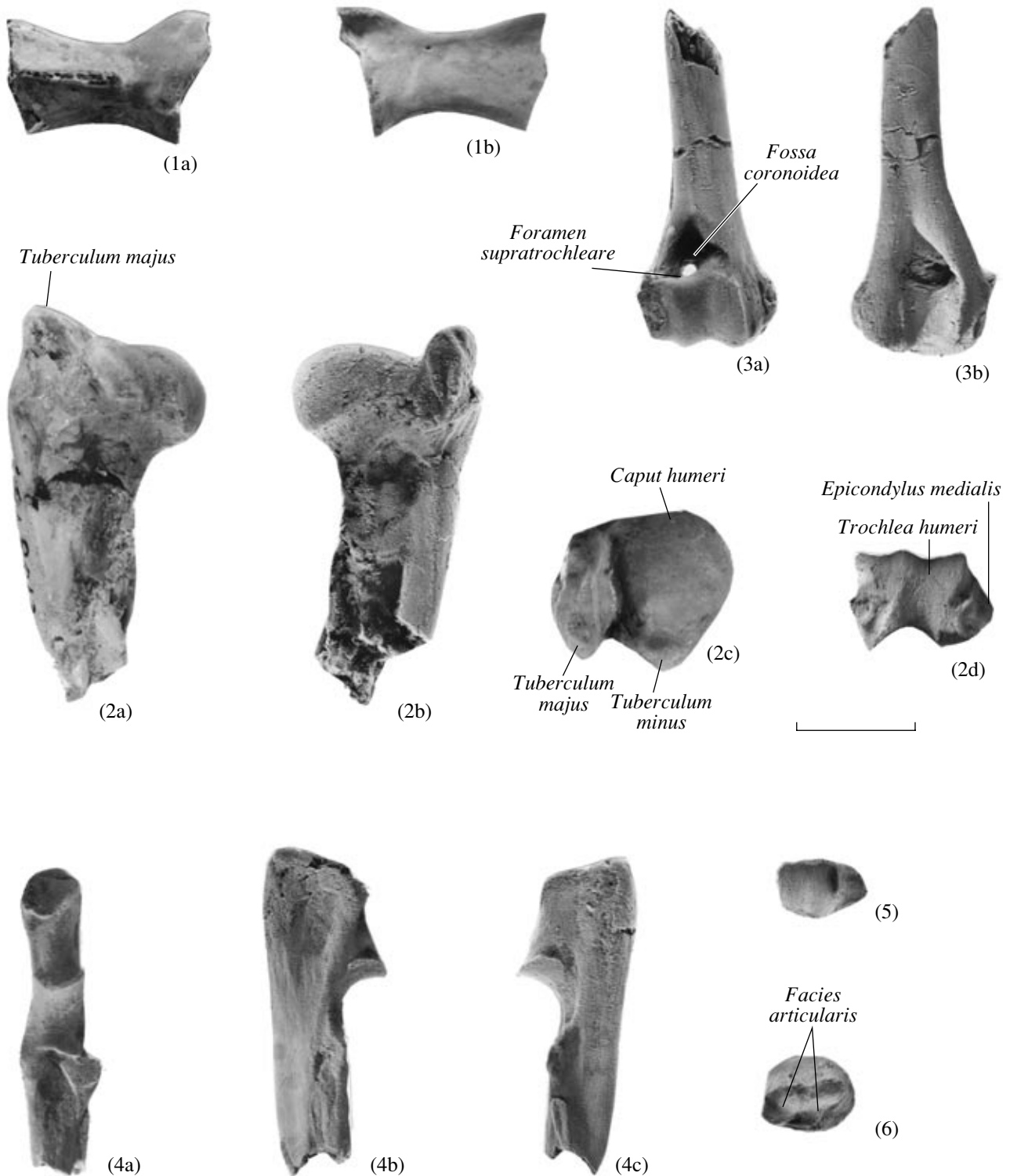
Fig. 24. Forelimb bones: (1) PIN, no. 2198, scapula: (a) lateral and (b) medial views; (2) PIN, no. 2198/154, proximal end of the humerus: (a) medial, (b) lateral, and (c) superior views; (3) PIN. no. 2198/163, distal end of the humerus: (a) anterior, (b) posterior, and (c) inferior views; (4) PIN, no. 2198/183, proximal end of the ulna: (a) anterior, (b) medial, and (c) lateral views; (5) PIN, no. 2198/182, radius, superior view; and (6) PIN, no. 2198/162, radius, inferior view. Scale bar, 1 cm.

head of the radius (caput radii) is weakly transversely enlarged and rather broad in anteroposterior diameter. The neck of the radius (collum radii) is short and hard to distinguish.

The proximal articular surface of the radius has two concavities of approximately the same width, which are separated from each other by a broad and shallow groove for the crest of the distal humeral trochlea. The

anteroposterior diameter of the lateral region of the proximal articular surface is only slightly shorter than the anteroposterior diameter of its medial region. A similar structure is characteristic of *Leptomeryx* and hypertragulids. In tragulids, the medial concavity is enlarged and the median groove is deeper. In the course of ruminant evolution, the difference between the concavities increased, and the median groove located between them became deeper.

The tuberosity of the radius (tuberositas radii) is located close to the proximal end of the bone.

The distal end of the radius is narrow. The styloid process of the radius (processus styloideus radii) is well developed.

The distal articular surface is primitive in structure and, in contrast to those of higher ruminants, consists of two facets for the scaphoid and lunar bones of the carpus, as in hypertraguloids, *Leptomeryx*, and *Tragulus meminna*. In a more advanced state, the distal articular surface acquires the third (lateral) facet for the articulation with the triquetrum.

The ulna of *Archaeomeryx* is stout and only slightly narrows to the distal end, in contrast to those of the majority of ruminants. The ulna has a well-developed and relatively high ulnar process, the olecranon. The tuber of the ulna (tuber olecrani) is stout. The medial and lateral coronoid processes (processi coronoideus medialis et lateralis) are narrow. The trochlear notch (incisura trochlearis) is relatively narrow and low. The radial notch (incisura radialis) is broad. Posterior to the latter, there is a well-developed crest of the muscle supinating the forearm (crista musculi supinatoris). Inferior to the radial notch, the anterior surface of the diaphysis is covered by the tuberosity of the ulna (tuberositas ulnae).

MANUS

The manus of *Archaeomeryx* preserves the structural features of primitive eutherians and considerably differs from the pattern typical of many artiodactyls. The manus of *Archaeomeryx* remains incompletely paraxonic and resembles the initial mesaxonic pattern by the most developed third digit.

In contrast to the majority of ruminants, *Archaeomeryx* has completely developed metacarpals II and V and the entire set of three phalanges of the second and fifth digits. Apparently, the first digit (pollex) was also developed, although it was most likely incomplete.

Carpals

In *Archaeomeryx*, the number of carpal bones only slightly decreased in comparison with the initial type of the limb pattern. The arrangement of bones is alternative, i.e., typical of ruminants and close to that in a generalized mammalian manus (Figs. 25, 26, 28). A reexamination of fossil material has shown the presence of the trapezium (PIN, no. 2198/199).

The first row of the carpus includes the scaphoid (os scaphoideum), lunar (os lunatum or lunare), triquetrum (os triquetrum or cuneiforme), and a very small pisiform bone (os pisiforme or os carpi accesorium).

In the second row of the carpus, there are the following four bones: the trapezium (os trapezium) for the first digit, fused magnum (os magnum or os capitatum) and trapezoid (os trapezoideum) for the second and third digits, and the unciform (os unciforme or hamatum) for the fourth and fifth digits.

Archaeomeryx demonstrates one of the initial stages of transformation of the initial type of the autopodium with the carpal bones positioned in the same plane towards a more compact arrangement characteristic of advanced ungulates.

In *Archaeomeryx*, the dorsal curvature of the carpus is well pronounced. The side bones of the carpus are strongly displaced backward.

The structural features of the carpal articular surfaces of *Archaeomeryx* suggest that manus was more mobile than those of later ruminants.

The scaphoid occupies the medial position in the first row of the carpus. The proximal articular surface of the scaphoid contacts with the medial facet of the distal epiphysis of the radius. It consists of two parts; the anterior part is convex and expanded, and the posterior part is trochlear and very narrow. The latter extends onto the palmar surface of the bone. The distal articular surface of the scaphoid rests on the trapezoidomagnum. This surface is weakly convex anteriorly and weakly concave posteriorly. The lateral surface of the scaphoid has facets for the lunar. Of these, the upper facet is conical and trochlear; it provides a considerable rotation of these two bones relative to each other.

The lunar is articulated by the upper articular surface to the lateral facet of the proximal articular surface of the radius. Anteriorly, the pointed distal end of the lunar wedges in between the unciform and the trapezoidomagnum and closely approaches the proximal end of metacarpal III. The proximal articular surface of the lunar is twisted. It consists of two oblique trochlear crests and a narrow median concavity between them. The strongly concave distal articular surface of the lunar rests posteromedially and anterolaterally on the trapezoidomagnum and unciform, respectively. The lateral surface of the lunar has the facets for the triquetrum. The posterior facet for the triquetrum looks like a strongly projecting lateral trochlea and serves as the fulcrum for the triquetrum.

The proximal and distal articular surfaces of the triquetrum are articulated with the ulna and the unciform, respectively. The proximal articular surface of the triquetrum is twisted and irregularly triangular in section; posteriorly, it extends onto the palmar surface and terminates close to the midheight of the bone. The distal articular surface has a rounded and weakly concave facet, which posteriorly becomes a narrow projection.

The unciform is the largest carpal bone. The unciform is high, very broad anteriorly, and narrow posteriorly. Its proximal surface is articulated with the lunar
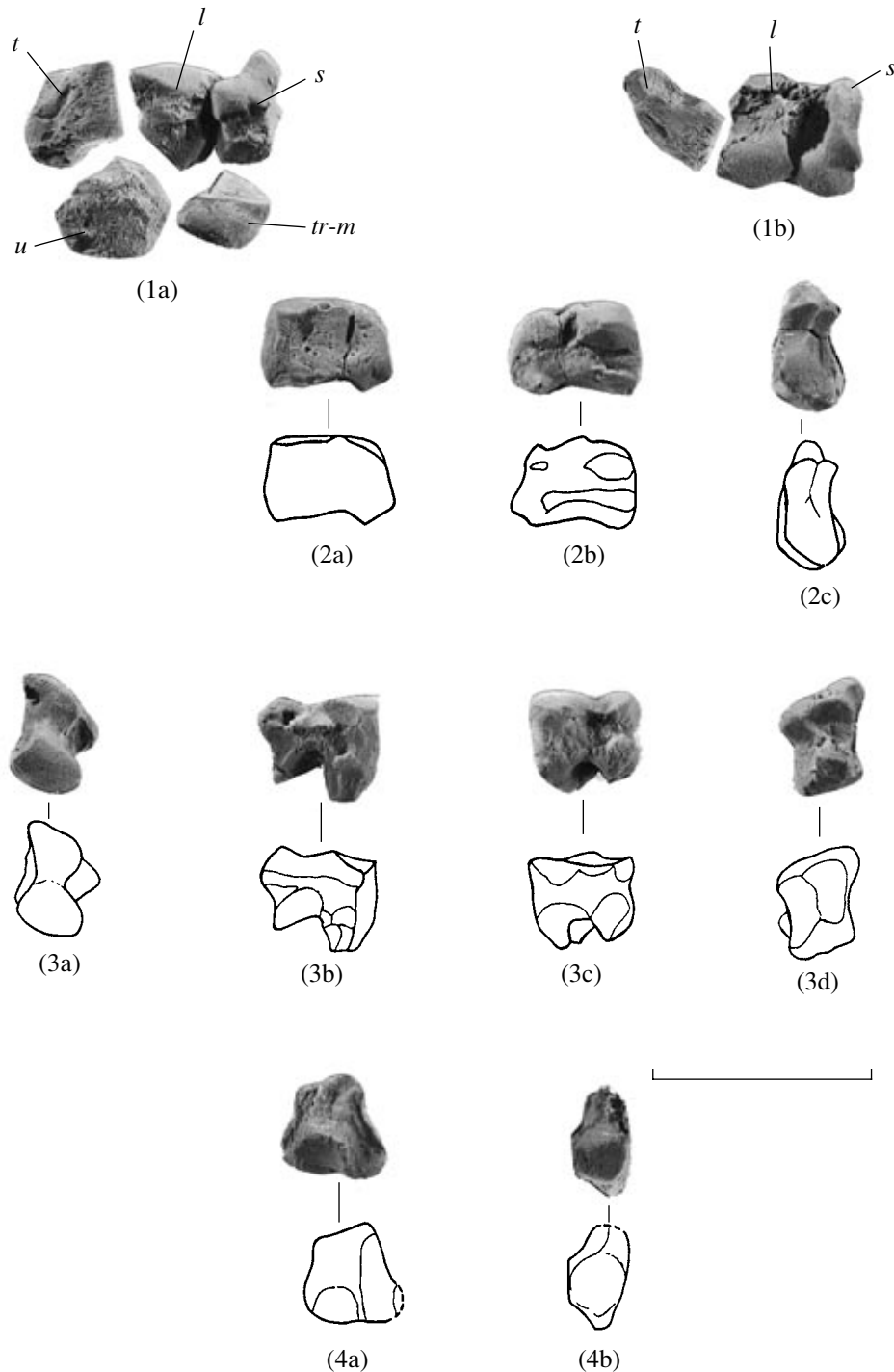
Fig. 25. Carpal bones: (1) carpus, (a) anterior and (b) superior views; (2) scaphoid: (a) medial, (b) lateral, and (c) distal surfaces; (3) lunatum: (a) proximal, (b) medial, (c) lateral, and (d) distal surfaces; and (4) triquetrum, (a) medial and (b) distal surfaces. Designations: (*l*) lunatum, (*t*) triquetrum, (*tr-m*) trapezoidomagnum, (*s*) scaphoid, and (*u*) unciform. Scale bar, 1 cm.

and triquetrum. The hook of the unciform (hamulus ossis unciformi) is thickened and slightly inclined outward. A small oval facet for the fifth metacarpal bone is placed on its lateral surface. Anteriorly and inferiorly, the medial side of the unciform adjoins the trapezoidomagnum and the third metacarpal, respectively. The distal surface of the unciform has two facets, a broad inner facet is articulated with the fourth metacarpal and a narrow outer facet is articulated with the fifth metacarpal.

The trapezoidomagnum is rather narrow. It is low anteriorly and very high posteriorly. The trapezoidomagnum rests on the second and third metacarpals, as
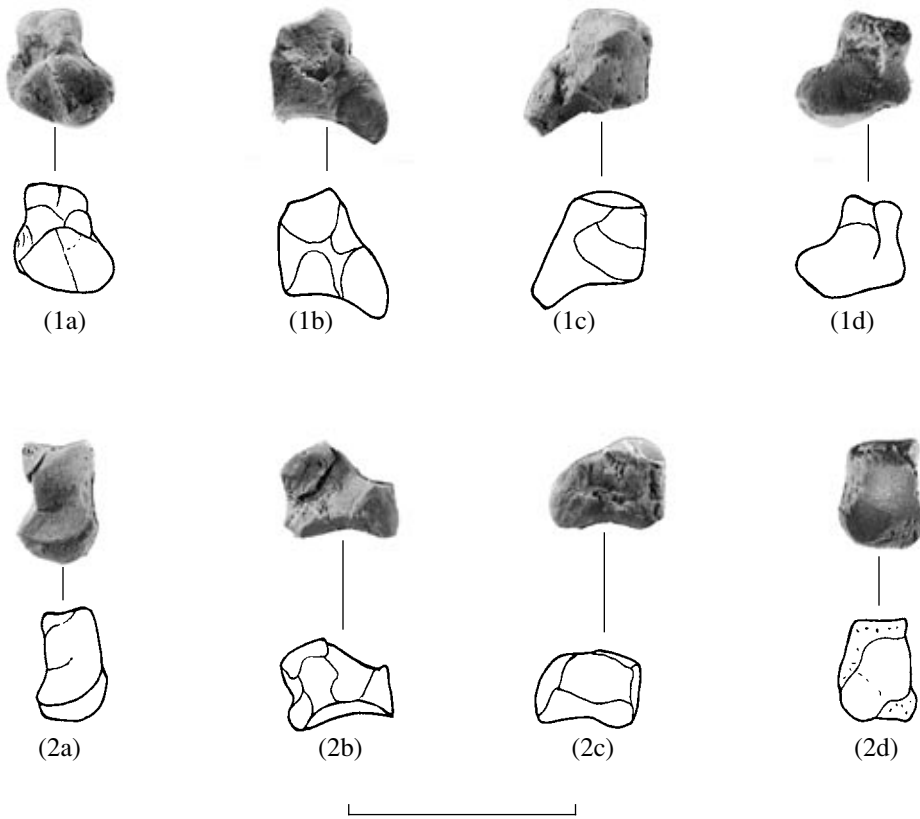
(1a)   (1b)   (1c)   (1d)

(2a)   (2b)   (2c)   (2d)

Fig. 26. Carpal bones: (1) unciform: (a) proximal, (b) medial, (c) lateral, and (d) distal surfaces; (2) trapezoidomagnum: (a) proximal, (b) lateral, (c) medial, and (d) distal surfaces. Scale bar, 1 cm.
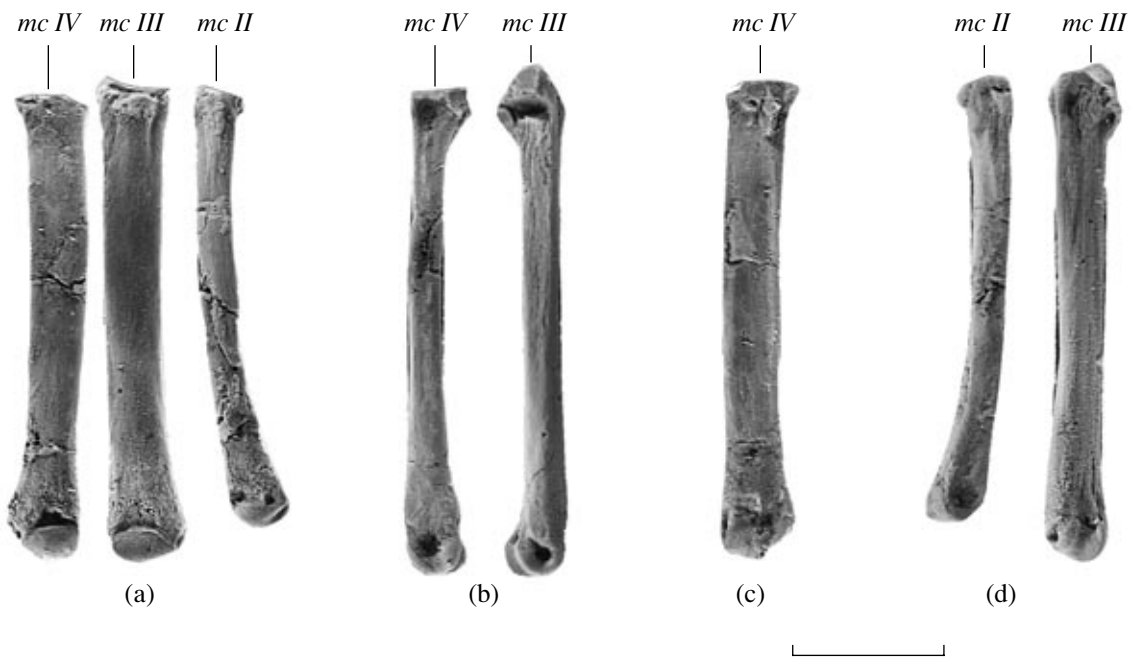

(a)   (b)   (c)   (d)

Fig. 27. Metacarpals: (a) anterior, (b) medial, (c) lateral, and (d) posterior views. Scale bar, 1 cm.
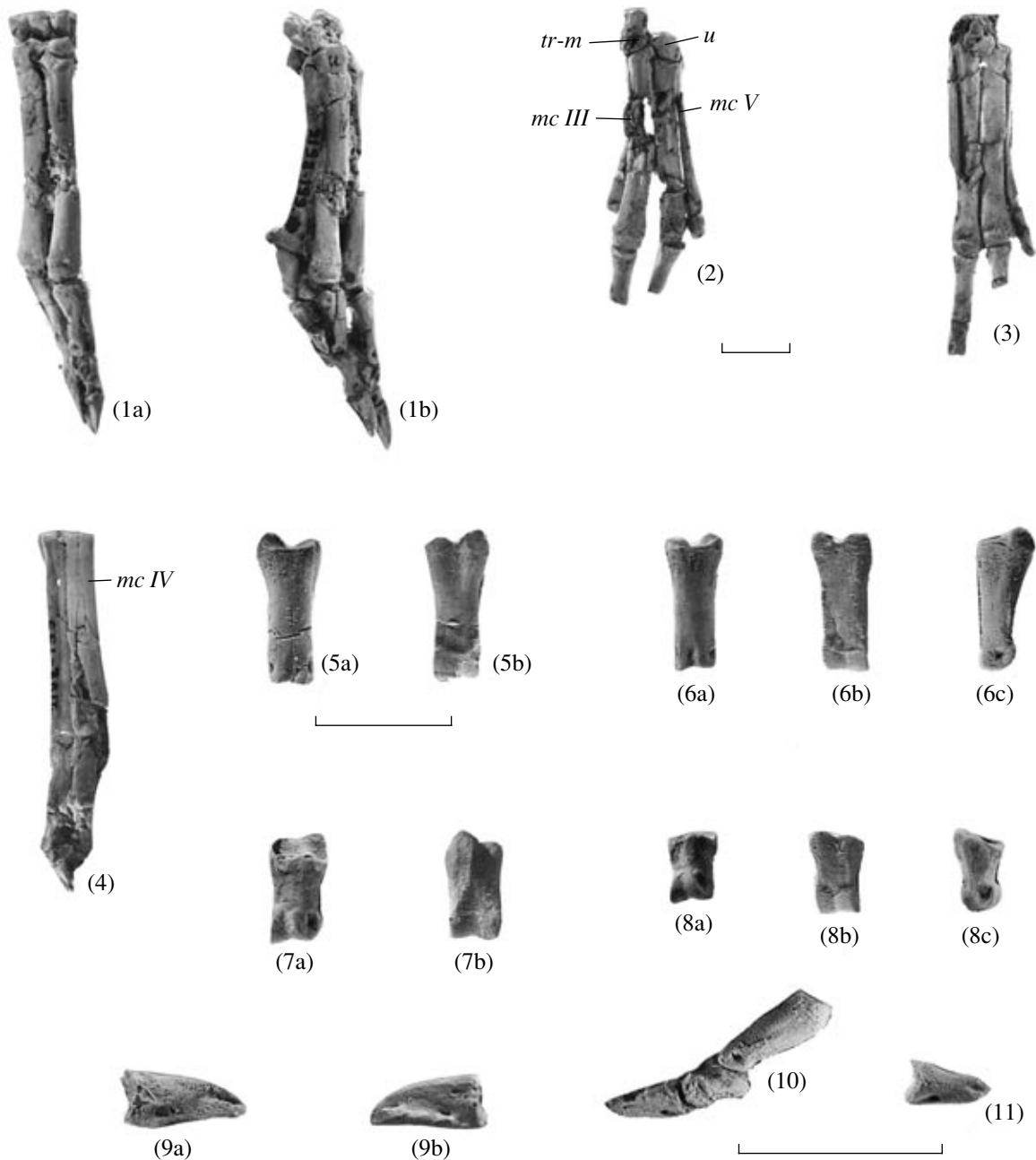
Fig. 28. Manus and phalanges of manus: (1, 12–15) PIN, no. 2198/199, manus: (a) anterior and (b) lateral views; (2) PIN, no. 2198, fragmentary manus; (3) PIN, no. 2198/157, fragmentary manus, anterior view; (4) PIN, no. 2198/199, fragmentary manus, anterior view; (5) PIN, no. 2198/162, first phalanx of digit 3: (a) anterior and (b) posterior views; (6) PIN, no. 2198/162, first phalanx of digit 4: (a) anterior and (b) posterior views; (7) PIN, no. 2198, second phalanx of digit 3: (a) anterior and (b) posterior views; (8) PIN, no. 2198/149, second phalanx of side digit: (a) anterior, (b) posterior, and (c) lateral views; (9) PIN, no. 2198, third phalanx of digit 3: (a) lateral and (b) medial views; (10) PIN, no. 2198/162, phalanges of digit 4; and (11) PIN no. 2198/162, third phalanx of side digit, lateral view. Designations: (*l*) lunatum, (*t*) triquetrum, (*tr-m*) trapezoidomagnum, (*s*) scaphoid, and (*u*) unciform; for other designations, see Fig. 22. Scale bar, 1 cm.

in *Hyemoschus*. In the more advanced *Leptomeryx, Gelocus*, and higher ruminants, it lies mainly on the third metacarpal.

The pisiform and trapezium are displaced posteriorly and strongly reduced. Posteriorly, the trapezium contacts with the trapezoidomagnum. The proximal surface of this bone has a facet for the scaphoid. The distal surface of the trapezium rests on the second and first metacarpals. The medial surface is articulated with the trapezoidomagnum and, apparently, with the second metacarpal. A separate trapezium was also present in *Lophiomeryx*. Among living ruminants, this remains
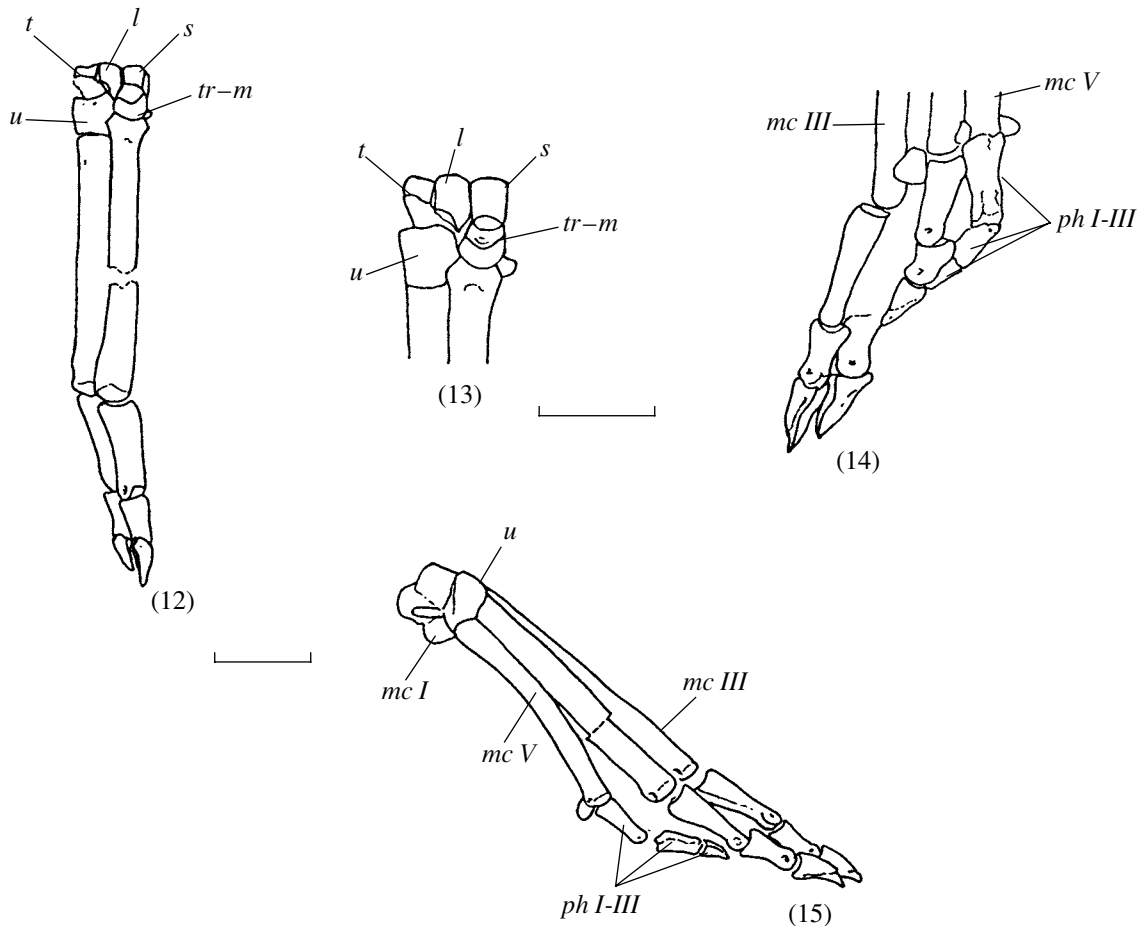
Fig. 28. (Contd.)

Metacarpals

In *Archaeomeryx*, as in the majority of tragulines, all metacarpals are present and separate (Figs. 27, 28). Webb and Taylor (1980) tentatively proposed the presence of metacarpal I in this animal. When reexamining the *Archaeomeryx* remains, they showed that the proximomedial surface of metacarpal II has a shallow depression (about 5 mm long) and the trapezoid extends medially beyond metacarpal II (for about 0.2 mm); consequently, the trapezoid could serve for the attachment of metacarpal I. An articulated manus (specimen PIN, no. 2198/199) displays the presence of metacarpal I. It is represented by a small, flat bone on the palmar side.

Metacarpal III is the longest metacarpal. Its proximal surface has two facets: a small oblique facet for the articulation with the unciform and a larger facet for the trapezoidomagnum.

Metacarpals II and V virtually lack a trace of reduction. They are only a little shorter and slenderer than the central metacarpals. The central metacarpals are expanded and as though displace the lateral metacarpals. The proximal ends of the lateral metacarpals only partially lean on the trapezoidomagnum and unciform and are somewhat displaced backward.

The distal articular surface remain almost hemispherical. The distal trochlear crests are only developed on the palmar surface of the distal trochleae.

Phalanges

The third phalanges of the central digits resemble in structure the ungual phalanges rather than the ungulate phalanges. The anterior ends of these phalanges are strongly curved downwards. The dorsal surface has a well-pronounced ungual sulcus (sulcus unguicularis), and some individuals have the ungual process (processus unguicularis). The plantar surface (facies solearis) is narrow, posteriorly expanded, and concave in the anterior part.

The first, second, and third phalanges of the lateral digits (second and fifth) are only slightly slenderer and shorter than those of the central digits.
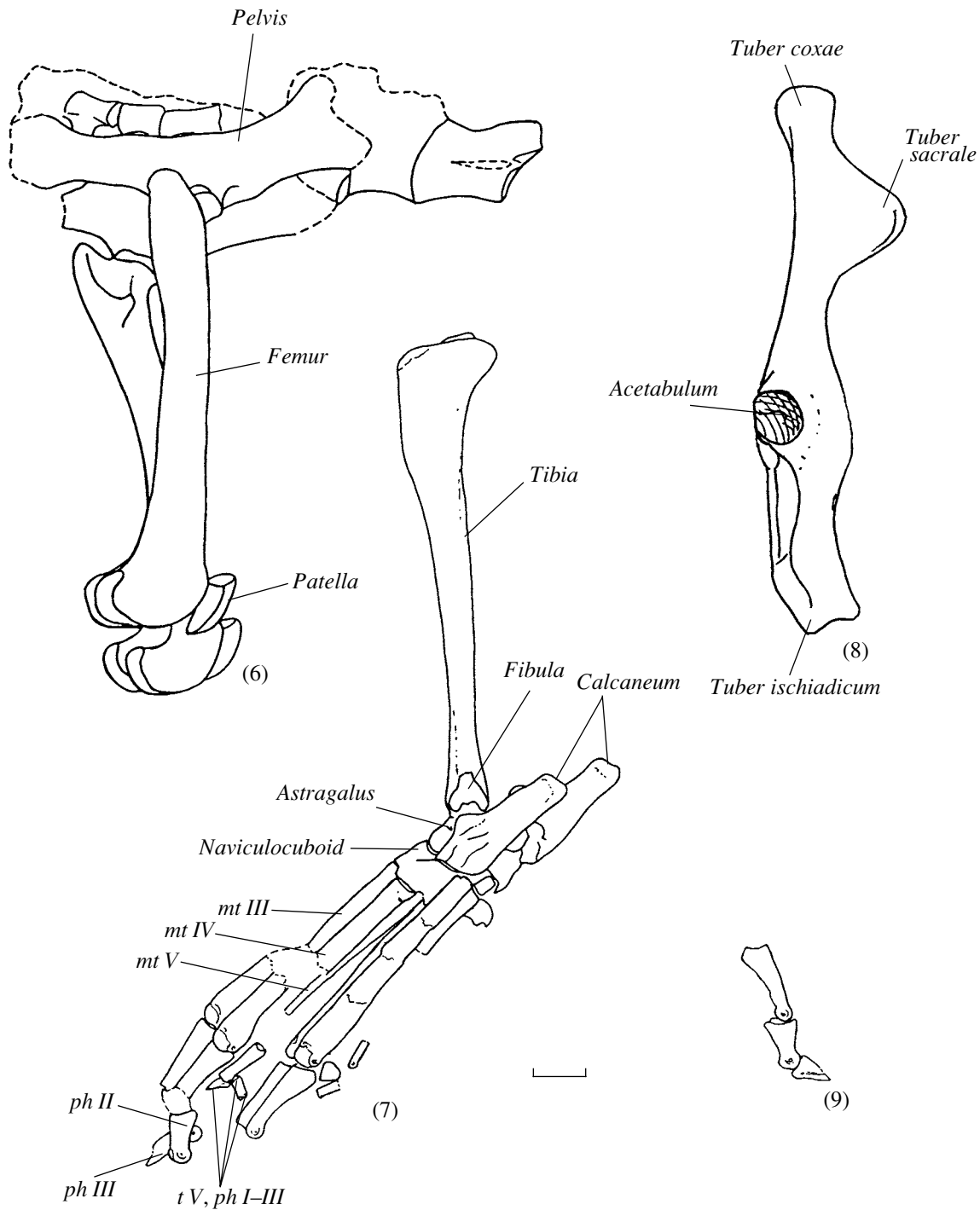
in only *Hyemoschus*. In all other tragulines and in all higher ruminants, the trapezium fused with the trapezoidomagnum.

(1)

(2a)

(2b)

(3)

(4)

Fibula

(5a)

(5b)

Fig. 29. Hind limb bones: (1, 6) PIN, no. 2198/160, pelvis and femurs; (2) PIN, no. 2198, femur: (a) posterior and (b) lateral views; (3) PIN, no. 2198/194, distal end of femur, posterior view; (4, 7) PIN, no. 2198/160, fragments of hind limbs, lateral view; (5) PIN, no. 2198/163, tibia and fibula: (a) anterior and (b) lateral views; (8) reconstructed pelvis, lateral view; and (9) PIN, no. 2198/160, digit 3, medial view. Designations: (*mt*) metatarsal, (*ph*) phalanx, and (*t*) digit. Scale bar, 1 cm.

HIND LIMB BONES

Pelvis

The pelvis is narrow and extended (Figs. 20, 29). The acetabulum is almost round in outline and faces ventrolaterally. The acetabular notch (incisura acetabuli) is narrow. The symphysis is extended.

The iliac bone (os ilium) has a long body (corpus ossis ilii) and a long and expanded flaring portion (ala ossis ilii). The alar portion has well-developed medial

and lateral tubers. The great sciatic notch (incisura ischiadica major) is deep.

The ischiadic bone (os ischium) has a long body (corpus ossis ischii) and a long ramus (ramus ossis ischii). Both the sciatic tuber (tuber ischiadicum), located on the ventral surface of the ramus and the sciatic spine (spina ischiadica), located on the dorsal surface of the body, are well developed. The lesser sciatic notch (incisura ischiadica minor), located on the dorsal surface of the bone, is not deep.

The pubic bone (os pubis) forms the ventral region of the pelvis. It consists of the body (corpus ossis pubis) and two rami: the cranial and caudal rami (ramus cranialis et ramus caudalis ossis pubis). These rami, along with the ischium, limit a long and narrow obturator foramen (foramen obturatum). In *Archaeomeryx*, the obturator groove (sulcus obturatorius) located at the dorsal border of this foramen is well developed.

The age and sex-associated variation is observed in measurements and certain other features of the pelvis. The collection includes medium-sized male pelves (PIN, nos. 2198/148, 154), a small pelvis of a presumable young female (PIN, no. 2198/149), and large pelves articulated with large sacral vertebra 1, which most likely belong to adult females (PIN, nos. 2198/159 and 160).

In males, the pelvis is narrower, the body of the ischium is shorter, the obturator foramen is longer, and the tuberculum pubicum is more massive than in females. The wings of the ilium in males appear to be in a more vertical position than in females.

In a young female, specimen PIN, no. 2198/210, the epiphyses of the limb bones are incompletely fused with the diaphyses and a number of sutures are clearly visible.

Femur

The femur is the most massive bone of the *Archaeomeryx* skeleton (Figs. 29, 30). The diaphysis of the bone is slightly twisted round the long axis and weakly curves forward.

The head of the femur (caput ossis femoris) is almost hemispherical in shape. The neck of the femur (column ossis femoris) is short and especially well distinguishable at the medial side of the bone inferior to the head. The greater trochanter (trochanter major) for the gluteus medius and gluteus profundus muscles is broad and prominent but only slightly higher than the femoral head. It is separated from the head by a deep trochanteric fossa (fossa trochanterica). The lesser trochanter (trochanter minor) for the iliacus and psoas major muscles is small and pointed. In the upper third of the bone, the gluteal tuberosity (tuberositas glutea) is well developed.

The proportions and morphology of the distal end of the *Archaeomeryx* femur closely resemble those of *Diacodexis* (Rose, 1996, text-fig. 2B) and leptictids (Rose, 1999, text-fig. 9).

The distal articular trochlea of the femur is relatively narrow and has a anteroposteriorly extended patellar surface (facies patellaris) for the patella. The medial condyle (condylus medialis) is only slightly larger than the lateral condyle (condylus lateralis). A deep extensor fossa (fossa extensoria) for the extensor digitorum longus muscle is present at the contact between the lateral condyle and the patellar surface. This fossa is especially well developed in ruminants and horses. Posterolateral to the extensor fossa, there is a distinct depression on the lateral epicondyle; it is probably the attachment area for the popliteus muscle.

The dorsal surface of the bone has small oval articular facets for the sesamoid bone [os sesamoideum (Vesalii)] located above each condyle. The Vesalii are placed in the tendon of the gastrocnemic muscle (musculus gastrocnemius).

Patella

The patella is the largest sesamoid bone (Fig. 30). It lies within the tendons of the quadriceps femoris muscle. The proximal end of the bone, the base of the patella (basis patellae), is weakly rounded, almost flat. The distal end, the top of the patella (apex patellae), is narrowed. The anterior surface is convex. The posterior surface is divided into two areas, which differ in size; the lateral area is larger and the medial area is smaller.

Tibia

The tibia is only slightly longer than the femur (Fig. 29). The shaft of the bone is relatively stout and triangular in section. Anteroposteriorly, it relatively strongly expands in the proximal part of the bone and strongly narrows in the lower one-third of the bone.

The dorsal (anterior) edge of the bone has a sharp tibial (cnemial) crest. At the proximal end of the latter, there is a relatively weak tibial tuberosity (tuberositas tibiae) for the patellar ligaments. The crest is moderately long, about 32% of the tibial length. Among tragulines, a long tibial crest is observed in *Leptomeryx* and *Hyemoschus*; a weakly developed tuberosity is observed in *Hypertragulus*.

The line for soleus muscle is well pronounced on the plantar surface of the bone.

The proximal end of the tibia is rather narrow and relatively weakly elongated anteroposteriorly (Fig. 30). It has medial and lateral condyles (condyli medialis et lateralis). A small articular facet for the fibula (facies articularis fibularis) is located on the lateral surface of the lateral condyle. The medial and lateral articular facets (facies articularis medialis et facies articularis lateralis) are separated from each other by the intercondylar eminence (eminentia intercondylaris), which bears the medial and lateral intercondylar tubercles (tuberculi intercondylare mediale et laterale) of approximately the
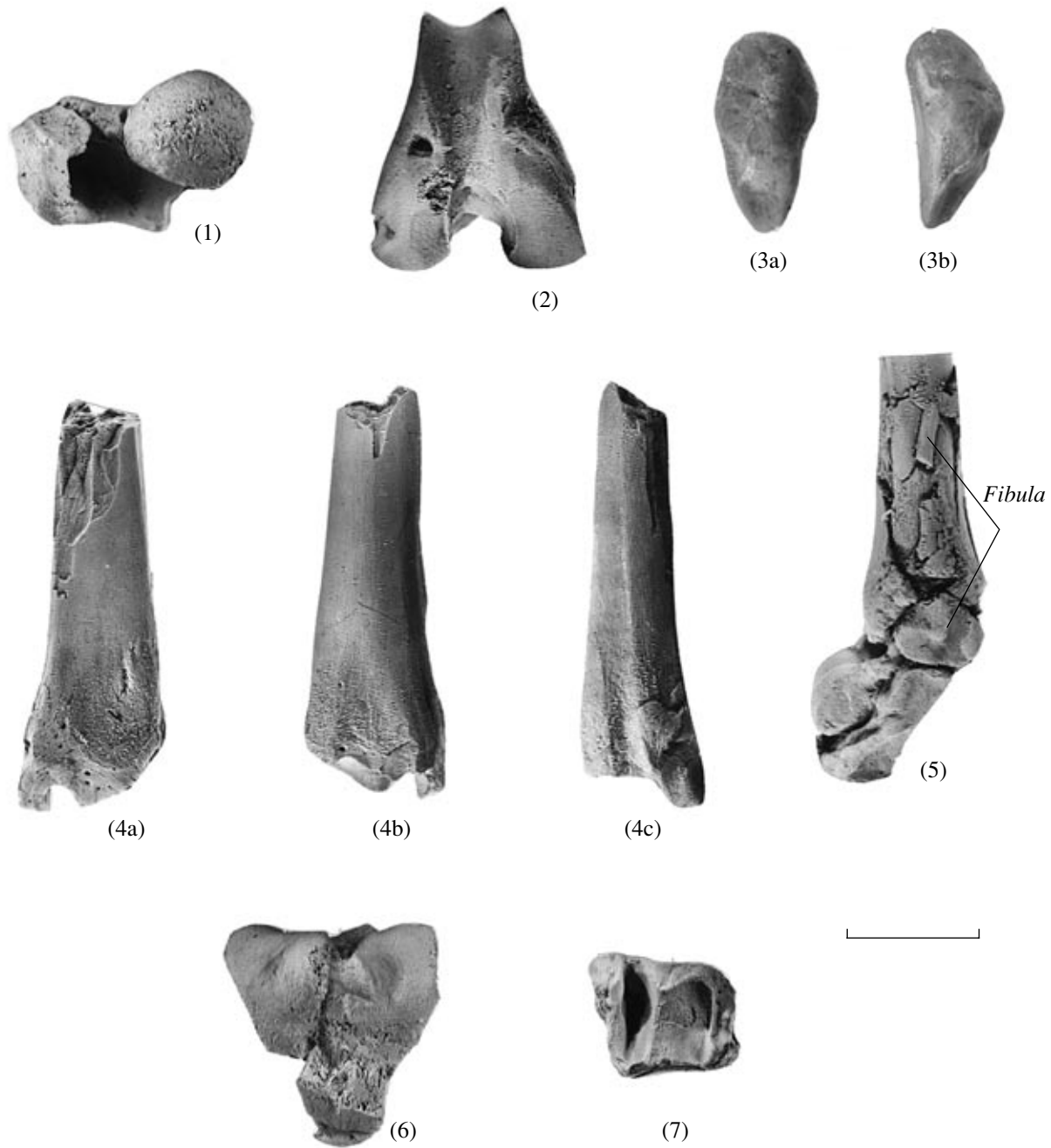
Fig. 30. Hind limb bones: (1) PIN, no. 2198, femur, superior view; (2) PIN, no. 2198/194, femur, inferior view; (3) PIN, no. 2198, patella: (a) anterior and (b) posterior views; (4) PIN, no. N 2198, distal end of tibia: (a) anterior, (b) posterior, and (c) medial views; (5) PIN, no. 2198/149, fragment of ankle joint, lateral view; (6) PIN, no. 2198/198, tibia, superior view; and (7) PIN, no. 2198, tibia, inferior view. Scale bar, 1 cm.

same height. A small posterior intercondylar area (area intercondylaris posterior) is located in a depression behind the medial intercondylar tubercle (tuberculum intercondylare mediale). A large anterior intercondylar area (area intercondylaris anterior) lies anterior to the intercondylar eminence. A moderately deep extensor sulcus (sulcus extensorius) is located on the dorsal margin anterior to the lateral condyle. It provides the

attachment area for the tendons of the long extensor of the digits (musculus extensor digitorum longus) and the third peroneal muscle (musculus peroneus tertius).

The distal end of the tibia has a well-developed medial malleolus (malleolus medialis; Fig. 30). Posterior to the latter, the medial surface of the distal end of the bone has a distinct malleolar groove (sulcus malleolaris). The distal articular surface of the tibia leans on
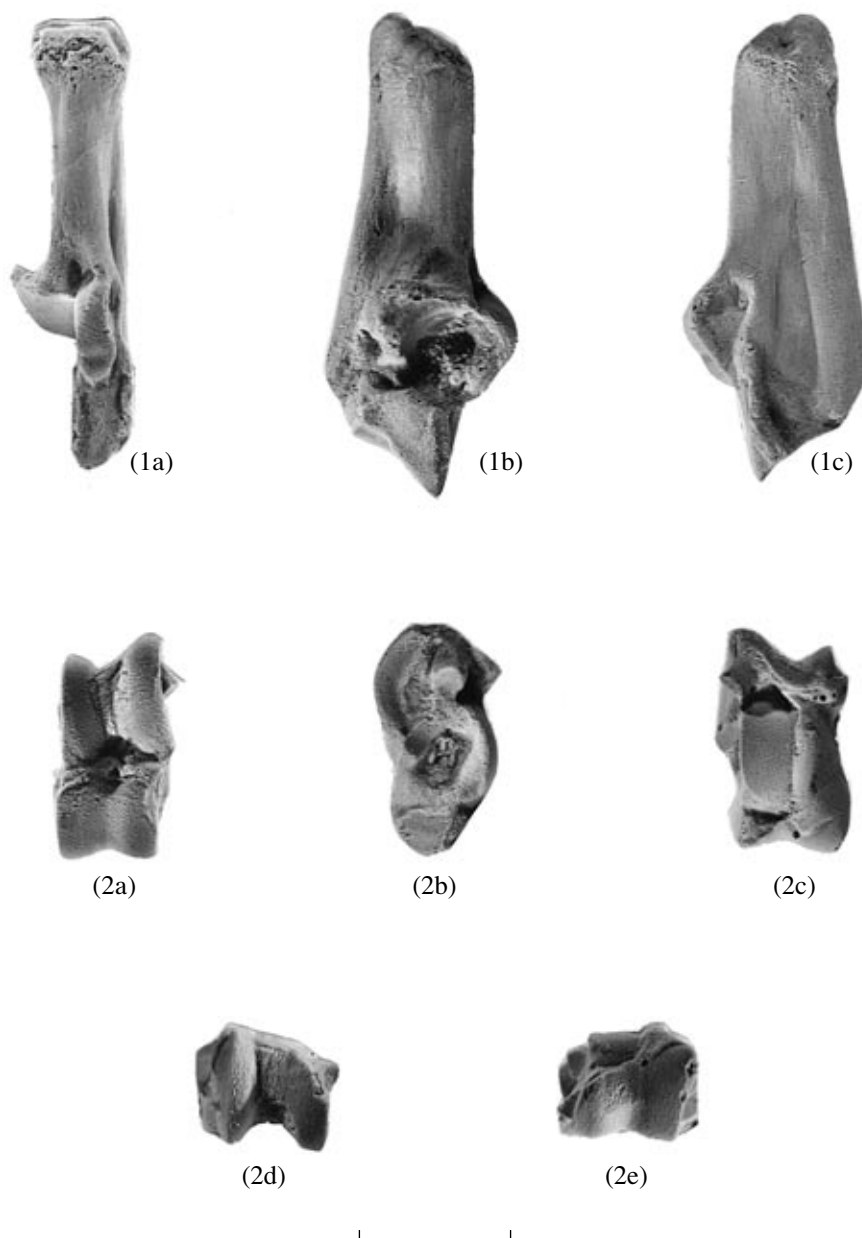
Fig. 31. Tarsal bones: (1) PIN, no. 2198, calcaneum: (a) anterior, (b) medial, and (c) lateral view; (2) PIN, no. 2198, astragalus: (a) anterior, (b) lateral, (c) posterior, (d) superior, and (e) inferior views; (3) PIN, no. 2198, calcaneum: (a) medial and (b) lateral views; and (4) PIN, no. 2198, astragalus: (a) anterior, (b) lateral, and (c) posterior views. Designations: (*DT*) distal trochlea, (*PT*) proximal trochlea, and (*PlT*) plantar trochlea. Scale bar, 1 cm.

the astragalus and fibula. The articular surface for the fibula is narrow. It consists of two short and concave facets of approximately the same size, which are separated from each other by a small groove for the shaft of the fibula.

In the advanced state, ruminants have a more anteroposteriorly elongated proximal region of the tibia, a better developed tibial tuberosity, and a shorter tibial crest. In addition, the articular surface for the fibula is a single and more complex facet, which is formed as a result of fusion of the two facets typical of the *Archae-*

omeryx developmental stage. In almost all ruminants, the facet for the os malleolus consists of two concavities and a small fossa between them.

Fibula

The fibula is complete but strongly reduced. It is positioned along the lateral side of the tibia and consists of a very thin shaft pressed to the tibia (PIN, no. 2198/200), a weakly expanded proximal end inferi-
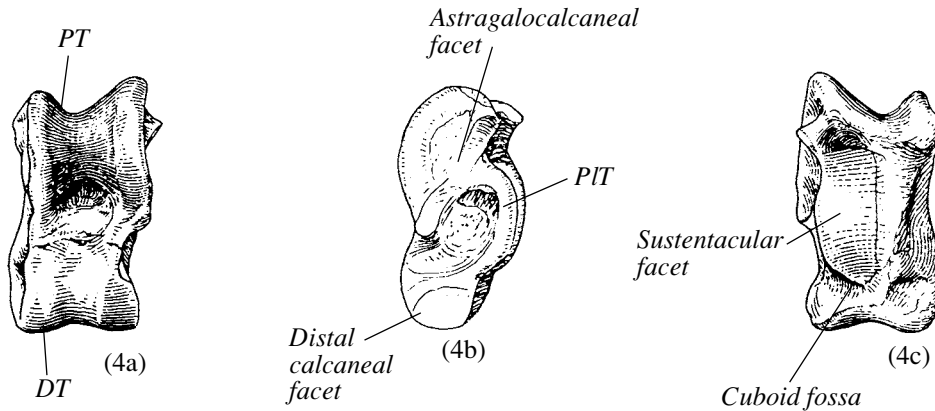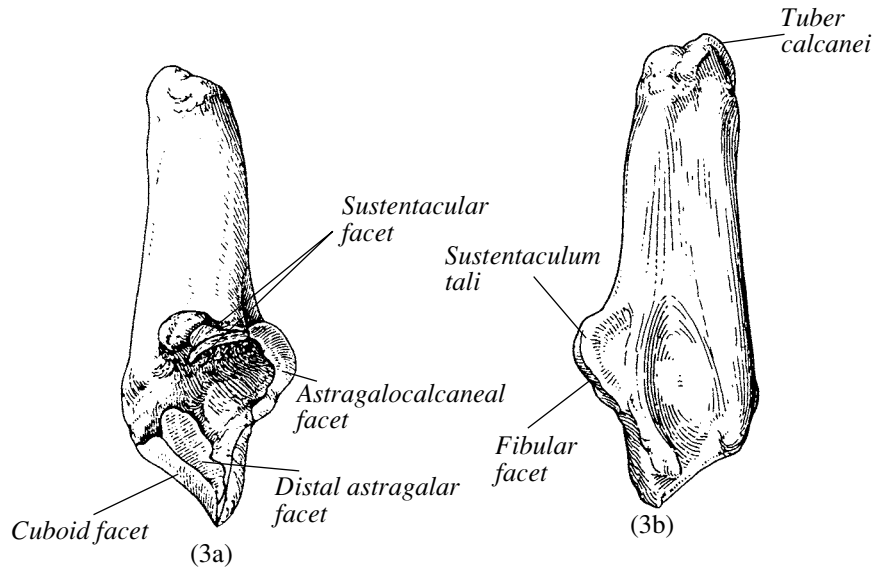
Fig. 31. (Contd.)

orly articulated with the lateral edge of the lateral tibial condyle, and a more massive distal end (Figs. 29, 30).

The shaft of the fibula of *Archaeomeryx* is extremely scarce. It was not observed in the specimens excavated by the expedition of the American Museum of Natural History.

The distal end of the fibula forms the lateral malleolus (malleolus lateralis), which is anteroposteriorly expanded and does not form a separate bone (os malleolus) characteristic of almost all ruminants. The proximal articular surface of the lateral malleolus contacts with the tibia, the medial surface contacts with the astragalus, and the distal articular surface contacts with the calcaneum.

In many tragulines, the proximal end of the fibula usually fused with the tibia; the distal end forms the os

malleolus. In *Hypertragulus, Hypisodus*, and *Tragulus*, the distal end of the fibula is also fused with the tibia.

PES

Tarsals

In *Archaeomeryx*, the number of tarsals decreased in comparison with the generalized eutherian type. The following six bones are present: the astragalus, calcaneum (calcaneus), scaphocuboid or naviculocuboid (scaphocuboideum or naviculocuboideum), and, probably, three tarsal bones, i.e., entocuneiform (tarsale I, cuneiforme I, or os cuneiforme mediale), mesocuneiform (tarsale II, cuneiforme II, or os cuneiforme intermedium), and ectocuneiform (tarsale III, cuneiforme III, or os cuneiforme laterale) (Figs. 29–34).
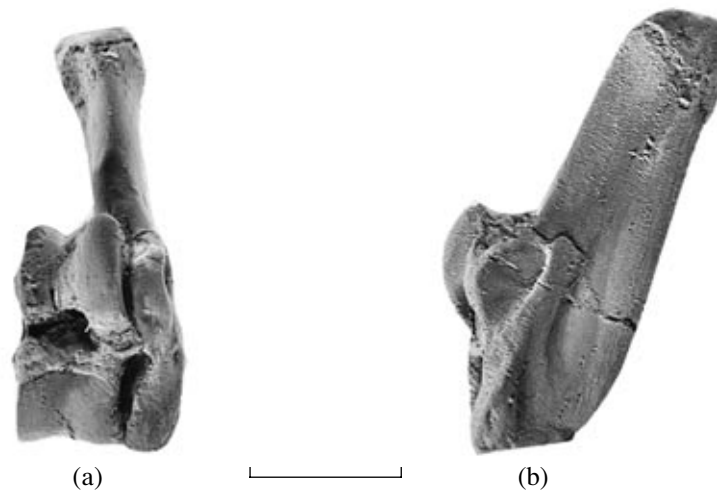
Fig. 32. Articulated astragalus and calcaneum, PIN, no. 2198/160, (a) anterior and (b) lateral views. Scale bar, 1 cm.

In the majority of ruminants, the navicular (os naviculare, os scaphoideum, or os tarsi centrale), cuboid (os cuboideum), and cuneiform II and III fused.

The astragalus (talus) is rather narrow and long. In contrast to those of the majority of artiodactyls, it is primitive tripulley (Fig. 31). Of its three trochleae (proximal, plantar, and distal), the proximal trochlea for the tibia is especially well developed. The axes of the trochleae are primitively nonparallel.

The proximal trochlea has a high lateral crest and a lower medial crest. The former is substantially shorter than the latter. The posterior edge of the proximal trochlea lacks median concavity. The depression under the proximal trochlea on the dorsal surface of the astragalus and the plantar hollow under the proximal trochlea of the astragalus are well developed. The neck of the astragalus remains as a narrow band between the proximal and distal trochleae on the anterior surface of the bone.

The almost semicylindrical plantar trochlea of *Archaeomeryx* is atypical of ruminants and apparently allows for not only vertical rotation (typical of the ruminant astragalus) but also certain inversion–eversion motion; according to Schaeffer (1947), this kind of motion was well pronounced in some early Paleocene arctocyonids and hyopsodontids. Among the extant mammal orders, a combination of these movements is characteristic of lagomorphs and rodents (Schaeffer, 1947).

The main axis of the plantar trochlea of the astragalus of *Archaeomeryx* extends close to the dorsal surface, similar to that of *Diacodexis*; however, it is positioned immediately above the neck of the astragalus. In *Archaeomeryx*, this axis and the longitudinal axis of the trochlea are at an angle of about 80°.

The distal trochlea of the astragalus of *Archaeomeryx* is less developed than those of other ruminants. It is low and narrower in transverse plane than the proximal trochlea. Moreover, the distal trochlea strongly narrows toward the lateral end; its lateral side is almost half as wide as the medial side. A well-pronounced ridge is present in the lateral part of the distal trochlea. This ridge corresponds to the boundary between the navicular and the cuboid.

On the plantar surface, the facet for the lateral process of the naviculocuboid occupies a primitive low position.

An elongated astragalocalcaneal facet is well pronounced on the lateral surface of the astragalus. Its long axis is weakly inclined to the longitudinal axis of the astragalus and nonparallel to the longitudinal axis of the facet for the sustentaculum tali of the calcaneum. Two stops (anteroinferior and posterosuperior) for the sustentaculum tali are well developed at the ends of the astragalocalcaneal facet. In higher ruminants, the lower stop serves in addition as the fulcrum for the os malleolus.

Regarding the degree of development and the position of the astragalocalcaneal facet, the astragalus of *Archaeomeryx* resembles a primitive ferungulate pattern rather than the astragalus of *Diacodexis*; in the latter form, the facet occupies a more vertical position (Schaeffer, 1947). In pecorans, the astragalocalcaneal facet is extremely weakly developed.

The interarticular fossa, which is located on the lateral side of the plantar trochlea, is large and deep.

In general, more advanced artiodactyls have a relatively short and broad astragalus. The proximal and distal trochleae are better developed. They are aligned in a row, and their axes are almost parallel or parallel to each other. The plantar trochlea of these animals is flattened. The sustentacular facet is elongated and broadened; its medial ridge is less prominent, and its longitudinal sulcus occupies a more central (median) position. Such transformation of the sustentacular facet is associated with the changes of the loads on its surface
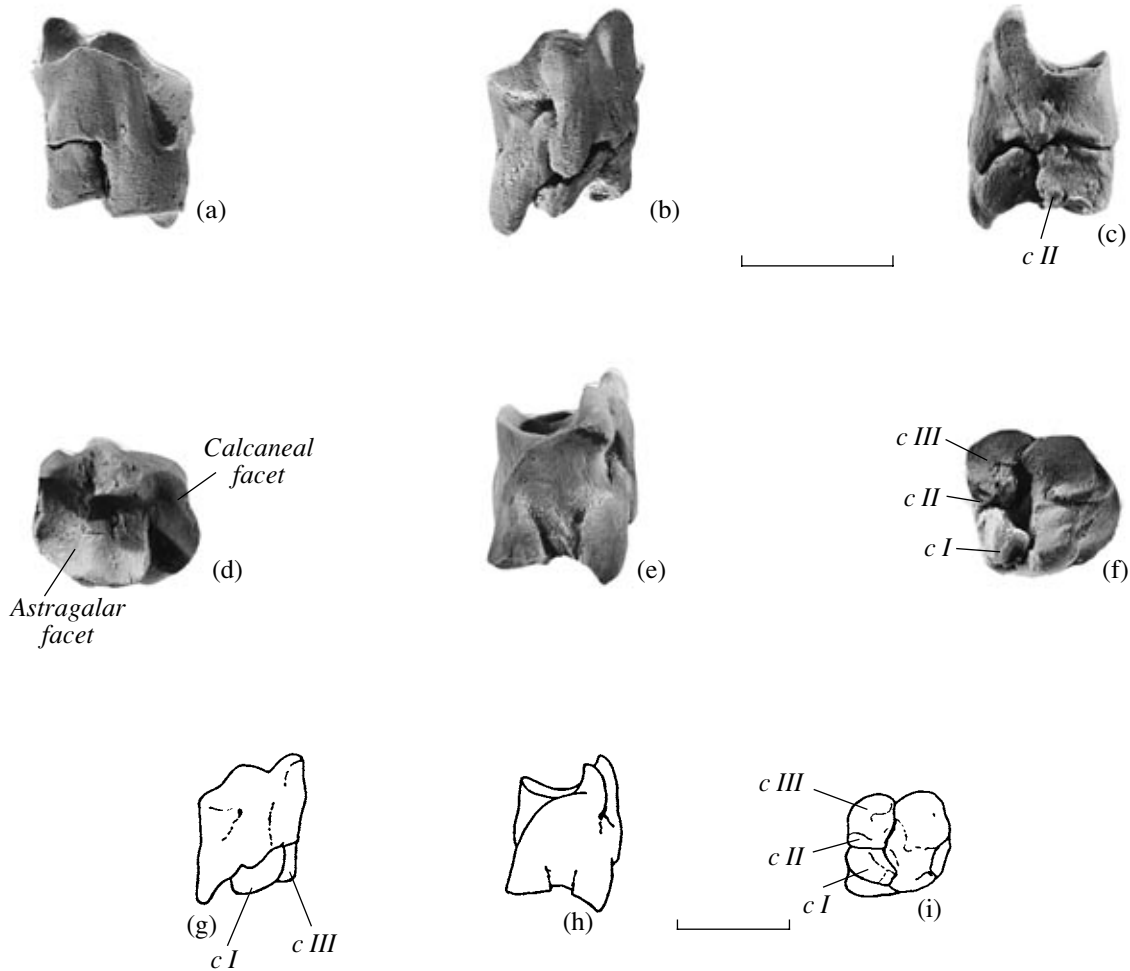
Fig. 33. Fragment of tarsus, PIN, no. 2198: (a) frontal, (b, g) posterior, (c) medial, (d) dorsal, (e, h) lateral, and (f, i) ventral views. Designations: (*c I*) entocuneiform, (*c II*) mesocuneiform, and (*c III*) ectocuneiform. Scale bar, 1 cm.

because of the improvement of the locomotory pattern, vertical straightening of limbs, and a decrease in the inclination of pes relative to the ground. These features of the sustentacular facet also provide a better contact between the astragalus and the calcaneum.

The calcaneum transmits the force of the gastrocnemic muscle (a strong extensor of the ankle joint, which is attached to the calcaneal tuber) to the pes.

The calcaneal tuber (tuber calcanei) and the articular region of the calcaneum are long (Figs. 31, 32). A long and deep sulcus for the peroneus longus muscle is well developed on the lateral surface of the calcaneum. The malleolar facet for the fibula (facies articularis malleolaris) is strongly convex and has a weakly pronounced depression in the lower part.

The sustentaculum tali of the calcaneum is relatively narrow and only slightly projects backward. Its articular surface reflects the morphology of the corresponding facet of the astragalus and is subdivided into two parts positioned at an angle, i.e., a broad lateral part and a very narrow medial part.

On the medial side of the articular region of the calcaneum, there are two facets for the astragalus. The lower facet is large and irregularly triangular in shape. The upper facet, which is commonly designated as the median articular facet (facies articularis media), is narrow. The cuboid facet (facies articularis cuboidea) is large and weakly concave.

The naviculocuboid is narrow and high (Figs. 33, 34). In some specimens (e.g., PIN, no. 2198/191), the line of fusion of the navicular and cuboid is clearly visible. The dorsal and two plantar projections are well developed on the proximal articular surface for the astragalus. The first projection is a flexor stop for the astragalus, and the plantar projections serve as its extensor stops.

The calcaneal facet on the naviculocuboid is long and broad. This facet is about one-third as wide as the naviculocuboid. Dorsally, the facet reaches the dorsal surface of the bone. The medioplantar angle of the distal surface of the naviculocuboid is strongly pulled backward. The sulcus for the tendon of the peroneus longus muscle, which is located on the distal surface of
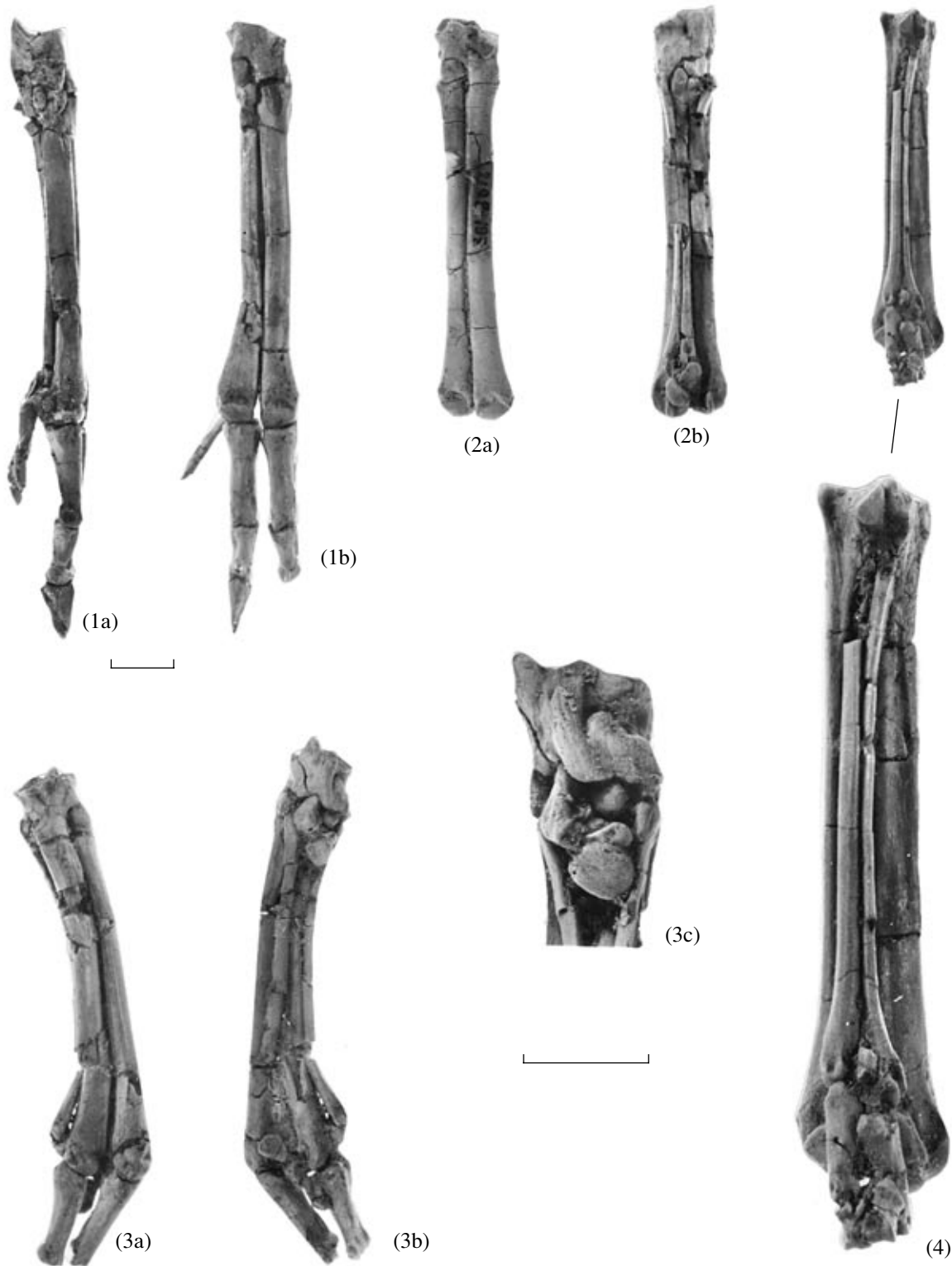
Fig. 34. Pes: (1, 5) PIN, no. 2198/160, fragmentary pes: (a) medial and (b) anterior views; (2) PIN, no. 2198/197, fragmentary pes: (a) anterior and (b) posterior views; (3, 7) PIN, no. 2198, fragmentary pes: (3a) anterior and (3b, 3c, 7) posterior views; and (4, 8) PIN, no. 2198/191, fragmentary pes, posterior view. Designations: (*c I*) entocuneiform, (*c II*) mesocuneiform, (*nav-cub*) naviculocuboid, (*mt I*) metatarsal I, (*mt II*) metatarsal II, (*mt III*) metatarsal III, (*mt IV*) metatarsal IV, (*mt V*) metarsal V, and (*se*) sesamoid bones. Scale bar, 1 cm.
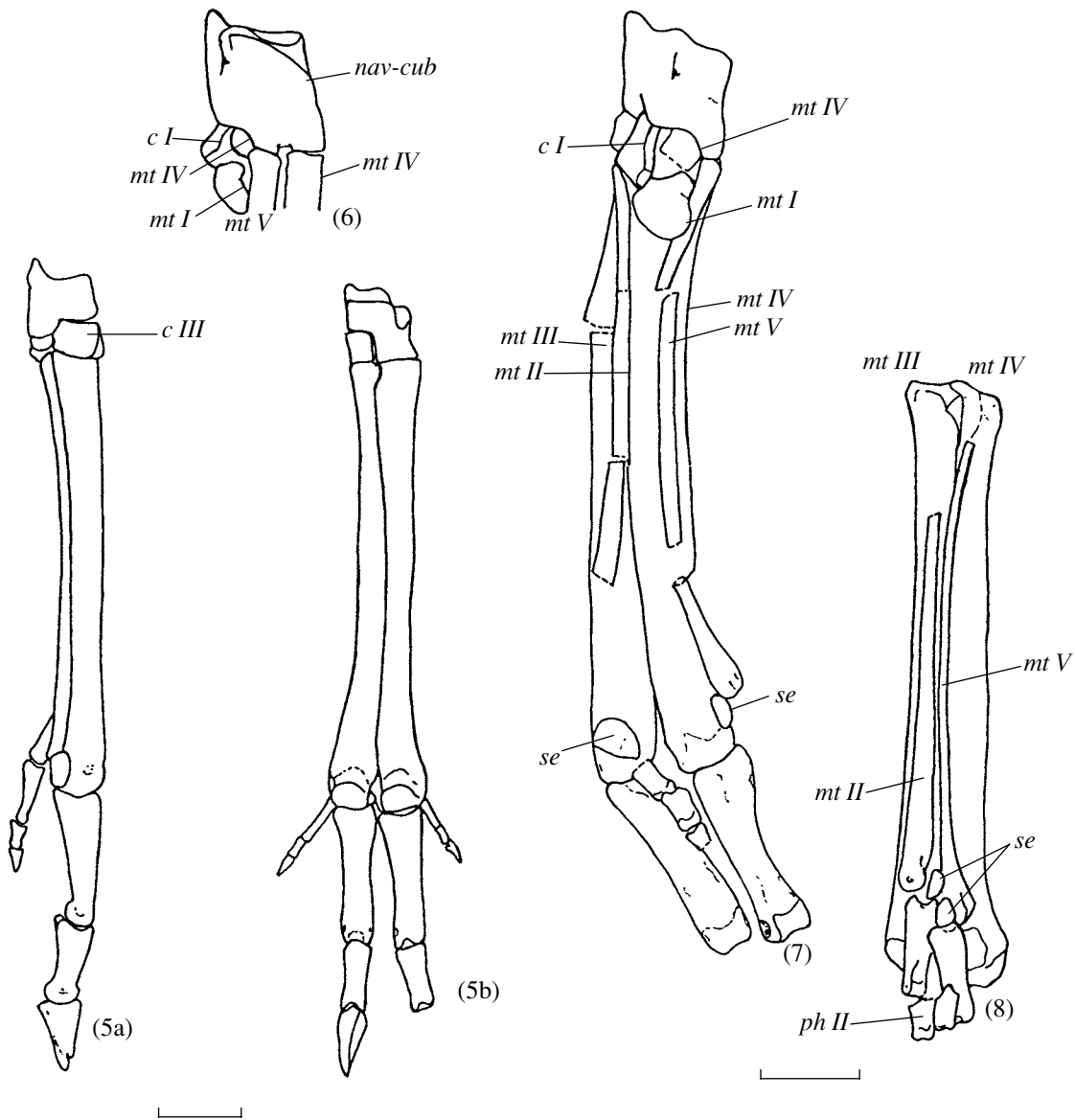
Fig. 34. (Contd.)

the naviculocuboid between the anterior and posterior metatarsal facets, is very weak. The tendon of the peroneus longus muscle is attached to cuneiform I; as it moves the latter, metatarsals II and III weakly rotate. The development of these characteristics of cuneiform I, which occurred in certain ruminants, allows them to change abruptly the direction of movements (to zigzag) at full speed (Leinders and Sondaars, 1974).

In the lateral part of the plantar surface of the naviculocuboid, there is a large concavity, which terminates at the vascular foramen. The plantolateral projection on the distal surface of the bone is strongly developed, hooklike, and directed downward. Metatarsals IV and V adjoin this projection.

The ectocuneiform and mesocuneiform (ossa tarsalia II + III) probably remain unfused in most individuals

(PIN, nos. 2198/148, 149, 160, 193, and 197) (Fig. 34, panels 1a, 1b). The mesocuneiform is substantially reduced. It is a small bone located between the ectocuneiform and the entocuneiform. In some articulated tarsi (e.g., in specimen PIN, no. 2198/197), the ectocuneiform is relatively short in anteroposterior dimension and has a small facet at the posterosuperior angle of the medial side, which probably adjoined the mesocuneiform. A small mesocuneiform articulated with the superiomedial surface of the ectocuneiform is known in some Paleocene eutherians from New Mexico (Szalay and Lucas, 1996, text-fig. 25). In this case, the mesocuneiform articulated medially with the entocuneiform. In specimen PIN, no. 2198/150, the ectocuneiform and mesocuneiform seem to be fused; this complex bone is
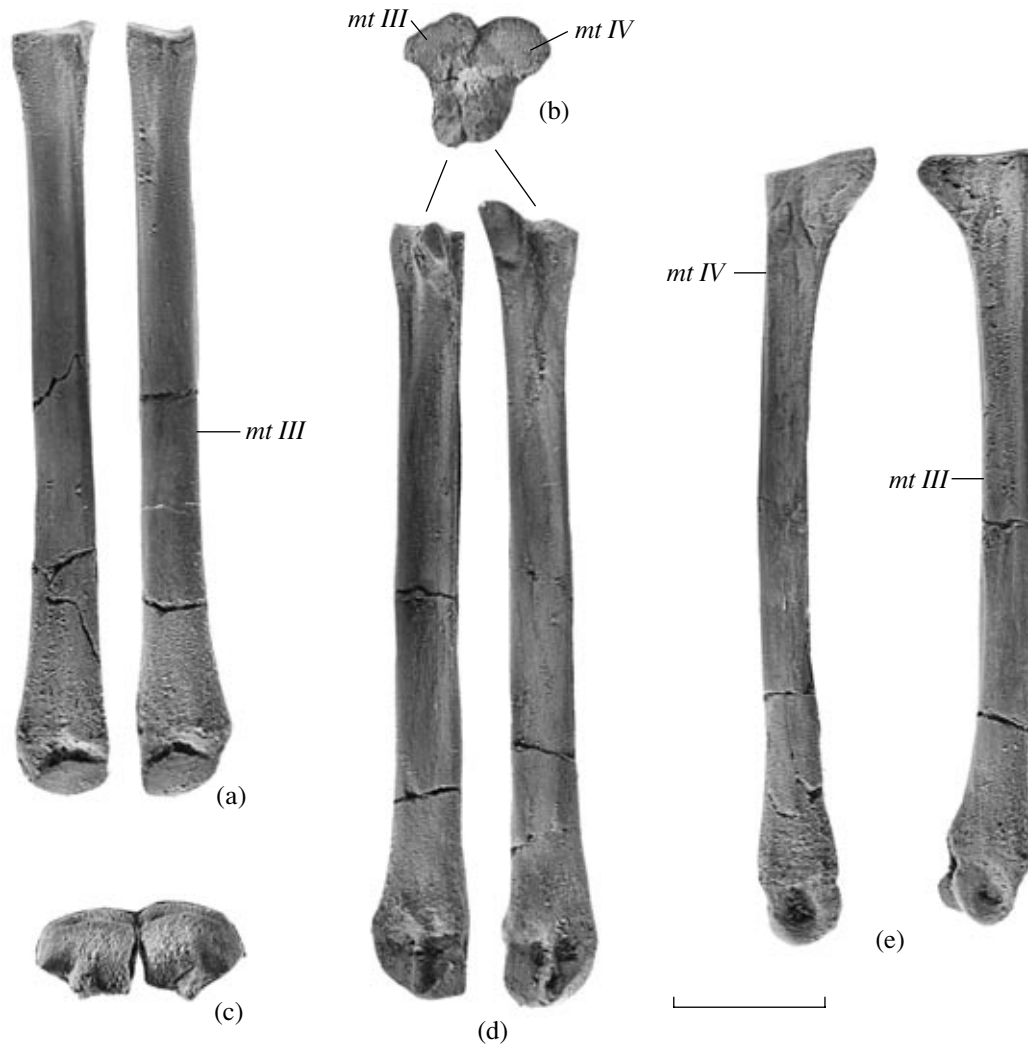
Fig. 35. Metatarsals, PIN, no. 2198/199: (a) anterior, (b) superior, (c) inferior, (d) posterior, and (e) medial views; for other designations, see Fig. 34. Scale bar, 1 cm.

somewhat larger than the ectocuneiform of other articulated tarsi.

The entocuneiform (os tarsale I) is large, close in size to the ectocuneiform. It is beanlike and flattened. It supports metatarsal I.

The lateral cuneiform (ectocuneiform) rests on metatarsal III and, partially, on metatarsal II. The entocuneiform is articulated with metatarsal II and I.

In the majority of ruminants, the ectocuneiform and mesocuneiform are fused; the entocuneiform is reduced and represented by a small bone. In extant adult tragulids, the ectomesocuneiform is fused with the naviculocuboid.

Metatarsals

All metatarsals of *Archaeomeryx* are separate. The second and fifth metatarsals (metatarsalia II et V) are only slightly shorter and almost twice thinner than the central metatarsals (Figs. 34, 35). Distally, they terminate somewhat proximal to the distal condyles of the central metatarsals.

The third and second metatarsals are articulated with the second and third cuneiforms, and the second metatarsal additionally contacts with the first cuneiform. The fourth and fifth metatarsals are articulated with the naviculocuboid.

A relatively massive and short platelike bone that is placed at the plantar surface posterior to the entocuneiform is probably a reduced first metatarsal. It has an irregular rounded plantar edge.

Phalanges

The first digit (hallux) is most likely lost.
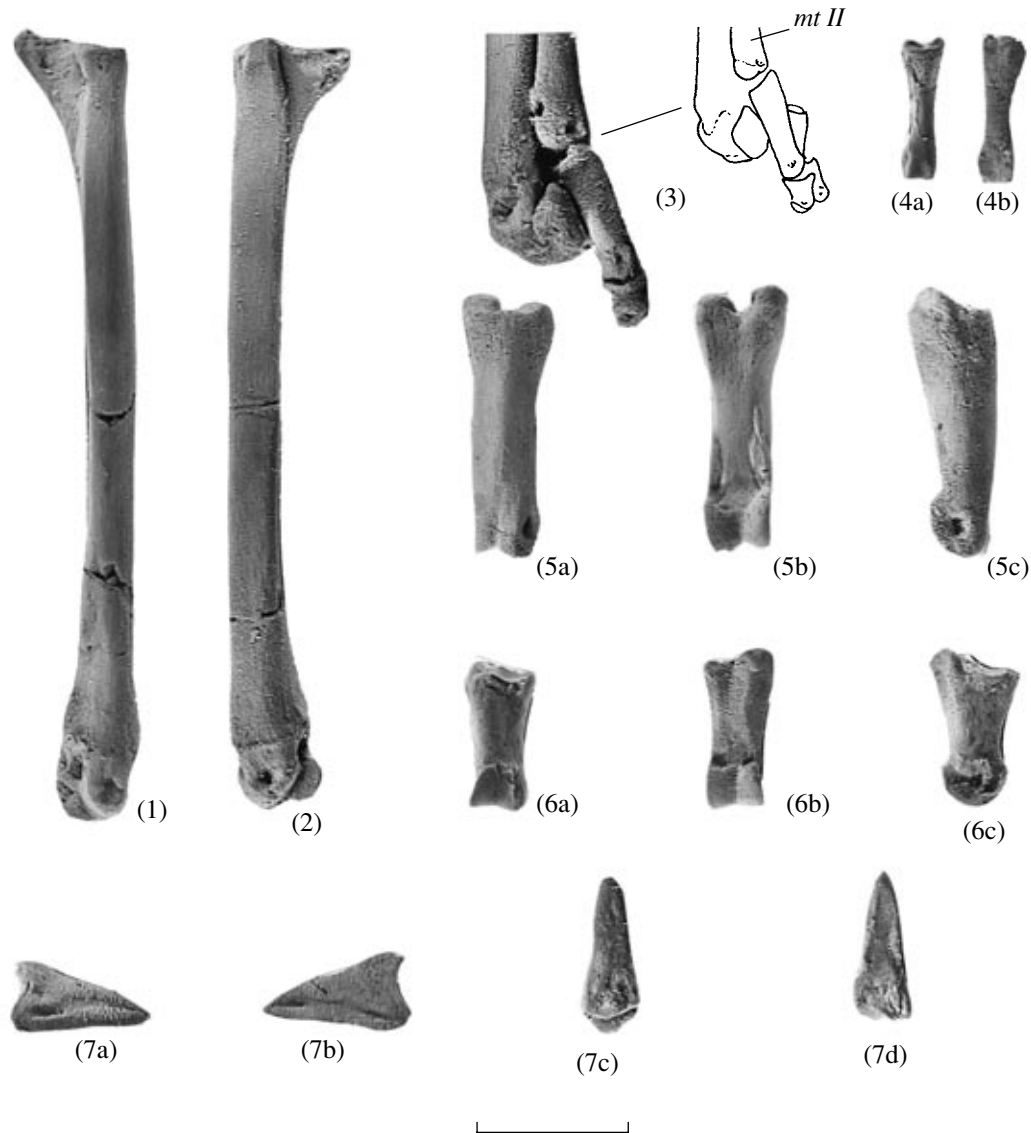
Fig. 36. Metatarsals and phalanges of pes: (1) PIN, no. 2198/199, metatarsal VI, lateral view; (2) PIN, no. 2198/199, metatarsal III, medial view; (3) PIN, no. 2198/191, fragment of pes, medial view; (4) PIN, no. 2198, first phalanx of side digit: (a) anterior and (b) posterior views; (5) PIN, no. 2198, first phalanx of median digit: (a) anterior, (b) posterior, and (c) lateral views; (6) PIN, no. 2198, second phalanx of median digit: (a) anterior, (b) posterior, and (c) lateral views; and (7) PIN, no. 2198, third phalanx of median digit: (a) lateral, (b) medial, (c) superior, and (d) inferior views. Scale bar, 1 cm.

The phalanges of the central (third and fourth) digits are well developed and large (Fig. 36). The first phalanges of the central digits are long. The second and third phalanges of the central digits are approximately equal in length. They are a little more than half as long as the first phalanx. The shape of the third phalanges of the central digits is typical of artiodactyls. The plantar surface of these phalanges is narrow and longer than those of the third phalanges of the forelimbs.

The side (second and fifth) digits are substantially thinner and half as long as the central digits. The distal end of the side digits reaches the lower third of the first phalanx of the central digits.

The first phalanx of the side digit is thin and long. It is approximately half as long as the first phalanx of the central digit. The second phalanx of the side digits is very short and broad. It is one-third as long as the first phalanx. The third phalanx of the side digits is short.

CHAPTER 4

MORPHOFUNCTIONAL ANALYSIS AND RECONSTRUCTION
OF THE MODE OF LIFE OF *ARCHAEOMERYX*

MORPHOFUNCTIONAL FEATURES OF SKULL AND POSTCRANIAL SKELETON

Morphofunctional analysis of *Archaeomeryx* shows adaptive changes in the skull, dental system, senses, and locomotor organs.

A detailed examination has shown that *Archaeomeryx* is distinguished from all known tragulines by a number of plesiomorphic characters of the skull and postcranial skeleton. These characters demonstrate relatively poor adaptation for feeding on plants and for rapid running in comparison with other ruminants.

Regarding many characteristics of feeding, locomotion, and organs of sense, *Archaeomeryx* resembles primitive eutherians; however, it has certain morphological characters that anticipate the appearance of higher ruminants.

The principal adaptations of *Archaeomeryx* are considered below.

FEEDING ADAPTATIONS

The structure of the jaw apparatus, temporomandibular joint, masticatory muscles, and dentition indicates that *Archaeomeryx* fed on mixed food, probably including insects, invertebrates, small vertebrates, and soft plants (mainly fruit, but leaves as well). The relative amount of plants in its diet was undoubtedly considerably less than in extant tragulids, which also consume some small animals.

Masticatory Apparatus

The structure and biomechanics of the masticatory apparatus of *Archaeomeryx* is most primitive among all known ruminants and has much in common with those of primitive insectivores, early ungulates, primates, and carnivores.

A very low upper jaw and jugal, a low position of the zygomatic arch, a low and curving body of the mandible, and a very weak development of the diastemata distinguish *Archaeomeryx* from other ruminants and resemble such primitive eutherians as *Kennalestes.*

The temporomandibular articulation of *Archaeomeryx* is located low and rather far from the posterior edges of the tooth rows, as in primitive mammals. The head of the mandible is weakly convex and allows for a wider opening of the mouth than is usually observed in ruminants.

The mechanics of jaw movements in *Archaeomeryx* remain relatively primitive and differ from those in the majority of other ruminants. Vertical movements of the jaws prevailed. The occlusion of teeth was mainly provided by the temporal muscle. The latter was thick and stout, and its base filled almost the entire postorbital region, as in carnivores. Anteriorly, dorsally, and posteriorly, this region is restricted to the temporal crests, a well-developed sagittal crest, and the occipital crest, respectively.

Weak lateral grinding movements were provided by the temporal and pterygoid muscles.

Higher ruminants are characterized by a relatively weak temporal muscle, extremely strong masseter, and strengthened pterygoid muscles.

In the course of ruminant evolution, the direction and magnitude of the masseter and pterygoid muscles changed in such a way that the tangent components of the resultant forces grew because of an increase in the height of appropriate regions of skull and mandible and because of a decrease in the distance between the points of application of forces (e.g., the insertions of the muscles) along the horizontal (Vislobokova, 1990b). These changes along with the decrease of the magnitude of the temporal muscle and the tangential component of its resultant force provided a greater efficiency of the masticatory apparatus for chewing with a substantial energy saving.

Dentition

The dentition of *Archaeomeryx* considerably differs from those of ruminants and resembles those of primitive eutherians. It is almost complete. Only the first upper premolars are lost, whereas, in some tragulids and all higher ruminants, the first premolars are lost in both the upper and lower jaws.

In contrast to almost all other ruminants, the lower canines of *Archaeomeryx* remain somewhat larger than the incisors and are not completely included in the incisor row. The small procumbent upper incisors, almost conical in shape, could be used for seizing animal and plant food objects. The presence of these teeth differs *Archaeomeryx* from all other ruminants. In size and shape, the teeth resemble those of some primitive eutherians and insectivores.

The small pointed upper canines and first lower premolars could serve for seizing, biting through, and holding animal and plant objects. The other premolars of *Archaeomeryx* performed mainly a cutting function, as in *Kennalestes*, insectivores, and carnivores. However, the brachyodont molars, with four weakly selenodont cusps, were already adapted to a certain degree for grinding plant food. The latter property is extremely developed in the majority of ruminants.

FEEDING POSTURE AND MOVEMENTS

The feeding posture, prevailing movements in the atlantooccipital joint, and the features of the cervical and thoracic regions of the vertebral column of *Archaeomeryx*, which are close to those of primitive eutherians, demonstrate one of the basic state of therian adaptation.

The position of skull, the structure of the occiput and atlantooccipital joint, and the features of the cervical and thoracic regions of the vertebral column of *Archaeomeryx* suggest a low position of the head and frequent lowering and raising the head, which is characteristic of animals picking food from the ground level. This means of feeding apparently dominated in early eutherians and remained in many artiodactyl lineages (particularly, in bovids).

In *Archaeomeryx*, the range of vertical movements in the atlantooccipital articulation was relatively small, about 40∞. The occipital condyles are small and narrow; the dorsal articular surface of the condyles is inclined cranially. The articular surfaces of the condyles converge at an angle of approximately 42∞, and the cranial articular fossae of the atlas are positioned at a right angle.

The range of head rotation, which is provided by the rotation of the atlas round the dens of the epistropheus, was severely limited in *Archaeomeryx*. The arc of the caudal articular fossae of the atlas, which articulated with the odontoid process of the epistropheus, was less than 30∞.

The movements were provided by well-developed muscles and ligaments originating from the occipital crest, supraoccipital, basioccipital, and the processes and crests of the vertebrae.

The adaptation for picking food from the ground surface is also indicated by the total length of the neck and head (159–165 mm, which exceeds even the length of a fully extended forelimb), the body shape, and the position of limbs (see below).

Archaeomeryx had a relatively long cervical region of the vertebral column, with a stout spinous process of the epistropheus and relatively long spinous processes gradually increasing in size from vertebra 3 to vertebra 7, as in *Tragulus*; however, they are wider than those of *Tragulus*. Cervical vertebrae 2–4 of *Archaeomeryx* have stout caudal expansions of the ventral crests for the musculus longus colli lowering the neck. The elongation of the segment of the supraspinal ligament between cervical vertebra 7 and thoracic vertebra 1 made this part of the *Archaeomeryx* vertebral column more flexible and contributed to shock absorption.

ADAPTATIONS OF ORGANS OF SENSE

Regarding the structure of brain and organs of sense, *Archaeomeryx* was more primitive than Recent tragulids, which, according to Voogd *et al.* (1998), show the most primitive artiodactyl pattern of sulci and many primitive brain features. For example, the brain of the water chevrotain (*Hyemoschus aquaticus*) has three main longitudinal sulci: the lateral rhinal, suprasylvial, and dorsomedial sulci; the latter sulcus is a continuation of the splenius sulcus (Voogd *et al.*, 1998). In shape and proportion of the brain regions and in some features of the sulcus pattern, the water chevrotain resembles the North American opossum (*Didelphis virganiana*) (see Voogd *et al.*, 1998, text-figs. 22.217a, 22.217h). Their olfactory bulbs are large, elongated, and anteriorly tapering. The cerebrum is low cranially and high caudally. The lateral rhinal sulcus is located rather dorsally (somewhat lower than the half height of the brain) and moderately extends caudally. The rostral part of the cortex does not cover the olfactory bulbs; between them, there is a short distance. The brain of *Archaeomeryx* was more primitive than that of *Hyemoschus* and similar to those of some primitive eutherians, insectivores, lagomorphs, and marsupials in the long olfactory bulb, the shape of hemispheres, and in a low cerebellum.

The features of organs of sense and brain structure of *Archaeomeryx* show that it had a well-developed sense of smell and less developed hearing and eyesight. *Archaeomeryx* apparently had a better sense of smell and worse hearing and vision than Recent tragulids. In its sense of smell, *Archaeomeryx* was probably intermediate between opossum and Recent tragulids.

Sense of Smell

A well-developed sense of smell in *Archaeomeryx* was used for the search for food, escape from enemies, and for biocommunication. The sense of smell was well developed in primitive eutherians, such as *Kennalestes*. It also plays an important role in the life of extant tragulids.

The long olfactory bulb in the brain of *Archaeomeryx* was only slightly shorter than one-fourth of the hemisphere length.

The olfactory bulb of *Didelphis* is a little shorter than half the hemisphere length. In *Hyemoschus*, the olfactory bulb is about 26% of the hemisphere length; in *Tragulus*, this ratio is 21% (Milne-Edwards, 1864, pl. VI, figs. 2, 5).

Hearing

The hearing of *Archaeomeryx* was relatively poor in comparison with those of other ruminants (including living tragulids); however, it was developed to a substantially greater extent than in early eutherians.

In *Archaeomeryx*, the tympanic region of the temporal is less developed than in other ruminants and almost lacks the external auditory meatus. A small tympanic bulla is extremely weakly inflated and overlaps only

two-thirds of the petrosal. In living tragulids, the tympanic bulla is strongly inflated and completely overlaps the petrosal; the external acoustic meatus is elongated.

The tympanic membrane, which was located at the base of the external auditory meatus, was apparently larger than that of *Tragulus*. It was about 3 mm in diameter.

In *Archaeomeryx*, the auditory ossicles, which amplify and transmit the sound waves, and seem to be very small, judging by the small-sized and shallow recessus epitympanicus enclosing these ossicles. The oval window, which transmits sound vibrations to the fluid of the inner ear, is also small-sized. In Recent tragulids, these structure are more advanced and larger in size. Consequently, the structures of the middle ear and the oval window of *Archaeomeryx* could amplify a relatively narrower range of sound waves compared to those of Recent tragulids.

The inner ear of *Archaeomeryx* was more primitive in structure and apparently less effective than those of many tragulines. The cochlea of the inner ear was simple, robust, not inflated, not expanded, and consisted mostly of one whorl, as in primitive mammals; therefore, it was poorly adapted for the generation of nerve impulses compared to those of many other tragulines, including Recent tragulids. Both *Tragulus* and *Hyemoschus* possess a more complex, thin, and relatively more inflated cochlea, the last two whorls of which are almost equal in size. It is not surprising that, being inhabitants of tropical forests, Recent tragulids have a less developed smell and better developed hearing than *Archaeomeryx*.

According to Voogd *et al.* (1998), the size of the auditory region of the anterior dorsal ventricular ridge (ADVR) in *Hyemoschus* shows that the hearing of this animal is better than that of *Didelphis*. In *Hyemoschus*, the lateral rhinal sulcus, bordering this region inferiorly, strongly curves inferiorly. In *Didelphis*, this sulcus only slightly curves inferiorly and the auditory region of ADVR is less expanded. The auditory region of ADVR in the brain of *Archaeomeryx* was probably of approximately the same size and position.

Vision

The vision of *Archaeomeryx* was probably weaker than in living tragulids. This is demonstrated by small orbits and a very small optic foramina for the optic nerve (nervus opticus) and external ophthalmic artery (arteria ophthalmica externa). These foramina are substantially smaller than those of living tragulids, in which they are confluent because of the enlarged eyes and a thick optic nerve transmitting the nervous impulses to the visual center of the brain.

LOCOMOTORY ADAPTATIONS

The structure and biomechanic features of postcranial skeleton of *Archaeomeryx* provide important infor-

mation on locomotory adaptations and ecology of this animal.

Regarding many locomotory adaptations, *Archaeomeryx* is undoubtedly the most primitive member of ruminants and more primitive than diacodexids and condylarths. In some respects, *Archaeomeryx* is close to primitive eutherians.

Very important information on the locomotion of *Archaeomeryx* was obtained by the study of its almost complete skeleton preserved in the sediments (PIN, no. 2198/200) and a very informative photo of four skeletons discovered by the Joint Soviet–Chinese Expedition (Fig. 37). This extremely rare (in paleontology) case of conservation of postmortem postures provides us with a better understanding of the characters of *Archaeomeryx* locomotion (Vislobokova and Trofimov, 2000b). The shape of the animal, curvature of the vertebral column and tail, position of limbs, and the angles between the articulated bones are fixed and correspond to the state during the standing jump, when the animal propels itself forward and up, owing to the automatism of the neuromuscular system.

Unlike the majority of ruminants, *Archaeomeryx* was better adapted for saltatorial (leaping) than for cursorial locomotion.

A rapid gait of *Archaeomeryx* was apparently similar to primitive rebounding leaps characteristic of most insectivores, marsupials, some rodents, and, as Gambaryan (1972) proposed, close to that of the ancestors of ungulates. This is a quadrupedal gait whereby the hind legs are brought anteriorly just after they lose contact with the ground.

This is probably the most primitive type of leaping observed in mammals. It is noteworthy that the locomotor mode of living tragulids resembles to a certain degree the movements of agouti and consists in small jumps followed by a rise of the posterior region of the trunk.

Gambaryan (1972) associated the development of primitive rebounding jumps with the initial semifossorial mammalian mode of life and with the prevalence of the hind limb support of the body. According to this hypothesis, early mammals used the forelimbs for raking away leaves, forest litter, and upper layers of soil in searching for invertebrates. The same limb functions were basically retained in *Archaeomeryx*.

The shape of body and vertebral column also demonstrate features suitable for these basal eutherian adaptations. The vertebral column of *Archaeomeryx* has a weaker thoracocervical curvature and stronger thoracolumbar and sacrocaudal curvatures than those of living tragulids (Fig. 38). In addition, the vertebral column of *Archaeomeryx* is positioned lower in the anterior part of the thoracic region, whereas, in the lumbar region, it is more curved and much more strongly raised than those of living tragulines. This counterbalances the light anterior part of the *Archaeomeryx* body and the considerably heavier posterior part.
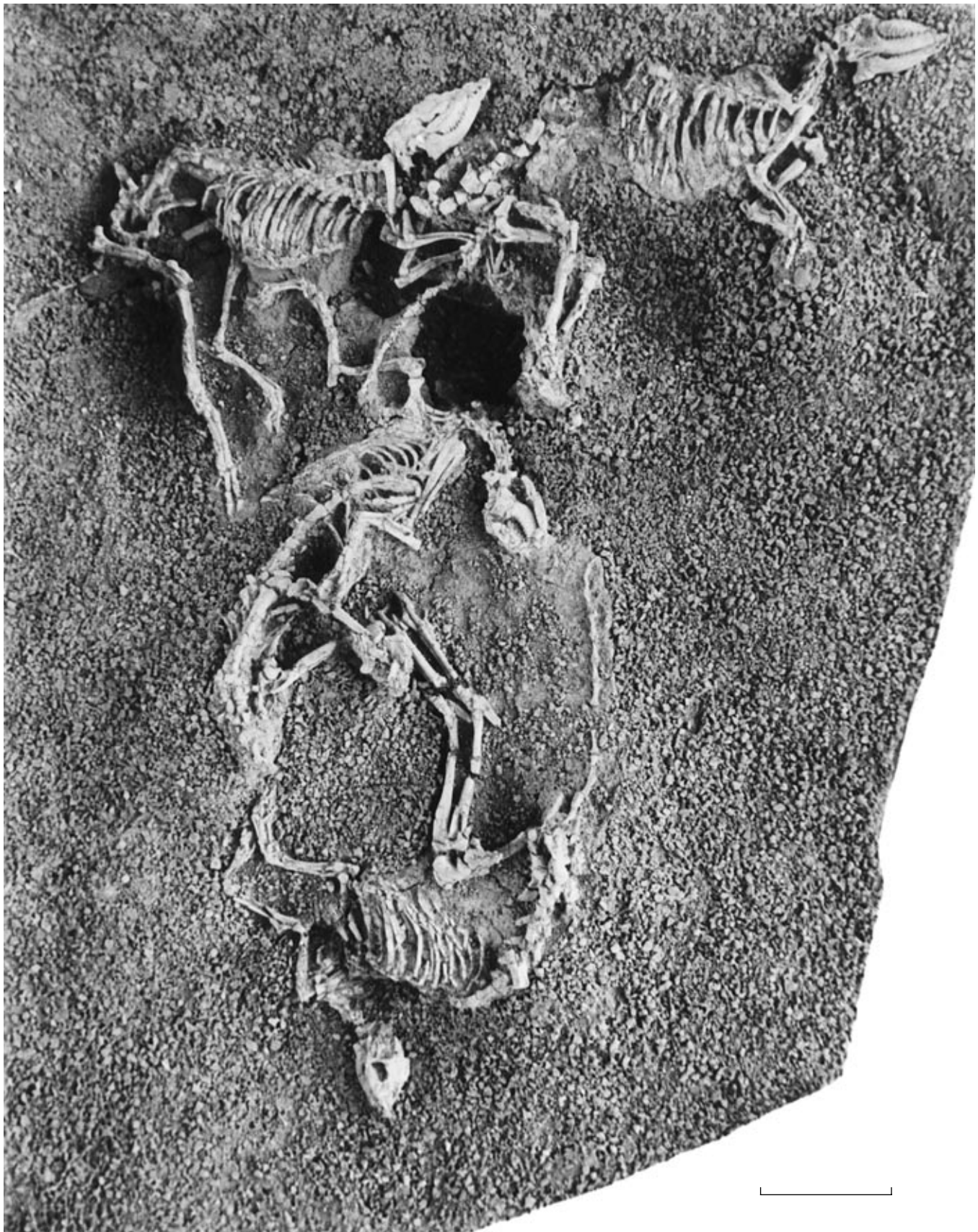
Fig. 37. Articulated skeletons in postmortem postures found by the Joint Soviet–Chinese Expedition. Scale bar, 10 cm.
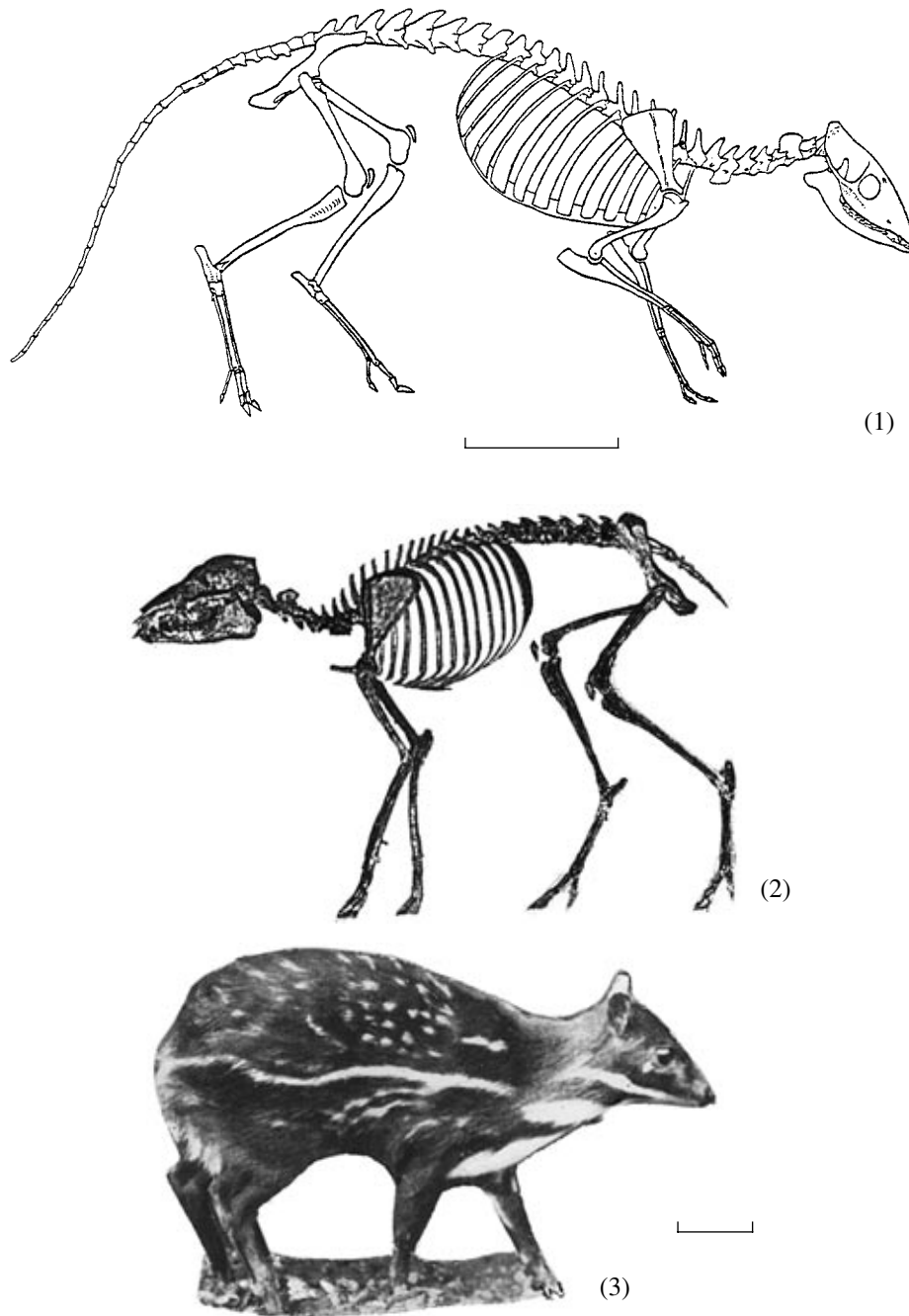
Fig. 38. Reconstructed Skeletons of *Archaeomeryx*, early ungulates and Recent water chevrotain: (1) *Archaeomeryx*; (2) *Hypertragulus calcaratus*, Harvard University, no. 3809; (3) *Hyemoschus* (after Abel, 1927, text-fig. 161); (4) *Chriacus truncatus* (after Rose, 1987, text-fig. 1A); (5) *Diacodexis* (after Rose, 1982, text-fig. 1); and (6, 7) *Messelobunodon* (after Franzen, 1981 text-figs. 6, 10). Scale bar, 10 cm.

In the case of rapid gait, the forelimbs of *Archaeomeryx* served as shock absorbers; the hind limbs performed the locomotor (pushing) and, partially, shock-absorbing functions. However, the rate of moving the hind limbs anteriorly during the suspended phase after leaving the ground was apparently lower than in the case of a true rebounding gait, but higher than in the case of a leaping gallop, which is characteristic of many living small mammals.

In the postmortem posture of *Archaeomeryx*, it is seen that the greatest curvature of the dorsum corresponds to the greatest extension of the hind limbs drawn under the trunk, as in lagomorphs, rodents, and carnivores. In suspension (while airborne), *Archae-*

Fig. 38. (Contd.)

omeryx apparently moved its hind legs forward not as far as the majority of ruminants; its fore and hind limbs did not cross, as in some rodents displaying primitive rebounding jumping (e.g., *Rattus*).

As living ungulates gallop, the forelimbs, along with the hind limbs, actively participate in locomotion and push the body forward.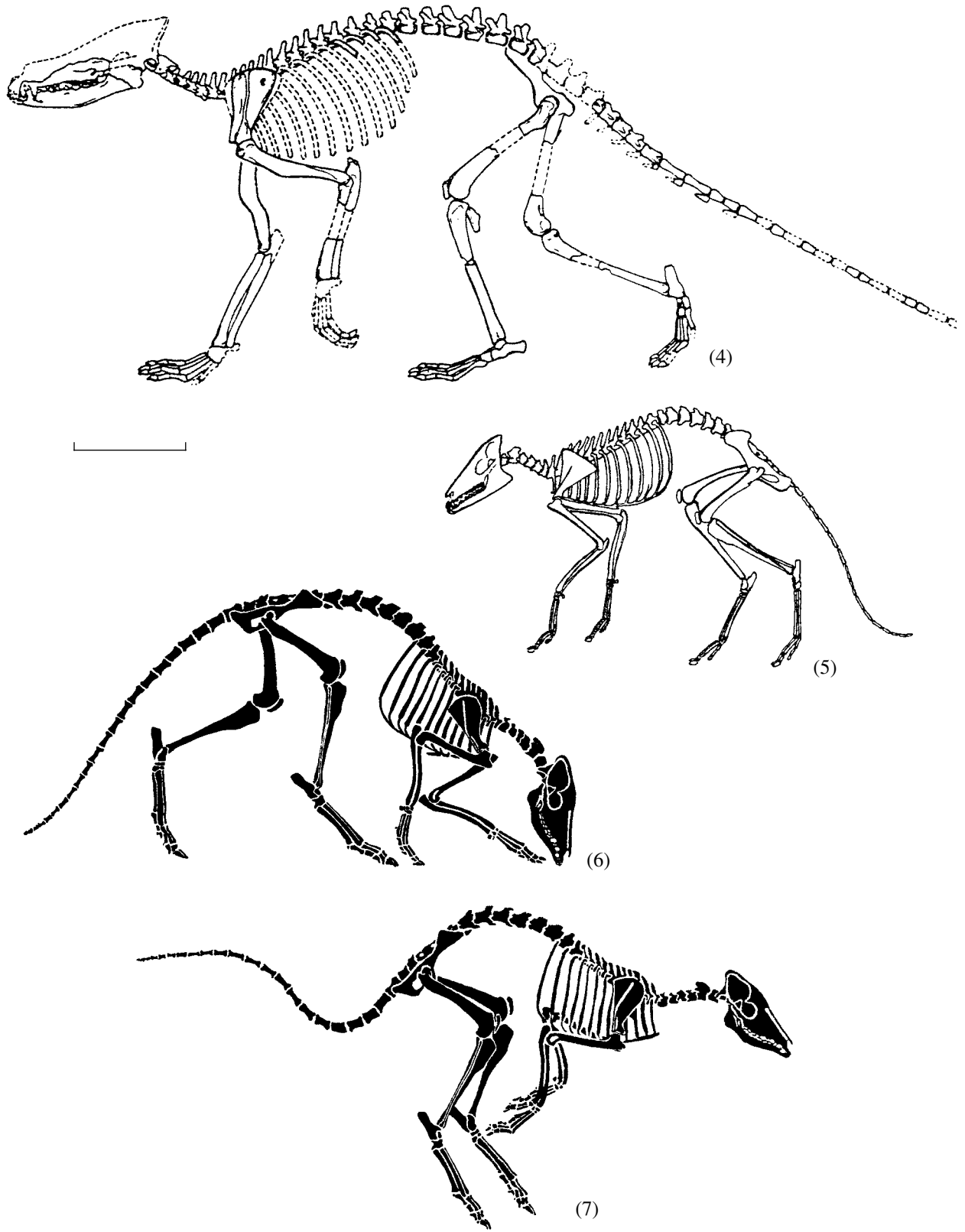 The dorsum of the majority of ungulates is much more rigid, the range of flexion–extension motion of limbs is greater, and a stride includes the cross stage where the fore and hind legs cross during the suspension in the gallop (e.g., in *Capreolus*).

The Main Features of Vertebral Column and Ribs

The flexion–extension movements of the vertebral column apparently played an important role in the locomotion of *Archaeomeryx*, as in some rodents, lagomorphs, and carnivores. In these animals, before a jump, the center of gravity is raised (above the starting position) by the extensors of the dorsum.

In ungulates, the rigidity of the vertebral column during running is provided by the complex of the supraspinous processes, supraspinous ligament, transverse processes of the lumbar vertebrae with the intertransverse ligaments, and locks of the articular processes of the lumbar and sacral vertebrae.

The supraspinous ligament is an important element of the shock-absorbing system and appears to be the most important element of this system in *Archaeomeryx*. The well development of this ligament in this animal is evidenced by a strong posterior projection of the occipital crest (the origin of the nuchal ligament) and by the presence of the spinous processes from the third cervical vertebra to the fourth caudal vertebra. The supraspinous ligament extended along the tops of these processes. In the majority of ungulates, the spinous processes on the cervical vertebrae behind vertebra 2 are usually absent or weakly developed and the tops of the spinous processes of the thoracic and lumbar vertebrae are anteroposteriorly widened. As they run, the first feature provides the head with better shock absorption and the second provides a greater rigidity of the back.

In *Archaeomeryx*, the shock absorbers of the head and neck are weaker, the lumbar region of the vertebral column is more flexible, and the thoracic and sacral regions are less rigid than those of the majority of ruminants.

The shock-absorbing difference in the length of the spinous processes of cervical vertebra 7 and thoracic vertebra 1, which is typical of the majority of ruminants, is rather weak in *Archaeomeryx*. However, the enlarged distances between the apices of these spinous processes and between the tops of thoracic vertebrae 3, 4, and 5 indicate the elongation of these regions of the supraspinous ligament, which serve for amortization.

A weak increase in the rigidity of this region of the back occurred by the anteroposterior enlargement of the top of the spinous process of thoracic vertebra 6.

In *Tragulus*, the tops of all spinous processes of the thoracic vertebrae, beginning with the third vertebra, are expanded and flattened. In the majority of ungulates, the rigidity of the back is provided by even greater anteroposterior expansion of the tops of the spinous processes.

The withers typical of ungulates is absent in *Archaeomeryx*; consequently, the load on this region of the vertebral column at the moment of landing was lower than in the majority of ungulates.

A substantial decrease in the distances between the spinous processes of thoracic vertebrae 10 to 13 indicates that this region of the *Archaeomeryx* vertebral column was relatively rigid.

The lumbar region of the vertebral column of *Archaeomeryx* was more mobile in the vertical plane than those of the majority of ungulates, in which the rigidity of this region is provided by strongly developed supraspinous and intertransverse ligaments and by the locks of the zygapophyses.

In *Archaeomeryx*, the supraspinous ligament in the lumbar region was probably weakly developed, and a fluent flexion–extension motion in this region was provided by the interspinous ligaments. The slightly anteroposteriorly expanded spinous processes of two last lumbar vertebrae made this section of the lumbar region of the vertebral column more rigid.

The intertransverse ligaments, which were attached to relatively short horizontal transverse costal processes, were probably weaker than those of the majority of ungulates.

The zygapophyses of all vertebrae, except for the posterior lumbar vertebra, do not form locks. The anteroposteriorly elongated and very narrow locks restricted extension in the lumbosacral articulation but allowed for certain lateral curvature.

An important primitive feature of *Archaeomeryx* is the preservation of certain mobility in the sacral region; this is atypical of the majority of ungulates.

A relatively high flexibility at the boundary of the lumbar and sacral regions is evidenced by the enlarged distance between the tops of the last lumbar and first sacral vertebrae, which reflects the elongation of the supraspinous ligament in this region. In a more derived condition, which is typical of higher ruminants, the elongation occurs by the anterior inclination of the spinous process of the lumbar vertebra and a vertical position or posterior inclination of the spinous process of the first sacral vertebra.

The sacrum of *Archaeomeryx* is less durable than those of other ungulates and usually consists of four isolated vertebrae. In *Leptomeryx* and *Tragulus*, the sacrum consists of five fused vertebrae, as in the majority of higher ruminants. In these animals, an increase in

Table 7. The ratios of the length of limb segments to the total length of the thoracic and lumbar regions of the vertebral column

No.	Segment	N	Min–Max	M
1	Brachium (B)	6	0.269–0.320	0.296
2	Antebrachium (A)	6	0.238–0.266	0.250
3	Manus (M)	4	0.212–0.292	0.425
4	B + A + M	4	0.738–0.879	0.795
5	Femur (F)	7	0.350–0.396	0.378
6	Crus (C)	6	0.377–0.428	0.419
7	Pes (P)	6	0.383–0.49	0.452
8	F + C + P	5	1.169–1.297	1.254

durability spreads to the first caudal vertebra, which is included in the sacrum.

In *Tragulus*, the lumbosacral region of the vertebral column is often strengthened by a bony sacroischiadic bridge. In other ruminants, the sacrum is usually firmly fused into one solid structure.

It is well seen that a number of features of the lumbosacral region of the *Archaeomeryx* vertebral column can be regarded as preadaptation restricting the flexion in this region in more derived ungulates. These features outline the following evolutionary tendencies typical of ungulates:

(1) massiveness of the posterior lumbar vertebrae (PIN, nos. 2198/159, 160);

(2) development of locks in the posterior lumbar vertebra; and

(3) partial fusion of the posterior sacral vertebrae (two or even three of them) in some individuals.

Archaeomeryx is also distinguished from the majority of artiodactyls and all ruminants (including *Hypertragulus, Hypisodus*, and living tragulids) by a very long and mobile tail, which was strong and probably served for balance during locomotion. Among artiodactyls, a similar long tail is observed in *Diacodexis* (Rose, 1982).

A strong development of the depressors of tail is evidenced by distinct fossae on the ventral surface of the second caudal vertebrae and well-developed transverse processes of succeeding vertebrae, particularly, those of vertebrae 3–6, to the ventral surfaces of which they are attached. A strong development of the elevators of tail manifests itself in the presence of the spinous processes on the first caudal vertebrae and the articular processes or their rudiments up to the posteriormost vertebrae, i.e., the places of their attachment. In all individuals (collection PIN), caudal vertebrae 4 and 5 are somewhat dorsocaudally raised.

The ribs of *Archaeomeryx* had flattened bodies, which are strongly expanded in thoracic vertebrae 3–8, where the fascicles of the thoracic portion of the musculus serratus ventralis thoracis originated. This muscle along with the thoracic region of the vertebral column and other thoracic muscles, served for shock absorbing,

as the forelimbs landed; in addition, they helped to extend the trunk anteriorly.

Limb Features

A large difference in the length between the fore and hind limbs, the ratios of the limb segments (Table 7), the range of flexion–extension motion in the joints, the structural features of the joints, a strong inclination of the autopodium to the ground surface, and the position of the insertion points of the main muscles show that *Archaeomeryx* had a well-developed saltatorial ability, whereas cursorial adaptations were very weak.

In addition, *Archaeomeryx* differs from the majority of coursers by the scapula, which occupies a relatively dorsal position, intermediate between those of typical coursers and noncoursers, rather than lies along the side of the deep thorax (as, e.g., in deer). The thorax is also intermediate in shape between those of the two groups.

Length and proportions of limbs. The elongation of the zygapodium and metapodials and reduction and fusion of a number of limb bones, which are characteristic of the ungulate evolution and were first investigated by Kowalevsky (1873–1874, 1875), were extremely weakly developed in *Archaeomeryx* (Colbert, 1941; Webb and Taylor, 1980).

The forelimb was approximately two-thirds as long as the hind limb and three-fourths as long as the thoracolumbar region of the vertebral column. The ratios are 0.625–0.69 ($M = 0.649$, $N = 4$) and 0.738–0.879 ($M = 0. 795$, $N = 4$), respectively (Table 7).

The tibia is longer than the femur. The crural index, i.e., the ratio of the tibia length to the femur length (tibia/femur), is 1.021–1.115 ($M = 1.07$, $N = 12$).

The autopodium of both fore and hind limbs is elongated to a much lesser extent than those of cursorial forms.

The manus of *Archaeomeryx* remains extraordinarily short for ungulates. It is almost half as long as the pes. The ratio of the manus length to the pes length is 0.478–0.636 ($M = 0.54$, $N = 5$). The manus length is

about 0.3 of the forelimb length, and the pes length is about 0.37 of the hind limb length. Regarding the relative length, the *Archaeomeryx* manus resembles those of lagomorphs and rodents.

In respect to the ratios between the limb segments and the relatively low position of the distal regions of the long posterior femoral muscles (extensors of the hip joint), *Archaeomeryx* is something intermediate between the powerful and high-rate types. This type is observed, in particular, in the Norway rat (*Rattus norvegicus*), although the pes of *Archaeomeryx* is somewhat longer than those of rats.

In small cursorial ungulates (including more advanced ruminants), the difference between the lengths of fore and hind limbs decreases (the index is higher than 0.75).

Limb simplification and decrease in mass. The simplification of limbs in *Archaeomeryx* is at a very low level, which is transitional from the basal therian structure (where the entire bone set is developed) to the ruminant structure characterized by considerably reduced ulna and fibula (to the malleolus bone) and by the loss and fusion of many autopodial elements.

The massiveness of hind limbs in relation to other parts of the body is relatively high. The femur and middle and distal limb segments are markedly more massive than those of more advanced ruminants of similar size. In higher ruminants, the limb structures is extremely simplified and the relative limb mass is considerably reduced. These cursorial adaptations provide them with a substantial economy of effort.

Joint mobility and limb extension. *Archaeomeryx* retained a greater mobility in the humeral and hip joints, in the antebrachium and crus, and in the manus and pes than living tragulids and other ruminants. It was capable of certain external rotation of the manus and pes, as early mammals.

However, the range of the flexion–extension motion and the maximum angles in the joints of *Archaeomeryx* were smaller than those of the majority of ruminants; i.e., its limbs were markedly less extended than in other ruminants. In more advanced ruminants, the movements in the limb joints are transferred to the parasagittal plane and the limbs are considerably straightened.

The short forelimbs of *Archaeomeryx* differed by a stronger pronation of the humeral joint and by a stronger supination of the elbow and carpal joints than in other ruminants.

As *Archaeomeryx* landed and leaned on the forelimbs, the flexion of the elbow joint and extension of the carpal and interphalangeal articulations occurred and braked the motion.

As the forelimbs achieved the maximum extension, they remained strongly flexed and directed laterally at the elbow joint to a greater degree than those of living tragulids, hypertragulids, and earliest cervids.

The metacarpophalangeal joints of *Archaeomeryx* are relatively primitive. The distal articular surfaces of the metacarpals are very low and have weaker crests than those of the metatarsals. The range of flexion–extension motion provided by these joints was substantially narrower than in the metatarsophalangeal joints and in the metacarpophalangeal joints of other ruminants.

In cursorial ruminants, the distal articular surfaces of the metapodials are very well developed and possess rather strong median crests.

The hind limb motion pattern of *Archaeomeryx* substantially differs from a true high-rate pattern, which is characteristic of higher ruminants.

The hip joint of *Archaeomeryx* demonstrates the preservation of adaptations, which could be usual for the basal eutherian pattern.

A primitive narrow and elongated pelvis of *Archaeomeryx* has a number of features suggesting a strong development of the extensors of the hip joint. The areas of their insertion are very well developed, e.g., the wing of the ilium strongly expands and has well-developed medial and lateral tubercles; the ramus ossis ischii is elongated; and the spina ischii and the tuber ischiadicum with the lateral and ventral processes are well developed. These muscles demonstrate further development in higher ruminants with their forward–backward limb movements. However, in *Archaeomeryx*, they were most likely adapted for primitive rebounding leaps, with the hind limbs prevented from a strong movement forward.

The fact that the hip joint retained the ability of rotation is evidenced by the hemispherical head and well-developed neck of the femur and by the presence of an incisure of the obturator foramen and the incisura ischiadica minor.

The ventrolateral orientation of the acetabulum allowed a stronger abduction of the femur than in the majority of ruminants.

Archaeomeryx has the most primitive hock joint among ruminants. A primitively elongated astragalus and a strong development of the extensor support for the calcaneum, which restricts extension in the plantar (talocalcaneal) articulation, may be a result of strong inclination of the pes relative to the ground surface.

The primitive short arches of the proximal and distal trochleae of the astragalus provided a narrower range of motion in the joints than those of the majority of artiodactyls.

The range of movements in the talocrural or proximal ankle joint (between the crus and the astragalus) was 43∞; in the distal (talonaviculocuboid) ankle joint and in the plantar joint, the ranges were approximately 36∞ and 22∞, respectively.
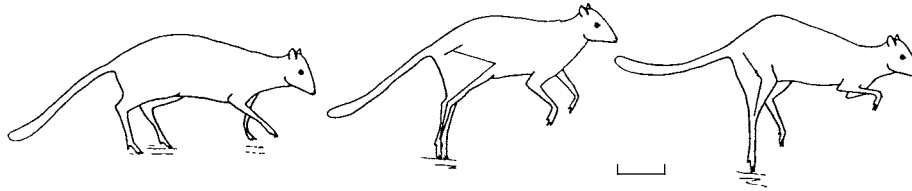
Fig. 39. Reconstructed limb position during leaping.

The divergence of the axes of these joints, inherited from the ancestors, caused rotation of the longitudinal axes of the calcaneum and pes during flexion. As a result, the calcaneal tuber deviated internally and the pes deviated externally.

The range of flexion–extension motion in the hip joint was at most 80∞. In modern *Capreolus*, it is about 150∞.

The atypical of ruminants almost semicylindrical plantar joint apparently provided rapid flexion and extension, as the calcaneum slid over the arc of the joint.

In the course of ruminant evolution, a decrease in the inclination of the limbs to the ground surface resulted in the changes of loads in the joint. The astragalus decreased in length, which was favorable for the development of efficient rapidly functioning joints. The plantar trochlea became an extensive and relatively flat sustentacular facet below which a cavity for synovial fluid damping abrupt flexional loads on the joint is retained.

Elastic flexional braking in the joints of the majority of ruminants is achieved by the increased tension of a strong plantar ligament. In *Archaeomeryx*, the latter was probably primitive and consisted of individual fascicles extending from the calcaneal tuber to metatarsals II–IV.

At the end of the propulsive phase (the phase of support, which precedes a jump), the hip and knee joints of the hind limbs flexed as strongly as possible and the angles in the joints were 41∞ and 52∞, respectively. As this occurred, the ankle and interphalangeal articulations were straightened to the maximum possible extent, as at the phase of transition from the preparatory stage to the accelerating stage (Fig. 39). At this phase, the angle in the hip joint was 132∞. The main loads were born by well-developed extensors of the hip, knee, ankle, and interphalangeal articulations (the gluteal and posterior femoral groups of muscles, gastrocnemic muscle, etc.). This phase of hind limb motion corresponds to the forelimb position at which each joint flexed, as at the beginning of the preparatory stage of the phase of free (unsupported) motion.

The steep jump was probably achieved not only by a strong thrust provided by the hind limbs but also by raising the center of gravity with the extensor of the dorsum before a jump.

The angle of the flexion of the metatarsophalangeal joints exceeded those of the metacarpophalangeal joints but was less than in many other ruminants.

Springing effect in the metatarsophalangeal joints. The metatarsophalangeal joints bore a relatively large load and, along with the interphalangeal joints, apparently provided a weak springing effect, so that the dorsal flexion of the metatarsophalangeal joint was accompanied by the plantar flexion of the proximal interphalangeal joint and dorsal flexion of the distal interphalangeal joint. This effect reached its maximum not only in the hind limbs but also in the forelimbs of some bovids inhabiting the regions of dry ground (Leinders, 1979).

Foot posture. An important distinction of *Archaeomeryx* from other ruminants is its partially digitigrade foot posture. This animal preserved a primitive manus leaning on the second and third phalanges of the central and lateral digits (Fig. 28). However, the pes of *Archaeomeryx* was already unguligrade, as in all ruminants.

In other known ruminants, an unguligrade foot posture, which is more effective for coursers, is present in both manus and pes. Leaning on the third phalanx, which is characteristic of them, enables for a rapid push against the substrate during running.

During leaning, the longitudinal axes of the second and third phalanges of the *Archaeomeryx* manus coincided rather than formed an acute angle, as in other ruminants. The articular surface of the third phalanx is almost vertical; therefore, in the state of the maximum extension, the plantar surface of the second phalanx was on the same line as the sole of the first phalanx.

In addition, the digits of the *Archaeomeryx* manus could widely diverge to provide a large bearing area, in particular, on moist ground. This adaptation is traced in living *Tragulus* by a strongly developed extensor carpi radialis muscle (extensor of the manus) and well-pronounced abductors and adductors of digits 2 and 5 (m. abductor indicus, m. adductor indicus, and m. adductor digiti minimi); in other ruminants, these muscles have disappeared (Carlsson, 1926).

The hind limbs were only supported by the third phalanges of central and lateral digits. This cursorial adaptation led to a decrease in the duration of the phase of leaning on the hind limbs in comparison with that in

Fig. 40. Reconstructed appearance of *Archaeomeryx optatus.*

primitive mammals and other nonungulates and provided a more rapid push. This push was performed by the hooves of the central digits.

The pes was inclined in relation to the ground surface to a lesser extent than the manus.

RECONSTRUCTION OF APPEARANCE AND MODE OF LIFE

Since Colbert (1941), the concept that *Archaeomeryx* resembles *Tragulus* in skeletal structure and ecology was established. However, presently, it is evident that Colbert's reconstruction of skull (Colbert, 1941, text-fig. 1) based on four specimens from the AMNH collection needs to be revised. This concerns the shape of the anterior opening of the nasal cavity, the structure of the occiput, and certain other features (Vislobokova and Trofimov, 2000a, 2000b). Colbert's reconstruction of the *Archaeomeryx* skeleton (Colbert, 1941, text-fig. 4), which is based on several specimens from the AMNH, actually resembles modern *Tragulus*. It is distinguished from the latter only by a longer and stronger elevated lumbar region of the vertebral column and by a very long tail. New morphological evidence allowed us to revise and improve the skeleton reconstruction, appearance, and mode of life of *Archaeomeryx*.

Summarizing the data on morphology and morphofunctional analysis given above, we can propose the following reconstruction of appearance and mode of life of *Archaeomeryx*.

Archaeomeryx was a small and graceful animal, approximately 130–150 mm high at the withers (i.e., smaller than a cat) (Fig. 40). It had a tapering snout, small ears, relatively short and lowly positioned trunk, curved back, long tail (almost as long as the trunk), very short pentadactyl forelimbs, and elongated and strong tetradactyl hind limbs. The body was 450–500 mm long, the thoracic and lumbar regions were 225–260 mm long, the manus was 55–70 mm long ($M = 64.2$, $N = 11$), the pes was 110–120 mm long ($M = 118.3$, $N = 18$), and the tail was longer than 304 mm. The animal was apparently at most 2 kg of weight, i.e.,

similar to small individuals of *Tragulus javanicus* (Vislobokova and Trofimov, 2000b).

Archaeomeryx was a highly organized and widely adapted gregarious animal that was not restricted to a narrow range of feeding specialization and was adapted for inhabiting diverse landscapes. It was active, with a relatively well-developed brain, and resembled early eutherians in the long olfactory bulbs and narrow and low cerebellum.

Similar to early marsupials and placentates, *Archaeomeryx* was adapted to feeding mainly on animals (insects, invertebrates, etc.) and fruit and was not a true herbivore. It possibly preferred a nocturnal mode of life requiring a well-developed sense of smell and hearing.

Archaeomeryx belongs to a special biological type resembling certain living marsupials (such as the opossum *Didelphis*) in feeding and certain rodents in locomotion rather than living tragulids and higher ruminants.

Archaeomeryx shows an example of a transition from insectivorous to herbivorous feeding, from a generalized pentadactyl limb (in which digit 3 is most developed) to paraxony (in which the force of gravity falls between enlarged digits 3 and 4), and from a primitive rebounding jump to gallop characteristic of the majority of ungulates.

Flerov (1962, 1971) believed that *Archaeomeryx* inhabited marshy forests and plant formations on the banks of rivers and lakes and escaped predators by taking cover and hiding in thickets. It is evident that *Archaeomeryx* did not inhabit open landscapes; however, it was adapted not only to the environmental condition of moist soil but also to those of dry ground.

The transformation of the first phalanges of *Archaeomeryx* into small hooves with a thickened posterior region of the sole provided a possibility of inhabiting relatively dry areas. However, the ability of digits to diverge and relatively wide soles of the third phalanges could be useful for inhabiting moist areas. It is not inconceivable that these animals could migrate and change their habitats depending on the seasons.

The dispersal of archaeomerycids coincided with a decrease in humidity in Central Asia in the Eocene. The range of these animals extended from the eastern regions of China to the north of the Huang He (Yellow River) to the Zaisan Depression (Kazakhstan) and partially fell in the North Chinese Floral Realm. The Eocene floras of this region represented a mixed coniferous, microphyllous, and broad-leaved deciduous forests dominated by angiosperms, including such temperate to subtropical forms as *Alnus, Betula, Carpinus, Fagus, Quercus, Rose, Acacia, Mimosites, Phellodendron*, etc. (Guo, 1990). They existed in subtropical or warm–temperate climate, which was less humid than the climate in the Paleocene and could be similar to the modern climate of the northern bank of the Chang Jiang River (Guo, 1990). In the *Archaeomeryx* burial in Ula Usu, fossil seeds, leaves of monocotyledons (such as sedges), stalks resembling horsetails, and medium-sized leaves resembling those of hornbeam (*Carpinus*) and beech (*Fagus*) were collected. *Archaeomeryx* probably consumed some of these plants.

The rate of ecological evolution of early ruminants was probably extremely slow. This is evidenced in particular by the fact that *Archaeomeryx* retained many features inherited from the generalized type of primitive eutherians and observed in primitive members of a number of mammalian orders. However, the main feeding and locomotor adaptations of *Archaeomeryx* showed a distinct shift toward the ruminant morphological type.

Ecosystem reorganization at the boundary between the Eocene and Oligocene, climatic changes, and an increase in the aridity of the inland regions of Asia promoted further improvement of this morphological type, the culmination of which was the appearance and adaptive radiation of higher ruminants.

CHAPTER 5

THE ROLE OF *ARCHAEOMERYX* IN THE EVOLUTION OF THE ARTIODACTYLA

ARCHAEOMERYX AND EARLY EUTHERIANS

Archaeomerycids represent one of the most archaic morphological types of the Tragulina. Direct ancestors of archaeomerycids have not yet been discovered, although it is evident that archaeomerycids have common roots with hypertraguloids and most likely originate from a currently unknown early group of tragulines (Vislobokova, 1998).

Among all the known mammals, early eutherians characterized by generalized structural pattern are most similar in morphology and ecology to the roots of early ruminants. The structure of skull, dentition, and postcranial skeleton of *Archaeomeryx* retain many primitive features that are characteristic of certain members of the earliest (Cretaceous) Eutheria (= Theria) belonging to a number of primitive groups (e.g., Deltotheriida, Leptictida, and Anagalida) and that are absent in archaic Late Cretaceous and Early Paleocene ungulates and archaic Early Eocene suiform artiodactyls.

These data are a very important argument in support of the hypothesis of a very early origin of the Ruminantia and the entire order Artiodactyla. The fact that *Archaeomeryx* retains the most important profound plesiomorphic features, which were largely involved in the adaptatiogenesis and shared by early eutherians, confirms a very early development of artiodactyls from the basal eutherian stock.

The first American researchers already defined such primitive features of *Archaeomeryx* as (1) the presence of the upper incisors; (2) small upper canines; (3) the presence of the first lower premolar; (4) very brachyodont molars; (5) separate radius and ulna; (6) relatively long vertebral column, especially, in the dorsal and lumbar regions; (7) separate sacral vertebrae; (8) pelvis not fused with sacrum; (9) a very long tail; (10) separate carpals, metacarpals, and metatarsals; and (11) complete side digits (Matthew and Granger, 1925a; Colbert, 1941).

Webb and Taylor (1980) supplemented this list by the following essential primitive characters: (1) small size of the fenestra vestibuli; (2) small and narrow stapedial muscle chamber placed almost behind the fenestra cochleae; (3) a moderately deep tensor tympani chamber pocketed in the lateral wall and placed almost opposite the fenestra vestibuli; and (4) the presence of the first metacarpal and, possibly, the presence of the trapezium.

The morphology of early eutherians has been relatively well investigated (see Kielan-Jaworowska, 1978; Kielan-Jaworowska *et al.*, 1979; Novacek, 1986, 1992; Nessov *et al.*, 1998; Archibald *et al.*, 2001; etc.).

Archaeomeryx resembles early eutherians and, particularly, *Kennalestes* from the Late Cretaceous of Asia in the shape and proportions of skull, basicranium, and certain features of the brain structure (e.g., weakly developed cerebral hemispheres, a narrow and low cerebellum, long olfactory bulbs, and a well-preserved paleopallium).

The brain structure is rather primitive even in living chevrotains (Voogd *et al.*, 1998, text-fig. 22.217h) and resembles those of primitive mammals (Romer and Parsons, 1978, text-fig. 417E) and opossum (*Didelphis virginiana*) in the strong development of the olfactory bulbs, primitive large dimensions of the paleopallium (olfactory lobe), a lateral (ventrolateral) rhinal fissure, and only weakly advanced neopallium of modest dimensions. In lateral view, the neopallium (= neocortex) of the water chevrotain *Hyemoschus* covers somewhat less than half the brain height. According to Voogd *et al.* (1998), these primitive features are very prominent in extant species of the Insectivora (e.g., tenrec *Tenrec*, hedgehog *Erinaceus*, etc.) and Tubulidentata (aardvark, *Orycteropus*). The brain of insectivores is considered to be the most primitive mammalian brain, and the brain of *Tenrec* is regarded to be close to that at the beginning of mammalian brain evolution (see Voogd *et al.*, 1998).

The paleopallium is still large in the measurements along the lateral wall of the cerebral hemisphere of living primitive higher ruminants, in particular, the musk deer *Moschus* (Voogd *et al.*, 1998, poster 1). The large dimensions of the paleopallium along with the well-developed olfactory bulbs are associated with the dominant state of the sense of smell in early eutherians, which they inherited from their ancestors. In advanced mammals, the paleopallium forms smaller olfactory lobes.

The primitive brain structure of *Archaeomeryx* is reflected in the proportions and dimensions of its braincase, which along with some basicranial features (e.g., the retention of an elongated region of the basicranium behind the external acoustic meatus, lateral exposure of the mastoid, etc.) resemble those of the most archaic eutherian groups. In other ruminants, the posterior region of the basicranium is strongly shortened and the mastoid is mostly in the occipital position.

A concave ventrolateral surface of the mastoid process of *Archaeomeryx* apparently served for the attachment of a strongly developed posterior region of the digastric muscle (musculus digastricus), similar to that of early eutherians. In higher ruminants, the longissimus capitis muscle is attached to the mastoid, which is displaced to the occipital plane.

Archaeomeryx shows certain primitive characters in the structure of the skull base and the temporal region.

A thick, elongated, and weakly posteriorly expanded basioccipital with a convex ventral surface and stout muscular tubercles extending onto the alisphenoid are primitive eutherian features; they are pronounced to a lesser degree in *Hypertragulus*.

The basisphenoid of *Archaeomeryx* is primitively elongated and has a convex ventral surface.

The alisphenoid of *Archaeomeryx* is positioned horizontally and, as in early eutherians (Novacek, 1986), lacks alisphenoid and pterygoid canals.

The petrosal of *Archaeomeryx* bears three main grooves (for the facial nerve, stapedial artery, and for the inferior petrosal sinus vein), which are characteristic of the primitive trisulcate type commonly observed in early ungulates; this type was first recorded in the Late Cretaceous *Protungulatum*-like form (Cifelli, 1982).

The tympanic region of the temporal in the skull of *Archaeomeryx* is developed to a much lesser extent than those of other tragulines, including *Lophiomeryx* (Vislobokova, 2001). The entotympanic (bulla tympani) covers only about two-thirds of the petrosal. The external acoustic meatus is extremely short. In addition, the vagina of the processus styloidei is poorly pronounced. In the course of ruminant evolution, the tympanic region increased, the external acoustic meatus lengthened, and the vagina of the processus styloidei became deeper and posteriorly enclosed.

In *Archaeomeryx*, a primitive small anterior opening of the nasal cavity is ovoid in outline and the nasals do not protrude anteriorly between the premaxillae; this is atypical of other ruminants and may correspond to a primitive eutherian state. A similar type of the anterior opening of the nasal cavity is present, in particular, in certain insectivores (*Erinaceus*).

In addition, *Archaeomeryx* resembles early eutherians in an extremely low position of the orbits and in the pattern of the orbital mosaic. The posterior opening of the infraorbital canal is in the maxilla and placed higher than the sphenopalatine foramen, as in early eutherians, in particular, deltatheriids and leptictids.

In the course of evolution of selenodont ruminants, the depth of the maxilla under the orbit increased, the orbit occupied a higher position, the orbital surfaces of the lacrimal and jugal increased, and the posterior foramen of the infraorbital canal was displaced to the lower edge of the lacrimal.

The proportions of masticatory muscles of *Archaeomeryx* also make it close to the most primitive eutherians. In contrast to the majority of ruminants, the main jaw adductor of *Archaeomeryx* is the temporal muscle, as in primitive eutherians and the majority of mammals. A strong development of this muscle in *Archaeomeryx* is evidenced by the well-developed and extremely long sagittal crest (in comparison with those of the other Tragulina), which closely approaches the bregma (the midpoint of the coronal suture), and by the well-developed and widely diverging temporal crests positioned almost perpendicular to the sagittal plane of skull. In addition, the large size of the temporal muscle is reflected in a deep fossa on the coronoid process of the mandible.

In the course of ruminant evolution, the role of the main adductor passed to the masseter. The temporal muscle gradually became weaker, whereas the masseter and the pterygoid muscles became stronger.

The dentition of *Archaeomeryx* preserves many features of the generalized eutherian type as follows:

(1) a complete number of incisors;

(2) procumbent incisors and canines;

(3) small-sized canines;

(4) extremely weakly developed diastemata;

(5) weak molarization of premolars;

(6) the position of the highest cusps of the premolars (protocone in the upper teeth and the protoconids in the lower teeth) closer to the anterior edge of the tooth crowns;

(7) pointed main tubercles;

(8) brachyodonty; and

(9) considerable narrowing of the tooth crowns toward the occlusal surface.

Archaeomeryx also resembles the generalized eutherian type in the occlusal pattern of the tooth rows.

A number of structural features of the *Archaeomeryx* mandible are also inherited from primitive eutherians. They are as follows:

(1) a low mandibular body curving under the posterior molars;

(2) a broad ramus;

(3) a very low position of the condylar process; and

(4) a narrow and strongly posteriorly projecting angular process.

Archaeomeryx retained a primitive radial structure of the enamel, which is typical of early eutherians.

The type of nutrition and the pattern of locomotion most likely also resembled those of early eutherians.

Most likely, archaeomerycids had a primitive structure of the stomach. In living tragulids, as in all ruminants, the esophageal region of the stomach is well developed; however, it is divided into only two parts (reticulum and rumen) instead of three; the third part (omasum) appears in higher ruminants.

The esophageal type of stomach, which is observed in living monotremes, allows one to propose that the prevalence of the esophageal region of stomach in ruminants is a plesiomorphic character inherited from early eutherians in which this region probably remained larger than the glandular region. The latter is strongly developed in the majority of Recent eutherians. In the course of ruminant evolution and development of rumination, the esophageal region became complicated and the glandular region was improved and transformed into a specific abomasum, which is characteristic of all Recent ruminants.

The proportions of the *Archaeomeryx* skeleton are also close to those of early eutherians. Similar to *Archaeomeryx*, early eutherians had an extended corpus, short forelimbs strongly inclined to the ground, and relatively long hind limbs.

Colbert (1941) showed that *Archaeomeryx* had large vertebrae, in particular, in the postcervical region and a longer back than those of Recent tragulids. He proposed that, similar to primitive mammals, *Archaeomeryx* had a longer back than *Tragulus*. In addition, he indicated such primitive features of the cervical vertebrae as a weak expansion of the neural arches and zygapophyses.

The structure of the *Archaeomeryx* manus still resembles in many respects the generalized pattern of the manus of early eutherians.

ARCHAEOMERYX AND EARLY UNGULATES

The earliest members of the Ungulata are *Protungulatum* known from the Upper Cretaceous of North America (Sloan and Van Valen, 1965; MacIntyre, 1972) and two genera of the order Procreodi belonging to the family Oxyclaenidae (McKenna and Bell, 1997). *Protungulatum* is usually referred to arctocyonids; however, according to McKenna and Bell (1997), it can be assigned with certainty only to the Ungulata. The earliest oxyclaenids first appeared in fossil record in the Early Paleocene of North America (*Chriacus*) and in the Late Paleocene of Asia (*Petrolemur*).

Other archaic ungulates are known only beginning with the Early Eocene. Most of them belong to the family Hyopsodontidae of the order Condylarthra. This family was represented by several genera known from Europe, Asia, and Africa. In addition, one member of the order Dinocerata (*Gobiatherium*) appeared in the Middle Eocene of Asia.

The morphology of *Archaeomeryx* allows us to propose that the divergence of artiodactyls and other ungulates occurred somewhere in the Cretaceous.

Regarding certain structural details, *Archaeomeryx* resembles the most primitive ungulate, *Protungulatum*, and some members of the order Procreodi (*Chriacus, Petrolemur*, and *Lantianus*). However, with reference to certain important characters, it is more primitive than each of them.

Among early ungulates, *Archaeomeryx* is most similar to *Protungulatum donnae* from the Late Cretaceous of Montana (Sloan and Van Valen, 1965; MacIntyre, 1972). However, a number of morphological features of *Archaeomeryx* indicate that early ruminants (and, hence, artiodactyls) originated from the common eutherian stock earlier than *Protungulatum*.

According to Prothero *et al.* (1988), a greater primitiveness of the order Artiodactyla in comparison with *Protungulatum* is demonstrated, in particular, by the following features: (1) the position of the opening of the facial canal on a level with or behind the fenestra vestibuli, (2) a very narrow trigonid of the lower molars, (3) the absence of the hypocone on the upper molars, and (4) the absence of the third trochanter in the femur. These features are clearly exhibited in *Archaeomeryx*.

The petrosal of *Archaeomeryx* resembles that of *Protungulatum donnae*, as described by MacIntyre (1972), in the position of the stapedial muscle fossa behind the fenestra vestibuli. However, the petrosal of *Archaeomeryx* is more primitive with reference to the position of the opening of the facial canal; the latter is opposite the fenestra vestibuli. In the course of mammal evolution, the opening of the facial canal and the stapedial muscle fossa were displaced anteriorly. In *Protungulatum*, the opening of the facial canal is already slightly displaced and lies anterior to the fenestra vestibuli.

Archaeomeryx and *Protungulatum* are similar in the structure of the lower jaw and premolars; however, they differ from each other in the molar structure. Regarding the molar pattern, *Archaeomeryx* is closer to a more archaic type than *Protungulatum*. The tendency to the increase in the number of cusps on molars is typical of *Protungulatum* and other early ungulates (oxyclaenids, arctocyonids, and condylarths) as well as of dichobunoids, cainotheriids, amphimerycids, etc. This tendency is not observed in *Archaeomeryx*, other tragulines, and higher ruminants. In *Archaeomeryx*, the hypocone is always absent, as in all ruminants, whereas, in *P. donnae*, the hypocone is absent in only some cases; in the majority of cases, it is already weakly developed (Sloan and Van Valen, 1965).

Archaeomeryx is less similar to members of the order Procreodi (Oxyclaenidae and Arctocyonidae). Some researchers consider the latter to be ancestors of artiodactyls. This point of view is based mainly on the similarity in dental structure between dichobunoids and certain genera of the Procreodi. However, the hypothesis proposed by Van Valen (1971) and supported by Rose (1996) for the origin of artiodactyls from *Chriacus*-like presumable arctocyonids lacks support from our data.

Notwithstanding the fact that *Chriacus* appears similar to *Diacodexis* in certain features, this genus is too specialized to be located at the root of artiodactyls and archaeomerycids. The essential differences in the morphology and adaptations of early artiodactyls and arctocyonids sensu Rose (1982, 1987) undoubtedly indicate that *Chriacus* is not ancestral to artiodactyls.

Recently, Rose (1996) discovered that *"Chriacus truncatus"*, a small arctocyonid from the Middle Paleocene of New Mexico, and *Diacodexis secans* from the Early Eocene of Wyoming have several common characters in the structure of hind limbs that are associated with the adaptation for running. *"Chriacus truncatus"* is represented by incomplete jaws, fragmentary femur and tibia, and two vertebrae. The two animals are simi-

lar in size and the anteroposterior diameter of the distal region of their femurs exceeds the transverse diameter. The tibia of *"Chriacus truncatus"* is slenderer than that of *Diacodexis secans* and is more primitive in possessing a longer crista tibiae.

In addition, *Chriacus* and other arctocyonids (Procreodi) are more primitive than dichobunoids in the following characters: (1) more massive forelimbs, (2) a well developed deltopectoral crest on the humerus, (3) a wider distal end of the humerus with a projecting medial epicondyle and a large epicondylar foramen, (4) pentadactyl manus and pes with laterally compressed and curving claws, and (5) the absence of tendency to the paraxony (Rose, 1985).

The arctocyonid–artiodactyl transition proposed by Rose (1996) presumed progressive elongation and lightening of the distal limb segments, reduction of muscular processes and crests, mediolateral compaction of manus and pes accompanied by an increase in paraxony, restriction of the mobility in the joints to the parasagittal plane, and transformation of claws into hooves.

The entire set of these changes should develop in the course of the formation and improvement of the paraxony; however, the features of postcranial skeleton of *"Chriacus truncatus"* (Rose, 1996) are obviously insufficient to consider this form as the ancestor of artiodactyls, because they occur in all ungulate branches.

The differences in dentition between *"Chriacus truncatus"* and *Diacodexis secans* discovered by Rose (1996) are most likely evidence of the divergence of the arctocyonid and dichobunid branches rather than arctocyonid–artiodactyl transition in the Paleocene–Eocene, as was proposed by Rose.

Regarding the dental structure, *"Chriacus truncatus"* appears more similar to hyopsodont condylarths than to diacodexid dichobunoids. *"Chriacus truncatus"* has a very large and laterally compressed lower canine and differs from *Diacodexis secans* by small and short lower premolars and by a well-developed entoconulid on both m2 and m3 (Rose, 1996). The larger number of cusps on the lower molars of *Chriacus* than on those of *Diacodexis* and a remarkable enlargement of its lower canine, which is atypical of dichobunoids, are evidence that *Chriacus* is a more advanced form than dichobunoids and belongs to the other evolutionary lineage.

Although the Procreodi and Dichobunoidea show certain common evolutionary trends, it is highly unlikely that the former were ancestors of the latter.

Archaeomeryx is clearly more primitive than *"Chriacus truncatus"* described by Rose (1996); consequently, it could not originate from the latter.

The other ungulate group regarded by some researchers as the ancestors of artiodactyls is the order Condylarthra (see Van Valen, 1971). Condylarths are known beginning with the Paleocene and are substan-

tially more advanced than *Protungulatum*. They are rather diverse in the Eocene and possess certain common adaptations with artiodactyls; however, direct relationships between archaeomerycids and condylarths are even less probable than between archaeomerycids and *Protungulatum* or the Procreodi.

In addition to the similarity in the petrosal, lower jaw, and dentition, *Archaeomeryx* and *Protungulatum* resemble each other in a primitive radial pattern of the enamel (Stefen, 1999; Vislobokova and Dmitrieva, 2000). Both genera have the radial enamel with arcade-shaped prisms. However, some prisms of *Protungulatum* are circular and have complete prism sheaths (Stefen, 1999). We regard the latter as a relatively advanced feature, the first step to an increase in the density of enamel. Increasing enamel durability is an important trend in the development of mammalian enamel. Progressive evolutionary tendency in enamel development usually correlates with the progressive complication of the dental pattern and independently occurs in different mammal lineages. Within the order Procreodi, certain Paleocene genera (e.g., *Chriacus*) have the Hunter-Schreger bands, whereas, in the order Condylarthra, the forms characterized by less complicated molars (*Protoselene*) have radial enamel (Stefen, 1999).

The fact that, in comparison with the known early ungulates (*Protungulatum*, oxyclaenid procreodi, hyopsodontid condylarths, etc.), *Archaeomeryx* is most plesiomorphic in a number of characters and shows a different trend in the complication of molar structure does not allow us to consider these groups to be the ancestors of artiodactyls.

Thus, a great primitiveness of *Archaeomeryx* in comparison with the earliest and most primitive ungulate corroborates the hypothesis proposed by Prothero *et al.* (1988) that artiodactyls are the most primitive among ungulates; consequently, they originated from the common eutherian stock earlier than *Protungulatum*. The geological age of *P. donnae* indicates the upper time limit of the appearance of the order Artiodactyla, which is the Late Cretaceous.

ARCHAEOMERYX AND DICHOBUNOIDS

A comparative morphological study of *Archaeomeryx* and early members of the suborder Suiformes provides new evidence for the pre-Eocene time of origin and basal adaptive radiation of artiodactyls and rejects a widely accepted hypothesis of the origin of ruminants from suiforms.

The majority of Early Eocene artiodactyls belong to suiforms. They are known from Europe, Asia, and North America. The Suiformes were especially diverse in the Eocene. About ten genera have been established in the Early Eocene and above 60 are known from the Middle Eocene (McKenna and Bell, 1997). A large number of genera belong to the superfamily Dichobunoidea,

the families Diacodexidae and Homacodontidae. However, the Early Eocene suiforms are mostly poorly preserved, and little is known about their morphology. In the Middle Eocene, the diversity of suiforms increased, since the first members of the Anthracotheroidea, Entolontoidea, Anoplotheriidae, and Helohyidae (genera *Gobiohyus* and *Pakkokuhyus* from Asia) appeared. In addition, *Aksyiria* dwelt in Asia.

Archaeomeryx is rather similar to the most primitive Early and Middle Eocene members of the Dichobunoidea, in particular, to the genera *Diacodexis* and *Messelobunodon*, which are relatively well understood with reference to their morphology (Guthrie, 1968; Brunet and Sudre, 1980; Franzen, 1981, 1983; Rose, 1982, 1985; Russell *et al.*, 1983; Sigogneau-Russell and Russell, 1983; Sudre *et al.*, 1983; Thewissen *et al.*, 1983; Sudre and Erfurt, 1996; etc.). However, in contrast to *Diacodexis* and *Messelobunodon, Archaeomeryx* retains a larger number of characters of the generalized eutherian type and provides more important data on the origin of artiodactyls. We agree with Rose (1982, 1987) that *Diacodexis* should not be placed at the base of the artiodactyl tree; however, this inference is not based on the similarity between this genus and selenodont artiodactyls (tylopods, ruminants, etc.) but is made in spite of this similarity.

Kowalevsky (1875) explained the evolution of ungulates by two main evolutionary processes, i.e., (1) simplification of skeleton, which is too complex to perform the simple movements that are required, and (2) adaptation to herbaceous food and development of the chewing ability.

The degree to which the paraxony is developed in *Archaeomeryx* is one of the lowest among artiodactyls. Such a feature as an extremely weakly developed paraxony of the forelimbs distinguishes *Archaeomeryx* from the majority of ruminants (including hypertraguloids and leptomerycids) and other artiodactyls (except for diacodexids). However, the paraxony of hind limbs is shared by all artiodactyls.

Dichobunoids are a highly specialized group adapted for cursorial and saltatorial locomotion (Rose, 1985). They demonstrate one of the first evolutionary steps toward the improvement of the paraxony. Dichobunoids have extended metapodials, a considerably elongated pes, and elongated tibia, which exceeds the femur in length. The distal region of the humerus is perforated, as is those of many high-speed species. The movements in the elbow joint are mainly restricted to flexion and extension.

Archaeomeryx and dichobunoids are similar in the following features:

(1) general structural pattern of skull and lower jaw;

(2) the presence of the upper incisors;

(3) small-sized canines;

(4) characteristic features of occlusion;

(5) the number of thoracic and lumbar vertebrae;

(6) relatively weak reduction of the ulna and fibula;

(7) the presence of the os pisiforme;

(8) a strong development of the third metacarpals; and

(9) a possible preservation of the first digit in the manus.

Archaeomeryx and dichobunoids also share a lateral position of the mastoid and a weak elongation and small height of the facial region. In addition, *Archaeomeryx* and dichobunoids have very long tails composed of approximately the same number of vertebrae. For comparison, the number of caudal vertebrae in *Messelobunodon* is up to 24 (Franzen, 1981).

However, dichobunoids are at a higher evolutionary level than archaeomerycids in a number of features. The morphology of archaeomerycids and dichobunoids suggests that they are the lowest developmental stages of two different evolutionary lineages of artiodactyls, which lead to the modern Ruminantia and Suiformes, respectively.

The key points in the divergence of the two groups are associated with a fast adaptation of dichobunoids to new relatively dry biotopes and a slower changes of archaeomerycids associated with a substantial energy saving. The similarity between tragulines and dichobunoids is most likely retained from their common ancestors and, partially, acquired owing to parallel adaptation to similar environments rather than inherited by tragulines from dichobunoids, as many researchers have presumed.

Archaeomeryx is especially similar to the earliest dichobunoids of the genus *Diacodexis* known from the Early Eocene. The morphology of postcranial skeleton of *Diacodexis* is relatively well understood mainly owing to the studies of Rose (1982, 1985). Apparently, *Diacodexis* and *Archaeomeryx* were similar in the type of feeding and in the pattern of locomotion. Rose (1985) showed that, despite the earlier geological age, *Diacodexis* is more advanced and better adapted for running and jumping than many later genera of the Suiformes.

Archaeomeryx and *Diacodexis* are similar in many primitive structural features and certain advanced characters associated with the improvement of the paraxony, although *Diacodexis* has primitive separate cuboid and navicular.

Common primitive features in the postcranial structure are as follows:

(1) a short and wide atlas;

(2) the presence of grooves on the ventral surface of the atlas, which extend externally from the ventral tubercle (according to Rose (1985), this feature is not characteristic of tragulines);

(3) a more cranial position of the neural arch of the epistropheus than in *Tragulus*; the arch terminates above the back of the odontoid process;

(4) the presence of a strong median ventral crest (spina) on the epistropheus;

(5) short centra of the thoracic vertebrae and elongated centra of the lumbar vertebrae;

(6) nonexpanded apices of the spinous processes of the lumbar vertebrae;

(7) the posterior bifurcation of the base of the spinous processes into the divergent crests, which stretch to the medial side of each postzygapophisis;

(8) long and flexible lumbar region of the vertebral column;

(9) long and stout tail;

(10) short first caudal vertebra with a completely developed neural arch, zygapophyses, and horizontal transverse processes;

(11) almost median position of the spine of the scapula;

(12) separate ulna and radius; in *Messelobunodon*, they fused distally (Franzen 1981);

(13) anteroposteriorly compressed radius, which is posteriorly concave in the proximal half;

(14) relatively short olecranon with a groove at the anteroproximal angle, which presumably served for the insertion of the triceps tendon (Rose, 1985);

(15) separate entocuneiform and possibly ecto- and mesocuneiforms; in *Diacodexis*, ecto- and mesocuneiforms seem to be incompletely fused (Rose, 1985);

(16) paraxony of the pes;

(17) complete development and only weak reduction of the second and fifth metatarsals, they are slightly shorter and thinner than the central metatarsals;

(18) metatarsal keels restricted to the plantar half of the distal articular surfaces;

(19) possible presence of metatarsal I; in *Diacodexis*, a small triangular facet on the caput of metatarsal II is probably preserved for the articulation with metatarsal I; in this genus, only a small rudimentary metatarsal I was present and probably fused with the entocuneiform, as in the Eocene equid genus *Propalaeotherium* (Rose, 1985);

(20) a more dorsal termination of the articular surfaces on the second phalanges of the hind limbs than those of the first phalanges; and

(21) very small hooves in forelimbs, which clearly differ from the hooves of modern tragulids.

Similar to *Archaeomeryx, Diacodexis* was adapted for leaping; however, this adaptation was most likely developed to a greater degree. In this genus, the ratio of the tibia length to the femur length (the crural index t/f) is 1.17 (Rose, 1982). This exceeds the values calculated for *Archaeomeryx* and modern tragulids. In *Messelobunodon*, the crural index is about 1.09 (Franzen, 1981), i.e., somewhat lower than in *Diacodexis*. The relative length of the manus in dichobunoids is higher than in *Archaeomeryx*.

Although *Archaeomeryx* is more advanced than dichobunoids in the level of the development of the carpus and tarsus, it is much more primitive than the latter not only in the absence of tendency to an increase in the number of cusps on the molars but also in many characters of skull, limbs, and in the proportions of postcranial skeleton.

If the skull of one of the most primitive *Diacodexis, Diacodexis pakistanensis*, from the Early Eocene of Pakistan, was correctly reconstructed by Russell *et al.* (1983, figs. 1, 2, 5), *Archaeomeryx* differs from dichobunoids by such primitive characters as a narrower braincase, a stronger posteriorly projecting occipital crest, a more anterior position of the orbits, and by the shape and certain structural features of the anterior opening of the nasal cavity.

A greater primitiveness of *Archaeomeryx* is also clearly seen in the features of dentition. In particular, *D. pakistanensis* has less procumbent incisors, more vertical canines, and the diastemata located not only between the first and second premolars but also between P2 and P3. We also regard the presence of the paraconule and a very weak development of the parastyle on the upper molars of the latter species as more advanced features than those of *Archaeomeryx*.

Similar to dichobunoids, *Archaeomeryx* is at a very low stage of the development of paraxony.

Regarding the ankle joint structure and the extent to which the side metapodials and digits are reduced, *Archaeomeryx* only slightly exceeds dichobunoids; however, the dorsal curvature of the carpus and pes, which is characteristic of *Archaeomeryx*, is extremely weakly developed in dichobunoids. In *Archaeomeryx*, the double-pulley astragalus (the most essential skeletal character of artiodactyls) has not yet been completely formed. As is shown above, the astragalus of *Archaeomeryx* has a primitive three-pulley structure and resembles a primitive ferungulate type introduced by Schaeffer (1947) in its elongated shape, weakly developed proximal and distal trochleae, nonparallel axes of the trochleae, and the oblique position of the long axis of the astragalocalcaneal facet. In a number of characters, the astragalus of *Archaeomeryx* is undoubtedly more primitive than that of *Diacodexis*.

Archaeomeryx is more primitive than *Messelobunodon* in the proportions of the skeletal segments. In *Archaeomeryx*, the thoracolumbar region of the vertebral column is more elongated and the forelimbs are much shorter than the hind limbs. In *Messelobunodon*, the vertebral column is relatively short, and the difference in length between the forelimbs and hind limbs is smaller than in *Archaeomeryx*. The ratio of the forelimb length to the hind limb length is 0.715; the ratio of the lengths of the central metacarpals and central metatarsals is 0.623, and the ratio of the lengths of the forelimb and hind limb to the total length of the thoracic and lumbar regions of the vertebral column are 0.864 and 1.208, respectively (Franzen, 1981, 1983).

The other advanced characters of the postcranial skeleton of *Diacodexis* include the following:

(1) dorsal extension of the metapophyses above the prezygapophyses in the lumbar vertebrae;

(2) the presence of a small third trochanter on the femur, as in one *Messelobunodon* skeleton (Franzen, 1983; Rose, 1985);

(3) substantial elongation of the tibia and the shortness of the crista tibia (more proximal termination of the crista tibia than in *Archaeomeryx*), it is approximately one-quarter as long as the tibia (as in *Tragulus*); and

(4) possible fusion of the distal ends of the tibia and fibula (see Rose, 1985).

In addition, the sacrum of *Diacodexis* consists of three weakly fused vertebrae, as in *Cainotherium*; and the phalanges of the pes are longer and thinner than in *Archaeomeryx*.

The essential differences between archaeomerycids and dichobunoids are evidence of the different adaptive trends in the development of these groups.

It is obvious that dichobunoids could not have been ancestors of ruminants, because they are more advanced in a number of evolutionary significant characters. This highly specialized group of suiforms also cannot be regarded as the basal group of the order Artiodactyla. Since *Diacodexis* is more specialized than other dichobunoids and *Archaeomeryx*, it could not be placed at the base of the Artiodactyla stock; this inference was well substantiated by Rose (1982). If *Diacodexis* were the basal form, later suiforms and *Archaeomeryx* would emerge as a result of reverse evolution, i.e., the evolution toward a decrease in herbivorous and running adaptations. These adaptations are the main components of the adaptatiogenesis of the Artiodactyla. The possibility of such reversion was proposed by Guthrie (1968). However, we believe that the reversion in this case is highly improbable, because the coevolution of artiodactyls and vegetation was characterized by well-pronounced positive directional trends. This coevolution occurred against the background of general climatic aridification and was accompanied by an increase in the diversity of angiosperms (Wing and Tiffney, 1987). Thus, the hypothesis of reverse evolution appears incorrect with reference to both ruminants and suiforms. In either case (not only for suiforms, as Rose (1985) believed), one would propose a secondary reversion to a generalized eutherian type. The probability of such process is extremely low. Some suiform branches probably evolved at a lower rate than dichobunoids or ruminants.

THE MAIN TRENDS AND PATTERNS OF RUMINANT EVOLUTION

Although ecological conditions, which were favorable for the adaptive radiation of small herbivorous mammals, existed even in the Paleocene, the first adaptive radiations of ruminants were only recorded in the Eocene. They occurred against a background of a considerable increase in the diversity of angiosperms.

The main events of this kind were as follows: (1) adaptive radiation in the Early Eocene or at the beginning of the Middle Eocene resulted in the appearance of the primitive Traguloidea, including the Archaeomerycidae, and Hypertraguloidea; (2) adaptive radiation at the Middle–Late Eocene boundary or at the beginning of the Late Eocene manifested in a considerable increase in the diversity of traguloids and hypertraguloids; and (3) adaptive radiation at the Eocene–Oligocene boundary provided the appearance of highly specialized herbivorous artiodactyls, i.e., higher ruminants (Pecora).

Being the ancestors of a number of the families of the Traguloidea and higher ruminants, archaeomerycids occupy a special position among the earliest ruminants.

The evolution of archaeomerycids was associated with the initial stage of the development of a specific digestive system and the formation of the paraxony (where the body is supported mainly by the third and fourth digits). These features are of fundamental importance and provided the basis of one of the most successful trends in the evolution of ungulates. These trends gave rise to numerous ruminants, which achieved the maximum diversity in the Neogene and currently remain a dominating mammalian group.

Apart from plesiomorphic characters, of which many are shared by other groups of primitive artiodactyls, archaeomerycids show important features providing the basis of further advantageous development of the evolutionary trend to which they belong.

Archaeomerycids undoubtedly display one of the initial stages of transition to a specific type of herbivorous feeding (rumination) and advantageous type of improvement of the paraxony, which is especially well developed in higher ruminants. In contrast to other selenodont artiodactyl forms, they combine characters that could provide the basis for advanced ruminant type.

The principal apomorphic features of archaeomerycids are as follows:

(1) reduction of the upper incisors;

(2) primitive ruminant type of cheek teeth; and

(3) the changes of the distal end of the fibula providing the basis for the formation of the os malleolus.

In addition, the following characteristics of *Archaeomeryx* are considered to be preadaptive for the development of higher ruminants:

(1) transmission of the body weight to the zygopodium mainly through the radius and tibia and

(2) dorsal curvature of the basipodium with the side elements displaced backward; i.e., the arrangement of the carpals and tarsals providing for subsequent efficient simplification of the distal region of limbs and formation of the os cannon, which is characteristic of the Ruminantia.

A clear posterior curvature of the carpus and tarsus of *Archaeomeryx* provided the basis for subsequent adaptive reduction of limb elements in the descendants of this genus. The initial stage of the displacement of the metapodials was also registered in *Diacodexis* (Rose, 1985, text-fig. 8).

The upper ankle joint of *Archaeomeryx* possesses all the principal structural features characteristic of higher ruminants. It is formed mainly by the articular surfaces of the tibia and astragalus, as in other ruminants; the distal end of the fibula is reduced to the state closely approaching the os malleolus. This multifunctional bone, characteristic of the pes of higher ruminants, serves not only as a transmitter of load to the pes but also as an element restricting flexion and as a shock absorber. In addition, it provides a stable articulation between the shin and the pes.

Some of these features are present in other groups of the Artiodactyla; however, they are combined with quite different general morphological structures. Apart from ruminants, the cuboid and navicular are fused in amphimerycids (Sudre, 1978) and in the suiform family Leptochoeridae (Gentry and Hooker, 1988). McKenna and Bell (1997) considered leptochoerids to be a subfamily of dichobunids. It is evident that amphimerycids do not belong to true ruminants, as has been shown in a number of studies (Webb and Taylor, 1980; Scott and Janis, 1992). Although some amphimerycids have their cuboid and navicular fused, they are actually closer in dental morphology to early suiforms and tylopods, as Matthew, Simpson, and some others researchers believed.

There is certain similarity between tragulines and cainotheriids; however, they undoubtedly belong to quite different evolutionary trends. Cainotheriids are a very highly specialized group of small selenodont artiodactyls. They are usually referred to the Tylopoda (Gentry and Hooker, 1988). Recently, McKenna and Bell (1997) included cainotheriids along with the Dacrytheriidae to the Anoplotherioidea (Suiformes). The morphology of cainotheriids was thoroughly examined due to rather extensive fossil remains of this genus. A complete skeleton of *Cainotherium* was described in detail by Hürzeler (1936).

Cainotherium is much more advanced than *Archaeomeryx* in a number of key adaptations related to the herbivory and rapid running. In addition to five crescent molars, *Cainotherium* also differs from *Archaeomeryx* by a greater elongation of limbs, strongly reduced side digits, etc., which indicate its more advanced state with reference to the limb simplification and more advanced adaptation for running.

Position of Archaeomerycids among Tragulines

The structural features of the palate (a weak medial concavity of the posterior edge), the absence of alisphenoid canal, elongated premolars, separate radius and ulna, a considerable dorsal curvature of the carpus and tarsus, and fused magnum and trapezoid make archaeomerycids similar to the other families of the superfamily Traguloidea (Tragulidae, Gelocidae, Leptomerycidae, Lophiomerycidae, and Bachitheriidae) and distinguish them from members of the superfamily Hypertraguloidea (Vislobokova, 2001).

Among the Traguloidea, archaeomerycids undoubtedly represent one of the most primitive lineages that could appear as a result of an early adaptive radiation of this group (Fig. 41). Apart from archaeomerycids, this radiation could give rise to lophiomerycids and tragulids.

We cannot agree with the hypothesis proposed by Webb and Taylor (1990) and recently supported by McKenna and Bell (1997) that *Archaeomeryx* is united with the Leptomerycidae and is considerably more advanced than the Hypertragulidae and Tragulidae. The conclusion of these researchers is based on the data that *Archaeomeryx* shares with the Gelocidae and higher ruminants such derived characters as a closed postorbital bar; lingually projecting paraconid, metaconid, and entoconid on the fourth lower premolar; and a concavo-convex articulation between the calcaneum and fibula.

The conclusion of Bouvrain and Geraads (1985) that the most primitive phylogenetic position of *Archaeomeryx* among the Tragulina (which is determined by the presence of the upper incisors and the first lower premolars, nonincisiform lower canines, a low articular facet of the epistropheus, and the presence of the trapezium and the first metacarpal) appears more correct.

Substantial cranial differences between archaeomerycids and lophiomerycids, which can be regarded as apomorphic features and confirm separate position of these groups, are observed in the basicranial structure.

In *Lophiomeryx*, the foramen ovale is located close to the center of the alisphenoid, the petrosal is strongly pressed to the basioccipital and the posterior edge of the alisphenoid, the ventral surface of the petrosal is substantially laterally raised, and a small auditory bulla closely adjoins the postglenoid process and is almost fused with the latter. In addition, the lateral wall of the recessus epitympanicus is formed by the squamosal portion of the temporal, as in the Tragulidae, Leptomerycidae, and higher ruminants. These structural features of *Lophiomeryx* can be considered to be the most important apomorphies of lophiomerycids.

The distinctive features of tragulids are well pronounced in the structure of the orbital and ear regions, in particular, in the strongly inflated auditory bulla, fused optic foramina, and the absence of postglenoid process. In addition, they are manifested in the fusion of the os malleolus with the tibia, ectomesocuneiform with naviculocuboid, etc.

Judging from the better developed masseter and certain features of the enamel ultrastructure (Vislobokova
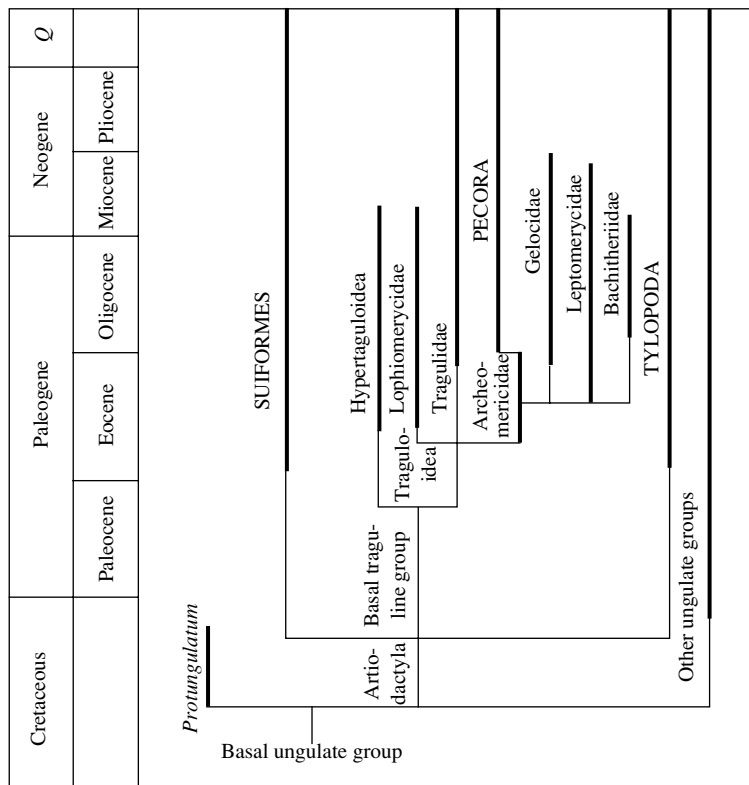
Fig. 41. Relationships of the Archaeomerycidae.

and Dmitrieva, 2000), lophiomerycids were better adapted for feeding on vegetation than archaeomerycids. Tragulids are even more advanced in this respect.

Lophiomerycids have relatively high cheek teeth with a very peculiar pattern of the occlusal surfaces, which clearly differs from a primitive ruminant type characteristic of archaeomerycids. The cheek teeth of tragulids are of the ruminant structural type.

Lophiomeryx and tragulids are more advanced than *Archaeomeryx* with reference to the development of the paraxony. The astragalus of these animals is already double-pulley, as in the majority of ruminants; however, the trochleae remained primitive nonparallel positions.

Archaeomerycids undoubtedly belong to a lower evolutionary stage than leptomerycids, gelocids, and bachitheriids.

These traguloid groups differ from archaeomerycids by substantial progressive changes in skull, dentition, and limbs that are associated with the adaptation to herbivory and progressive simplification of limbs.

Leptomerycids, gelocids, and bachitheriids are more advanced than archaeomerycids not only in commonly known characters, such as a more developed selenodonty and fused metatarsals III and IV, but also in many other characters. In particular, they are characterized by considerable progressive changes in the shape and proportions of skull, a more advanced petro-

sal, more developed tympanic region, advanced type of the anterior opening of the nasal cavity (with anteriorly projecting nasals), strong development of the nasolacrimal fissure, etc.

The distinctive features of leptomerycids include almost fused optic foramina, a slitlike oval foramen, and an advance pattern of the orbital mosaic (similar to those of the Tragulidae and Pecora). The differences between archaeomerycids and leptomerycids are as profound as those between leptomerycids and tragulids and correspond to the family rank (Vislobokova, 2001).

Archaeomeryx and Higher Ruminants

New data on the morphology of *Archaeomeryx* corroborate the views of Matthew and Granger (1925a) who considered *Archaeomeryx* to be the ancestral type of higher ruminants (Pecora) and reject a very popular hypothesis of the origin of higher ruminants from gelocids.

Actually, *Archaeomeryx* lacks the aberrant specialization characteristic of other known tragulines. This lowly specialized member of the Tragulina is more similar morphologically to the basal groups of the Pecora than to any other tragulines, which are characterized by more advanced adaptations for herbivory and rapid locomotion. The latter often surpassed contemporary pecorans in the evolutionary development of dentition and limbs.

As was shown above, *Archaeomeryx* differs from other tragulines in a number of morphological characters that promoted the appearance of higher ruminants.

The earliest Pecora are represented by several genera from the Oligocene of Central Asia. Among them, there are the cervoid *Eumeryx* and the bovoid *Palaeohypsodontus.* Although some researchers included these genera in the composition of lower ruminants (tragulines), new data on their morphology show that they undoubtedly belong to higher ruminants.

The morphological continuity is especially clear between *Archaeomeryx* and early cervoids (superfamily Cervoidea), which were assigned by Vislobokova (1990b) to the subfamily Dremotheriinae; earlier, Webb and Taylor (1980) included them, along with the hornless pecoran families Gelocidae and Moschidae, in the Moschina.

The subfamily Dremotheriinae (*Eumeryx* and *Dremotherium*) comprises small hornless animals resembling modern tragulids in appearance and characterized by an elongated body and relatively short forelimbs and long hind limbs. The earliest remains of these animals come from the Lower Oligocene of Central Asia and Kazakhstan.

Dremotheriines inherited from *Archaeomeryx* general patterns of skull structure, dentition, and skeleton. The differences between the two groups are associated with the adaptation to dry ground, feeding exclusively on plants, development of rumination, and the presence of a well-developed upper canine used for defense. Progressive evolution toward the development of rumination is manifested in the elongation of the facial skull region, improvement of the temporomandibular articulation, changes in the proportions of masticatory muscles, a higher degree of molarization of the premolars, development of the *Palaeomeryx* fold in the lower molars, etc.

The changes in the facial region of skull of dremotheriines include an expansion at the canines, increase in height, elongation of the anterior opening of the nasal cavity, and nasal shortening. The elongation of the diastema between the lower canine and the first lower premolar (where the upper canine is placed when the jaws occlude) is mainly associated with the initial enlargement of the upper canine.

The enlargement of the anterior opening of the nasal cavity is undoubtedly an advantageous feature for a rapidly moving animal.

The development of rumination was accompanied by the changes in dentition: the upper incisors and the first lower premolar disappeared; the diastema between P2 and C increased in length; the lower canine became indistinguishable from incisors; and the selenodonty, hypsodonty, and molarization of the premolars increased. In addition, the structure of the dental enamel became more advanced (Vislobokova and Dmitrieva, 2000).

The development of rumination in early cervoids occurred almost simultaneously with the adaptation to rapid running. The transition to the new type of feeding required the enlargement of the home range to preserve the living resources of their biotopes and avoid excessive nutrient loading and overexploitation. Consequently, this transition required the development of ability to cover large distances.

Dremotheriines are more advanced than *Archaeomeryx* in limb structure. The central metapodials fused to form the os cannon, and the side metapodials are complete or partially reduced. The median gully on the metatarsals of dremotheriines is already closed distally, as in all cervoids; however, the distal articular surfaces on the metapodials are incompletely developed, as in tragulines.

There is a close structural similarity between *Archaeomeryx* and the most primitive dremotheriines of the genus *Eumeryx* from the Oligocene of Asia (Kazakhstan, Mongolia, and northern China), which are known by only fragmentary jaws and separate limb bones. The two genera are similar in the following characters: (1) the presence of p1; (2) brachyodont molars, which are strongly narrowed toward the occlusal surface; (3) elongated premolars; (4) weak molarization of premolars; and (5) the shape of the principal cusps and certain other dental elements.

In *Eumeryx*, as in *Archaeomeryx*, the styles of the upper molars are very strongly developed; the parastyle is especially stout, whereas the pillar of the metacone is extremely weak. The astragalus is narrow and elongated and the keels of the distal trochleae of the metapodials are extremely weakly developed, as in *Archaeomeryx*.

The more advanced *Dremotherium*, skulls of which from the Early Miocene of Saint-Gerand-le-Puy are housed at the National Museum of Natural History in Paris, is also similar to *Archaeomeryx*.

The braincase structure of *Dremotherium* (see Sigogneau, 1968) has much in common with that of *Archaeomeryx*; however, the basicranium is markedly broader and the sagittal crest is shorter. In *Dremotherium*, the mastoid occupies the occipital position, as in all pecorans. The auditory bullae are small and rough but almost completely cover the petrosal. The main axis of the auditory bulla is at an angle of about 45∞ to the sagittal plane of skull (in *Archaeomeryx*, this angle is 35∞). The external acoustic meatus is shorter than those of other cervoids but clearly longer than that of *Archaeomeryx*. The facial skull region of *Dremotherium* is higher and somewhat longer than that of *Archaeomeryx*. It is approximately three-quarters as long as the basal length of skull. The nasals terminate posterior to the anterior orbital rim, as in *Archaeomeryx*; however, they already project anteriorly between the premaxillae. The ethmoidal (nasolacrimal) fissure is developed between the lacrimal and maxilla. The lower canine is already indistinguishable from the

incisors. In the advanced species of *Dremotherium*, the first lower premolar is lost. The enamel is more compact and well differentiated than that of *Archaeomeryx* (Vislobokova and Dmitrieva, 2000).

Archaeomeryx shows clear resemblance to *Amphitragulus* in the structure of skull, lower jaw, and dentition. The latter genus is known for its incomplete skulls, jaws, teeth, and limb bones. *Amphitragulus* is usually assigned to the Cervidae. McKenna and Bell (1997) included this genus in the family Palaeomerycidae. The skull structure of this animal was examined in detail by Sigogneau (1968) and Vislobokova (1990).

Archaeomeryx and *Amphitragulus* share the following characters: (1) narrow basicranium and occiput; (2) well-developed sagittal, frontal, and occipital crests; (3) relatively short frontals, which are comparable in length to the interorbital width; (4) elongated nasals (their posterior edges reach the line connecting the orbital centers); (5) anteriorly raised basicranial base; and (6) similar position of the opening of the infraorbital canal.

In *Amphitragulus*, the postglenoid process is sharp and does not curve posteriorly (as in *Archaeomeryx* and in contrast to later cervids); however, it is broader than that of *Archaeomeryx*. In the structure of the lower jaw, *Amphitragulus* retains the curvature of the mandibular body, the shape of the angular process, and a low position of the condylar process, which is typical of *Archaeomeryx*.

In *Amphitragulus*, the first lower premolar is present and located at a short distance from the second premolar, as in *Archaeomeryx*. However, the diastema between the first lower premolar and the lower canine is longer and the degree of molarization of the premolars is higher. The *Palaeomeryx* fold on the lower molar is well developed.

The early history of giraffoids is extremely poorly recorded. It is not inconceivable that a number of *Amphitragulus*-like forms known by the dental structure belong to ancient giraffoids. Earlier, they were referred to *Amphitragulus*; however, currently, they are considered to be separate genera (Ginsburg and Morales, 1988; Gentry, 1994; Gentry *et al.*, 1999; etc.). Should this be the case, the evolutionary development of dentition in early giraffoids would in many respects be similar to that of early cervoids.

In early bovoids, the changes of dentition apparently occurred somewhat faster than the development of limbs. The earliest bovid *Palaeohypsodontus* from the Oligocene of Asia has higher tooth crowns than early cervoids. The molar enamel is substantially complicated in comparison with that of *Archaeomeryx* (Vislobokova and Dmitrieva, 2000). However, the distal ends of bovoid metapodials fused to a lesser extent than those of cervoids.

The Main Features of the Evolution of the Ruminantia

The knowledge of the evolutionary pattern of the Ruminantia is relatively complete and critically important in studying the general principles of macroevolution.

The evolution of ruminants exhibits typical phenomena of the life flow through the geological time. The life flow manifests itself in the evolutionary development and improvement of adaptations (adaptatiogenesis), which follow common patterns in various groups and show specific energy characteristics of the main evolutionary lineages. The life flow is a **canalized process of adaptatiogenesis**, which has at least two main components: genetic and environmental. It is well known that macroevolution is strongly influenced and corrected by environmental changes.

The canalized process of adaptatiogenesis is the evolutionary transmission of whole summation of properties (including genetic codes of the species and above-species groups) from one evolutionary unit to another. The minimization of energy costs and the best use of outer and inner resources are the major principles of the life flow. The possibility to achieve the best results in the simplest way provides species (and higher taxonomic groups) with energetic advantage over the others.

In geological history, this process is recorded in the sequences of fossil species connected by the ancestor–descendant relationships and composing the higher rank groups according to the profundity of their relationships. In these series of fossil species, the evolutionary changes are well traced in the morphological structure; however, they undoubtedly occurred at the genetic level as well. At the same time, fossil data (including those on ruminants) show that macroevolution was strongly influenced by the environmental changes and correlated with them. An increase in generic and family diversity of ruminants clearly coincided with the main climatic and environmental changes.

The life flow follows a spiral pattern, which is supported by the intention of an evolutionary unit (species or group) to equilibrium (preservation of balanced state and integrity in the course of the development of new features) and minimization of energy costs.

Through geological time, the main direction of a definite life flow is determined by its distinct **adaptive dominant**. Any considerable and weakly coordinated deviation from the general structural pattern (e.g., in hypertragulids) and extremely narrow specialization (e.g., in hypisodontids) increase the probability of subsequent extinction of evolutionary lineages in which they occur.

The formation of the main distinctive features of a taxon occurs contemporaneously with the transmission of common features, which are characteristic of the previous stages of lineage evolution. As in many other

cases, the evolution of ruminants concerned a mosaic of plesiomorphic and derived features. In addition to the characters of different levels of specialization, certain weakly changeable (conservative and primitive) characters also take part in the canalized process of adaptatiogenesis. Thus, the mosaic pattern of evolution occurs at every moment of geological time and in any cross section of an evolutionary branch. Such a mosaic pattern is especially well pronounced in the evolution of the Ruminantia.

The paleontological history of this group gives a rare possibility to observe the formation of its characters from ancestors to extant species. Despite the commonly accepted idea that ancestral groups are extremely rare in the fossil record, archaeomerycids, which are the least specialized ruminants and one of the basal traguline groups, not only remained in the fossil record but existed for a rather long time, at least 10 Ma, and gave rise to a number of groups, including the Pecora, which flourish to date.

In the history of ruminants, certain morphological structures had an especially great adaptive significance. New adaptations were usually developed based on preadaptations occurring in the ancestors.

A great role in the evolution of the Ruminantia was played by the development of essentially new properties, rumination and specific adaptive structure of feet, which allowed a number of species to achieve a considerable **evolutionary advantage** leading to **adaptive radiation**, the appearance and wide dispersal of numerous species. These properties, initially discovered by Kowalevsky, provided a substantial evolutionary advantage of ruminants due to the optimization of energy costs and rational use of the environment.

Paleontological data suggest that rumination and energy efficient simplification of skeleton independently developed in different branches of the Ruminantia. However, preadaptations to these evolutionary trends already existed in *Archaeomeryx* (see above).

Early adaptive radiations of the Ruminantia were associated with ecological differentiation of species. The essential point in ruminant evolution was adaptation to relatively dry habitats, in particular, open woodlands. This caused the changes of the exosomatic organs (digestive and locomotor systems). Apparently, the rate of these changes was especially high at the Eocene–Oligocene transition, when ruminants adapted to feeding on more rough plant food and rapid locomotion in new biotopes. There is a convincing body of evidence that the main lineages of the Pecora appeared in Asia in the center of origin of their ancestors (Vislobokova, 1997, 2001). At that time, a number of primitive higher ruminants placed at the base of different phylogenetic lineages appeared. They include *Eumeryx* (basal genus of the Cervoidea) and *Palaeohypsodontus* (probable basal genus of the Bovoidea). Advanced forms of tragulines appeared as well. They were represented by bachitheriids, the gelocid *Prodremotherium*

(which is close in its key adaptations to the basal forms of the Giraffoidea), etc.

Comparative morphological analysis of *Archaeomeryx* and other ruminants corroborated that various groups of tragulines and higher ruminants most likely originate from the nonspecialized *Archaeomeryx*, although not all transitional forms are discovered and studied in detail. A high variability of *Archaeomeryx* could be a reason for the increased speciation in different parts of the generic range, which occurred in response to environmental changes.

Apparently, the development of specialization in different groups of the Ruminantia occurred almost simultaneously with the development of many other characters shared by higher ruminant rather than were superimposed over the higher ruminant basis prepared at the preceding evolutionary stages, as was assumed by some researchers (for example, Webb and Taylor, 1980). Such development is associated with **the canalized process of transmission of the gene pool, which is corrected by environmental press and spontaneous mutations**.

The simultaneous development of specialization and shared characters in high-rank groups, which is clearly traced in ruminant evolution, testifies that the roots of many large lineages actually go much deeper into the geological history than is usually believed. As a rule, extensive fossil material shows a stage of high diversity rather than the first appearance of a group.

Typical of evolutionary process is the development of similar characters in different and, in particular, far divergent ruminant lineages and in some groups of selenodont artiodactyls. Many ruminant groups show certain resemblance in the evolutionary development of teeth and limbs. The appearance of similar features in different lineages apparently follows from the similarity of their inner arrangement formed in the course of the development of history, morphogenetic complex (similarity of developmental mechanics), and features of the ancestral species, including certain stable preadaptations. Although the developmental mechanics operated in different ruminant lineages and in different environments, the results were often surprisingly similar.

In the course of the development of rumination and improvement of skeleton, the following changes occurred in parallel in different groups of the Ruminantia:

(1) loss of the upper incisors;

(2) inclusion of the lower canines in the incisor row and development of incisiform canines;

(3) increase in selenodonty;

(4) molarization of premolars;

(5) increase in hypsodonty;

(6) decrease in relative length of the premolar row;

(7) elongation of the facial region of skull;

(8) reduction of the ulna;

(9) reduction of the fibula;

(10) loss of the os trapezium;

(11) fusion of the central metapodials into the os cannon;

(12) loss of metapodials I;

(13) improvement of paraxony; and

(14) reduction of side metapodials.

In the light of modern data, the concept of Kowalevsky and Matthew concerning the monophyletic origin of higher ruminants appears to be quite correct. There is clear continuity between *Archaeomeryx* and primitive higher ruminants in the evolutionary development of many characters. Although the earliest ruminants insignificantly differed from tragulines, the initial differences substantially influenced subsequent evolution.

In addition to the changes shared by all ruminants, different branches of the Pecora developed the following common modifications:

(1) reduction of the sagittal and temporal crests;

(2) reduction of the occipital crest (except for the Palaeomerycidae and Dromomerycinae);

(3) elongation of the facial region of the skull;

(4) posterior displacement of orbits;

(5) reduction of the upper canines;

(6) development of the appendages (antlers, horns, and pronghorns) on the skull in correlation with the reduction of the upper canines;

(7) increase in molarization of the premolars;

(8) increase in hypsodonty;

(9) elongation of limbs; and

(10) development of a four-chambered stomach.

Some of these characters composing the pecoran pattern were characteristic of advanced tragulines as well.

The most noticeable originality of the pecoran evolution is the development of cranial appendages (antlers, horns, and pronghorns) in different groups (Bubenik and Bubenik, 1990). This distinctive feature belongs to the most important pecoran apomorphies.

In deer, this is the appearance of antlers, which are true apophyses of the frontal, and the development of their shedding. The essential point in the evolution of the Bovidae was the appearance of horns, which were dermal in origin, and the development of horny sheaths. The Giraffidae are distinguished by the appearance of the ossicones, which are also dermal in origin, but incompletely fused with the skull.

The branches of the Pecora share certain derived morphological characters. Each has some common features with other groups. However, even early members of different higher ruminant groups possess definite transitional preadaptations representing the sets of characters, which directionally developed in their descendants. A particular set of characters formed the structural basis of each higher ruminant group.

Early cervids, which were not yet true deer, showed a definite set of features characteristic of all primitive members of more advanced cervid groups (Vislobokova, 1990a, 1990b). This set, which was most successful for their evolutionary trend, appeared as a result of progressive transformation of preceding morphological structure and allowed early cervids to pass to the next adaptive level.

The following characters of early cervoids can be referred to the precervoid pattern:

(1) increase in the size of upper canines;

(2) development of the fold of the protocone on the upper molars and the *Palaeomeryx* fold on the lower molars;

(3) brachyodonty;

(4) appearance of the preorbital fossa;

(5) development of the nasolacrimal fissure;

(6) specific features of the petrosal;

(7) formation of the distally closed gully on the metatarsus; and

(8) fusion of the proximal end of metatarsal II with the os cannon.

Some advanced tragulines have certain features of higher ruminants. When using such features in cladistic analysis, incorrect phylogenetic trees are obtained. Complete sets of basal characters of different pecoran groups first appear in only the members of their basal groups.

The same characters in different ruminant branches changed at different rates, depending on many factors, in particular, the adaptive dominant and environment. The adaptation of bovids to rough plant food caused relatively fast changes of dentition (hypsodonty, selenodonty, and molarization of the premolars). Among tragulines, fast adaptation to relatively rough plant food was characteristic of gelocids, leptomerycids, and, especially, hypisodontids. The advanced structure of dentition was usually accompanied by a more advanced limb structure than in the forms characterized by primitive dentition. Among higher ruminants, relatively slow evolutionary changes of dentition occurred in giraffids, which adapted to feeding on leaves of shrubs and trees. At the same time, they had an especially strongly elongated facial region of skull, cervical vertebrae, and forelimbs. In different ruminant branches, individual characters differ in the rates of evolutionary development. For example, in giraffids, the tooth crowns are low, whereas p4 is relatively strongly molarized.

Thus, one can recognize that only the data on the phylogeny and transmission of the entire set of characters in each group over the geological time, which are discovered by a detailed comparative morphological study, are a great help in the understanding of the history of any group, whichever existed on the Earth.

"On the principle of the multiplication and gradual divergence in character of the species descended from a common parent, together with their retention by inheritance of some characters in common, we can understand the excessively complex and radiating affinities by which all the members of the same family or higher group are connected together" (Darwin, 1859).

CONCLUSIONS

This detailed study gives evidence that *Archaeomeryx* is morphologically intermediate between early eutherians and Recent ruminants. There is a considerable gap in the fossil record, which hampers the investigation of the early history of the order Artiodactyla and the suborder Ruminantia. The task of future researchers is to bridge this gap, which is about ten million years. To date, the study of *Archaeomeryx* has shown the important points of the origin and development of the suborder Ruminantia, one of the most abundant and diverse groups of large mammals. In addition, morphological data on *Archaeomeryx* enable us to revise the viewpoints on the origin of the order Artiodactyla.

Possessing many preadaptive characters of higher ruminants (Pecora), *Archaeomeryx* gave rise to various families of highly specialized tragulines and higher ruminants at the Eocene–Oligocene transition.

Functional morphological analysis of *Archaeomeryx* provides the possibility of tracing adaptive changes of the skull, dentition, and postcranial skeleton for a better understanding of the evolutionary trends and features of the initial ecological evolution of the earliest ruminants. No evidence was found for the existence of reverse evolution of the tooth and limb structure in any early branch of ruminants. All groups followed the path of progressive evolution directed to the complication of teeth and simplification of limbs.

The morphology of *Archaeomeryx* provides the basis for a critical review of a number of popular hypotheses concerning the origin and evolution of artiodactyls and presents an important component for the reconstruction of phylogenetic relationships within the Artiodactyla.

The low evolutionary level of the development of key artiodactyl adaptations in *Archaeomeryx* is evidence of the very early origin of this order from the common eutherian trunk. Although pinpointing the actual ancestor of artiodactyls is still a good distance in the future, a great primitivity of *Archaeomeryx* in comparison with the most primitive Late Cretaceous ungulate *Protungulatum donnae* leads us to believe that adaptive radiation of ungulates could have appeared already in the Cretaceous. The intermediate species between early eutherians and archaeomerycids are not known; however, it is evident that they belonged to neither the suborder Suiformes, nor arctocyonids, nor condylarths.

SUMMARY

Археомерикс служит связующим звеном между древнейшими эутериями и современными жвачными. В палеонтологической летописи существует значительный пробел, касающийся ранней истории подотряда Ruminantia и отряда Artiodactyla в целом. Заполнить этот пробел продолжительностью в десятки миллионов лет – задача следующих исследований. Но уже сейчас изучение археомерикса позволяет выявить важные стороны становления подотряда Ruminantia – одного из самых многочисленных и разнообразных среди млекопитающих и по-новому подойти к проблеме происхождения отряда Artiodactyla.

Обладая многими предадаптивными признаками высших жвачных (Pecora), археомерикс на рубеже эоцена и олигоцена дал начало разнообразным семействам специализированных трагулин и высших жвачных.

Морфофункциональный анализ археомерикса позволяет проследить приспособительные изменения черепа и зубной системы, органов чувств и передвижения, а также лучше понять направления изменения признаков и особенности начальной экологической эволюции древнейших жвачных. Все группы развивались по пути прогрессивной эволюции, в направлении усложнения зубов и упрощения конечностей. Ни в одной из ранних ветвей жвачных не прослеживаются черты обратной эволюции в строении зубов и конечностей.

Морфология археомерикса становится хорошей основой пересмотра ряда устоявшихся представлений, касающихся происхождения и эволюции парнопалых, и важной составляющей реконструкции их филогенетических отношений. Низкий эволюционный уровень развития ключевых адаптаций парнопалых у археомерикса является подтверждением очень раннего ответвления этого отряда от эутериевого ствола. Хотя поиск реального предка парнопалых – дело будущего, большая примитивность археомерикса по сравнению с наиболее примитивным позднемеловым представителем арктоционид Protungulatum donnae позволяет предполагать, что расхождение артиодактильной и арктоционидной ветвей могло осуществиться еще в мелу. Промежуточные формы между древнейшими эутериями и археомериксом пока не известны, но, очевидно, что они не принадлежали ни к подотряду Suiformes, ни к арктоционидам, ни к кондиляртрам.

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REFERENCES

Abel, O., *Lebensbilder aus der Tierwelt der Verzeit*, Jena, 1927.

Archibald, J.D., Averianov, A.O., and Ekdale, E.G., Late Cretaceous Relatives of Rabbits, Rodents, and Other Extant Eutherian Mammals, *Nature*, 2001, vol. 414, pp. 62–65.

Bouvrain, G. and Geraads, D., Un squelette complet de *Bachitherium* (Artiodactyla, Mammalia), de l'Oligocène de Céreste (Alpes de Haute Provence): Remarques sur la systématique des ruminants primitifs, *Comp. Rend. Acad. Sci. Paris, Sér. 2*, 1985, vol. 300, no. 2, pp. 75–78.

Bouvrain, G., Geraads, D., and Sudre, J., Révision taxonomique de quelques Ruminants oligocènes des phosphorites du Quercy, *Comp. Rend. Acad. Sci. Paris, Sér. 2*, 1986, vol. 302, no. 2, pp. 101–104.

Brunet, M. and Sudre, J., Deux neoveaux Dichobunidés (Artiodactyla, Mammalia) de l'Oligocène inférieur d'Europe, *Proc. Koninkl. Nederl. Akad.*, 1980, ser. B, vol. 83, no. 2, pp. 121–143.

Bubenik, G.A. and Bubenik, A.B., *Horns, Pronghorns, and Antlers*, New York: Springer, 1990.

Carlson, S.J. and Krause, D.W., Enamel Ultrastructure of Multituberculate Mammals: An Investigation of Variability, *Contrib. Mus. Paleontol. Univ. Michigan*, 1985, vol. 27, no. 1, pp. 1–50.

Carlsson, A., Über die Tragulidae und ihre Beziehungen zu den übrigen Artiodactyla, *Acta Zool.*, 1926, vol. 7, pp. 69–100.

Cifelli, R.L., The Petrosal Structure of *Hyopsodus* with Respects to That of Some Other Ungulates, and Its Phylogenetic Implications, *J. Paleontol.*, 1982, vol. 56, no. 3, pp. 795–805.

Colbert, E.H., Distribution and Phylogenetic Studies on Indian Fossil Mammals: Part V. The Classification and the Phylogeny of the Giraffidae, *Am. Mus. Novit.*, 1935, no. 800, pp. 1–13.

Colbert, E.H., Fossil mammals from Burma in the American Museum of Natural History, *Bull. Am. Mus. Nat. Hist.*, 1938, vol. 74, no. 6, pp. 255–436.

Colbert, E.H., The Osteology and Relationships of *Archaeomeryx*, an Ancestral Ruminant, *Am. Mus. Novit.*, 1941, no. 1135, pp. 1–24.

Cope, E.D., The Classification and Phylogeny of Artiodactyla, *Proc. Am. Philos. Soc.*, 1887, vol. 24, no. 126, pp. 377–400.

Darwin, C., *The Origin of Species by Means of Natural Selection*, London: John Murray, 1859.

Flerov, K.K., *Moschus* and Deer, in *Fauna SSSR. Mlekopitayushchie* (Fauna of the USSR: Mammals), Moscow–Leningrad: Akad. Nauk SSSR, 1952.

Flerov, K.K., On the Main Trends in the Ecological Evolution of Ruminants, *Paleontol. Zh.*, 1962, no. 4, pp. 31–42.

Flerov, K.K., On the Ancient Ruminants, *Byull. Mosk. O–va. Ispyt. Prir., Otd. Biol.*, 1971, vol. 76, no. 6, pp. 52–58.

Flower, W.H., On the Arrangement of the Orders and Families of Existing Mammalia, *Proc. Zool. Soc. London*, 1883, pp. 178–186.

Franzen, J.L., Das erste Skelett eines Dichobuniden (Mammalia, Artiodactyla), geborgen aus mitteleozänen Ölschiefern der "Grube Messel" bei Darmstadt (Deutschland, S-Hessen), *Senckenberg Lethaea*, 1981, vol. 61, no. 3/6, pp. 299–353.

Franzen, J., Ein zweites Skelett von *Messelobunodon* (Mammalia, Artiodactyla, Dichobunidae) aus der "Grube Messel" bei Darmstadt (Deutschland, S-Hessen), *Senckenberg Lethaea*, 1983, vol. 64, no. 5/6, pp. 403–445.

Franzen, J.L., Skeletons of *Aumelasia* (Mammalia, Artiodactyla, Dichobunidae) from Messel (M. Eocene, W. Germany), *Cour. Forsch.-Inst. Senckenberg*, 1988, vol. 107, pp. 309–321.

Gabounia, L., Contribution a la connaissance des mammifères paleogenes du Bassin de Zaissan (Kazakhstan Central), *Géobios*, 1977, mem. spec. no. 1, pp. 29–37.

Gambaryan, P.P., *Beg mlekopitayushchikh* (Running in Mammals), Leningrad: Nauka, 1972.

Gentry, A.W., The Miocene Differentiation of Old World Pecora (Mammalia), *Hist. Biol.*, 1994, vol. 7, pp. 115–158.

Gentry, A.W. and Hooker, J.J., The Phylogeny of the Artiodactyla, in *The Phylogeny and Classification of the Tetrapods*, vol. 2: *Mammals*, Oxford: Clarendon, 1988, pp. 235–272.

Gentry, A.W., Rossner, G.E., and Heizmann, P.J., Suborder Ruminantia, in *Land Mammals of Europe*, Munchen: Friedrich Pfeil, 1999, pp. 225–258.

Geraads, D., Bouvrain, G., and Sudre, J., Relations phylétiques de *Bachitherium* Filhol, ruminant de l'Oligocène d'Europe occidentale, *Palaeovertebrata*, 1987, vol. 17, no. 2, pp. 43–73.

Gill, T., Arrangement of the Families of Mammals and Synoptical Table of the Characters of the Subdivision of Mammals, *Smithson. Misc. Coll.*, 1872, vol. 11, pp. 1–98.

Ginsburg, L., Essai de phylogenie des Eupecora (Ruminantia, Artiodactyla, Mammalia), *C. R. Acad. Sci., Sér. 2*, 1985, vol. 301, no. 17, pp. 1255–1257.

Ginsburg, L. and Morales, J., Les ruminants du Miocéne inférieur de Laugnac (Lot-et-Garonne), *Bull. Mus. Nat. Hist. Nat. Paris, Sér. 4*, 1989, vol. 11, sec. C, no. 4, pp. 201–231.

Godina, A.Ya., Gromova, V.I., Sokolov, I.I., *et al.*, The Order Artiodactyla, in *Osnovy paleontologii. Mlekopitayushchie* (Fundamentals of Paleontology: Mammals), Moscow: Gos. Nauch.-Tekh. Izd. Lit. Geol. Okhran. Nedr, 1962, pp. 337–410.

Guo, S., A Brief Review on Megafloral Successions and Climatic Changes of the Cretaceous and Early Tertiary in China, in *Proc. Symp. Paleofloristic and Paleoclimatic Changes in the Cretaceous and Tertiary*, Prague: Geol. Surv., 1990, pp. 23–38.

Guthrie, D.A., The Tarsus of Early Eocene Artiodactyls, *J. Mammal.*, 1968, vol. 49, pp. 297–302.

Hamilton, W.R., The Lower Miocene Ruminants of Gebel Zelten, Libya, *Bull. Brit. Mus. Nat. Hist.*, 1973, vol. 21, pp. 73–150.

Hürzeler, J., Osteologie und odontologie der Caenotheriden, *Abh. Schweiz. Paläontol. Ges.*, 1936, vol. 58/59, pp. 1–112.

Janis, C., Tragulids as Living Fossils, in *Living Fossils*, New York: Springer, 1984, pp. 87–94.

Janis, C., Grades and Clades in Hornless Ruminant Evolution: The Reality of the Gelocidae and the Taxonomic Position of *Lophiomeryx* and *Bachitherium*, *J. Vertebr. Paleontol.*, 1987, vol. 7, no. 2, pp. 200–216.

Janis, C. and Scott, K., The Origin of the Higher Ruminant Families with Special Reference to the Origin of the Cervoidea and Relationships within the Cervoidea, *Am. Mus. Novit.*, 1987, no. 2893, pp. 1–85.

Janis, C. and Scott, K., The Phylogeny of the Ruminantia (Artiodactyla, Mammalia), in *The Phylogeny and Classification of the Tetrapods*, vol. 2: *Mammals*, Oxford: Clarendon, 1988, pp. 273–282.

Jehenne, Y., Description du premier crane du genre *Prodremotheium* Filhol, 1877 (Ruminant primitif de del'Oligocène eurasiatique), *Géobios*, 1977, mém. spéc. vol. 1, pp. 233–237.

Kielan-Jaworowska, Z., Evolution of the Therian Mammals in the Late Cretaceous of Asia, *Palaeontol. Polon.*, 1978, vol. 38, pp. 3–41.

Kielan-Jaworowska, Z., Bown, T.M., and Lillegraven, J.A., Eutheria, in *Mesozoic Mammals: The First Two-Thirds of Mammalian History*, Berkeley: Univ. California Press, 1979, pp. 221–259.

Koenigswald, W. von, Rensberger, J.M., and Pretzschner, H.U., Changes in the Tooth Enamel of Early Paleocene Mammals Allowing Increased Diet Diversity, *Nature*, 1987, vol. 328, no. 6126, pp. 150–152.

Koenigswald, W. von, Martin, T., and Pretzschner, H.U., Phylogenetic Interpretation of Enamel Structure in Mammalian Teeth: Possibilities and Problems, in *Mammal Phylogeny: Placentals*, New York: Springer, 1992, pp. 303–314.

Kowalevsky, W.O., On the Osteology of the Hyopotamidae, *Proc. R. Soc. London*, 1873a, vol. 21, pp. 147–165.

Kowalevsky, W.O., On the Osteology of the Hyopotamidae, *Phil. Trans. R. Soc. London*, 1873b, vol. 163, pp. 19–94.

Kowalevsky, W.O., Monographie der Gattung *Anthracotherium* Cuv. und Versuch einer naturlichen Klassifikation der fossilen Huftiere *Palaeontographica*, 1873–1874, vol. 22, pp. 131–346.

Kowalevsky, W.O., Osteology of Two Fossil Species from the Ungulate Group, *Entelodon* and *Gelocus aymardi, Izv. O–va Estestvoispyt. Antropol. Etnogr.*, 1875, vol. 16, no. 1, pp. 1–59.

Kowalevsky, W.O., Osteologie des *Gelocus aymardi, Palaentographica*, 1877, vol. 24, pp. 145–162.

Leinders, J.J., Some Aspects of the Ankle Joint of Artiodactyls with Special Reference to *Listriodon* (Suina), *Proc. Koninkl. Nederl. Akad. Wetensch.*, 1976, vol. 79, pp. 45–54.

Leinders, J.J. and Sondaars, P.Y., On Functional Fusion in Footbones of Ungulates, *Z. Saugetierkunde*, 1974, vol. 39, no. 2, pp. 109–115.

MacIntyre, G.T., The Trisulcate Petrosal Pattern of Mammals, in *Evolutionary Biology*, New York: Plenum Press, 1972, vol. 6, pp. 275–303.

Matthew, W.D., Reclassification of the Artiodactyls Families, *Bull. Geol. Soc. Am.*, 1929, vol. 40, no. 2, pp. 403–408.

Matthew, W.D., A Phylogenetic Chart of the Artiodactyla, *J. Mammal.*, 1934, vol. 15, pp. 207–209.

Matthew, W.D. and Granger, W., New Mammals from the Shara Murun Eocene of Mongolia, *Am. Mus. Novit.*, 1925a, no. 196, pp. 1–11.

Matthew, W.D. and Granger, W., New Ungulates from the Ardyn Obo Formation of Mongolia, with Faunal List and Remarks on Correlation, *Am. Mus. Novit.*, 1925b, no. 195, pp. 1–12.

McKenna, M.C. and Bell, S.K., *Classification of Mammals above the Species Level*, New York: Columbia Univ. Press, 1997.

Milne-Edwards, A., *Recherches anatomiques, zoologiques et paléontologiques sur la famile des chevrotains*, Paris: Impr. E. Martinet, 1864.

Miyamoto, M.M. and Boyle, S.M., The Potential Importance of Mitochondrial DNA Sequence Data to Eutherian Mammal Phylogeny, in *The Hierarchy of Life: Molecules and Morphology in Phylogenetic Analysis*, Amsterdam: Elsevier Sci. Publ., 1989, pp. 437–450.

Miyamoto, M.M., Kraus, F., Laipis, P.J., Tanhauser, S.M., and Webb, S.D., Mitochondrial DNA Phylogenies within Artiodactyla, in *Mammals Phylogeny*, New York: Springer, 1992, pp. 268–281.

Moyà-Solà, S., Morphology of Lower Molars of the Ruminants (Artiodactyla, Mammalia): Phylogenetic Implication, *Paleontol. Evol.*, 1988, vol. 22, pp. 61–70.

Nessov, L.A., Archibald, J.D., and Kielan-Jaworowska, S., Ungulate-like Mammals from the Late Cretaceous of Uzbekistan and Phylogenetic Analysis of Ungulatomorpha, *Bull. Carnegie Mus. Nat. Hist.*, 1998, vol. 34, pp. 40–88.

Novacek, M.J., The Skull of Leptictid Insectivorans and the Higher-Level Classification of Eutherian Mammals, *Bull. Am. Mus. Nat. Hist.*, 1986, vol. 183.

Novacek, M.J., Pattern of Diversity in the Mammalian Skull, in *Skull*, Chicago: Univ. Chicago Press, 1993, vol. 2, pp. 438–545.

Pilgrim, G.E., The Dispersal of the Artiodactyla, *Biol. Rev.*, 1941, vol. 16, pp. 134–163.

Presley, R., The Primitive Course of the Internal Carotid Artery in Mammals, *Acta Anatom.*, 1979, vol. 103, pp. 238–244.

Prothero, D.R., Manning, E.M., and Fischer, M., The Phylogeny of the Ungulates, in *The Phylogeny and Classification of the Tetrapods*, Oxford: Clarendon, 1988, vol. 2, pp. 201–234.

Qiu, Zh., Late Eocene Hypertragulids of Baise Basin, Kwangsi, *Vertebr. Palasiat.*, 1978, vol. 16, no. 1, pp. 7–12.

Romer, A.S., *Vertebrate Paleontology*, Chicago–Illinois: Univ. Chicago Press, 1966.

Romer, A.S. and Parsons, T.S., *The Vertebrate Body*, Philadelphia: Saunders Co., 1978.

Rose, K.D., Skeleton of *Diacodexis*, Oldest Known Artiodactyl, *Science*, 1982, vol. 216, no. 4546, pp. 621–623.

Rose, K.D., Comparative Osteology of North American Dichobunid Artiodactyls, *J. Paleontol.*, 1985, vol. 59, no. 5, pp. 1203–1226.

Rose, K.D., Climbing Adaptations in the Early Eocene Mammal *Chriacus* and the Origin of Artiodactyla, *Science*, 1987, vol. 236, no. 4799, pp. 314–316.

Rose, K.D., On the Origin of the Order Artiodactyla, *Proc. Nat. Acad. Sci. USA*, 1996, vol. 93, pp. 1705–1709.

Rose, K.D., Postcranial Skeleton of Eocene Leptictidae (Mammalia), and Its Implications for Behavior and Relationships, *J. Vertebr. Paleontol.*, 1999, vol. 19, no. 2, pp. 355–372.

Russell, D.E., Thewissen, J.G.M., and Sigogneau-Russell, D., A New Dichobunid Artiodactyl (Mammalia) from the Eocene of Northwest Pakistan, *Proc. Koninkl. Nederl. Akad. Wetensch.*, 1983, vol. B86, no. 3, pp. 285–300.

Savage, D.E. and Russell, D.E., *Mammalian Paleofaunas of the World*, London: Addison-Wesley, 1983, pp. 1–432.

Schaeffer, B., Notes on the Origin and Function of the Artiodactyl Tarsus, *Am. Mus. Novit.*, 1947, no. 1356, pp. 1–24.

Schlosser, M., Beiträge zur Kenntnis der Stammesgeschichte der Hufthiere und Versuch einer Systematik der Paar- und Unpaarhufer, *Morphol. Jahrb.*, 1886, vol. 12, pp. 1–133.

Scott, K.M. and Janis, C.M., Relationships of the Ruminantia (Artiodactyla) and Analysis of the Characters Used in Ruminant Taxonomy, in *Mammal Phylogeny: Placentals*, New York: Springer, 1992, pp. 282–302.

Scott, W.B., The Mammalian Fauna of the White River Oligocene: Artiodactyla, *Trans. Am. Philos. Soc., N. Ser.*, 1940, vol. 28, no. 4, pp. 363–746.

Shimamura, M., Yasue, H., Ohshima, K., *et al.*, Molecular Evidence from Retroposons that Whales form a Clade within Even-toed Ungulates, *Nature*, 1997, vol. 388, pp. 665–670.

Sigogneau, D. Le genre *Dremotherium* (Cervoidea). Anatomie du crâne, denture et moulage endocranien, *Ann. Paléontol.*, 1968, vol. 54, no. 1, pp. 39–64.

Sigogneau-Russell, D. and Russell, D., A New Dichobunid Artiodactyl (Mammalia) from the Eocene of Northwest Pakistan, *Proc. Koninkl. Nederl. Akad. Wetensch.*, 1983, vol. 86, no. 3, pp. 319–330.

Simpson, G.G., Studies of the Earliest Mammalian Dentitions, *Dental Cosmos*, 1936, pp. 2–24.

Simpson, G.G., The Fort Union of the Crazy Mountain Field, Montana and Its Mammalian Faunas, *Bull. US Nat. Mus.*, 1937, no. 169, pp. 1–287.

Simpson, G.G., The Principles of Classification and a Classification of Mammals, *Bull. Am. Mus. Nat. Hist.*, 1945, vol. 85, pp. 1–350.

Sloan, R.E. and Van Valen, L.M., Cretaceous Mammals from Montana, *Science,* 1965, no. 1948, pp. 220–227.

Stefen, C., Evolution of Enamel Microstructure of Archaic Ungulates ("Condylarthra") and Comments on Some Other Early Tertiary Mammals, *Paleobios*, 1999, vol. 19, no. 3, pp. 15–36.

Stirton, R., Comments and Relationships of the Cervoid Family Palaeomerycidae, *Am. J. Sci.*, 1944, vol. 242, pp. 633–655.

Sudre, J., Les artiodactyles de l'Eocène moyen et périor d'Europe occidentale; systématique et évolution, *Mém. Trav. Ecol. Prat. Haut. Etud.*, 1978, vol. 7, pp. 1–229.

Sudre, J., *Cryptomeryx* Schlosser, 1886, Tragulidé de l'Oligocène d'Europe, relations du genre et considérations sur l'origin des ruminants, *Palaeovertebrata*, 1984, vol. 14, no. 1, pp. 1–31.

Sudre, J. and Erfurt, J., Les artiodactyles du gisement Ypresien terminal de Prémontré (Aisne, France), *Palaeovertebrata*, 1996, vol. 25, nos. 2–4, pp. 391–414.

Sudre, J., Russell, D.E., Louis, P., and Savage, D.E., Les Artiodactyles de l'Eocène inférieur d'Europe, *Bull. Mus. Nat. Hist. Nat., Sér. 4*, 1983, vol. 5, sec. C, no. 3, pp. 281–333.

Szalay, F.S. and Lucas, S.G., The Postcranial Morphology of Paleocene *Chriacus* and *Mixodectes* and the Phylogenetic Relationships of Archontan Mammals, *Bull. New Mexico Mus. Nat. Hist. Sci.*, 1996, no.7, pp. 1–47.

Taylor, B.E. and Webb, S.D., Miocene Leptomerycidae (Artiodactyla, Ruminantia) and Their Relationships, *Am. Mus. Novit.*, 1976, no. 2596, pp. 1–22.

Thewissen, J.G.M., Russell, D.E., Gingerich, P.D., and Hussain, S.T., A New Dichobunid Artiodactyl (Mammalia) from the Eocene of Northwest Pakistan, *Proc. Koninkl. Nederl. Akad. Wetensch.*, 1983, vol. B86, no. 3, pp. 153–180.

Todd, N.B., Chromosomal Mechanisms in the Evolution of Artiodactyls, *Paleobiology*, 1975, vol. 1, no. 2, pp. 175–188.

Tong, Y., Zeng, S., and Qiu, Z., Cenozoic Mammal Ages of China, *Vertebr. Palasiat.*, 1995, vol. 33, no. 4, pp. 290–314.

Trofimov, B.A., Origin, History, and Some Characters of Evolutionary Development of Archaic Ruminants (Ruminantia), in *Kovalevskii V.O. Sobranie nauchnykh trudov* (Kowalevsky: Collected Research Works), Moscow: Akad. Nauk SSSR, 1956, vol. 2, pp. 287–298.

Van Kampen, P.N., Die Tympanalgegend der Saugetiershadels, *Morphol. Jahrb.*, 1905, vol. 34, pp. 321–722.

Van Valen, L., Toward the Origin of Artiodactyls, *Evolution*, 1971, vol. 25, no. 3, pp. 523–529.

Viret, J., Artiodactyla, in: *Traité de Paléontologie,* Paris: Masson et Cie, 1961, part 6, vol. 1, pp. 887–1021.

Vislobokova, I.A., The Basic Features of Historical Development and Classification of the Ruminantia, *Paleontol. Zh.*, 1990a, no. 4, pp. 3–14.

Vislobokova, I.A., *Iskopaemye oleni Evrazii* (Extinct Deer from Eurasia), Moscow: Nauka, 1990b.

Vislobokova, I.A., Eocene–Early Miocene Ruminants in Asia, *Mem. Trav. E.P.H.E., Inst. Montpellier*, 1997, no. 21, pp. 215–223.

Vislobokova, I., A New Representative of the Hypertraguloidea (Tragulina, Ruminantia) from the Khoer-Dzan Locality in Mongolia, with Remarks on the Relationships of the Hypertragulidae, *Am. Mus. Novit.*, 1998, no. 3225, pp. 1–24.

Vislobokova, I.A., Evolution and Classification of Tragulina (Ruminantia, Artiodactyla), *Paleontol. Zh.*, 2001, vol. 35, suppl. 2, pp. 69–145.

Vislobokova, I.A. and Dmitrieva, E.L., Changes in Enamel Ultrastructure at the Early Stages of Ruminant Evolution, *Paleontol. Zh.*, 2000, vol. 34, suppl. 2, pp. 242–249.

Vislobokova, I.A. and Trofimov, B.A., The Family Archaeomerycidae (Tragulina): Classification and Role in the Evolution of the Ruminantia, *Paleontol. Zh.*, 2000a, vol. 34, no. 4, pp. 455–461.

Vislobokova, I.A. and Trofimov, B.A., *Archaeomeryx:* Morphofunctional Analyses and Ecology, *Paleontol. Zh.*, 2000b, vol. 34, no. 6, pp. 662–669.

Voogt, J., Nieuwenhyus, R., and van Dongen, P.A.M., Mammals, in *The Central Nervous System of Vertebrates,* Berlin: Springer, 1998, vol. 3, pp. 1637–2098.

Webb, S.D. and Taylor, B.E., The Phylogeny of Hornless Ruminants and a Description of the Cranium of *Archaeomeryx, Bull. Am. Mus. Nat. Hist.*, 1980, vol. 167, pp. 117–158.

Wible, J.R., The Eutherian Stapedial Artery: Character Analyses and Implication for Superordinal Relationships, *Zool. J. Linnean Soc.*, 1987, vol. 91, pp. 107–135.

Wing, S. and Tiffney, B., The Reciprocal Interaction of Angiosperm Evolution and Tetrapod Herbivory, *Rev. Paleobot. Palynol.*, 1987, vol. 50, pp. 179–210.

Zheng, J., Description of Some Late Eocene Mammals from Lian-Kan Formation of Turfan Basin, Sinkiang, *Mem. Inst. Vertebr. Palaeontol. Palaeoanthrop. Acad. Sin.*, 1978, vol. 13, pp. 116–125.