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# **Evolution and Classification of Tragulina (Ruminantia, Artiodactyla)**

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*(Received June 30, 2000)*

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Vol. 35, Suppl. 2, 2001

The supplement is published only in English by MAIK "Nauka/Interperiodica" (Russia).  
*Paleontological Journal* ISSN 0031-0301.

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**Abstract**—The main evolutionary trends of the Tragulina are traced and the systematics and phylogeny of this taxon are revised based on the study of the comparative morphology of fossil and Recent species and on the estimation of the polarity and taxonomic value of features. Nine families are included in the Tragulina. The existence of two main traguline groups is confirmed, and the names Traguloidea and Hypertraguloidea are restored for these groups. The retention of many plesiomorphic characters shared with ancient eutherian mammals and the possession of very deep apomorphies distinguish tragulines from other artiodactyls and support a pre-Eocene origin of the Tragulina connected with the early radiation of artiodactyls.

## INTRODUCTION

Tragulines are the most primitive extinct and extant ruminants which flourished during the second part of the Paleogene and gave rise to the pecorans at the beginning of the Oligocene. The pecorans are one of the most numerous and widespread groups among Recent mammals. Hence, the study of tragulines helps us to understand one of the most significant and intriguing chapters in the evolution of mammals.

According to the fossil record, the history of tragulines covers more than 50 million years from the Middle Eocene to the present, but it seems that their history is much longer. The appearance of tragulines was one of the earliest and most successful attempts at the development of herbivorous adaptations and strategies to avoid predators. Even at the early stages of evolution, there was a rather wide spectrum of forms adapted to various plant foods. They inhabited all the continents of the Northern Hemisphere. Most of them remained largely herbivorous, also feeding on some small animals (mollusks, insects, etc.), as living chevrotains do.

Notwithstanding the more than 150 years that these ruminants have been studied, and the number of cladistic analyses that have been undertaken during the past two decades, the taxonomy and phylogeny of the group remain disputable with respect to many questions. This concerns not only rare forms represented by fragmentary material, but also many well-studied genera. Major problems include the monophyly of the Tragulina and the relationships, rank, and taxonomic position of most groups.

Apart from the morphological data (Kaup, 1833; Gray, 1845; Milne-Edwards, 1864; Flower, 1867; Garrod, 1877; Carlsson, 1926; Flerov, 1931; Janis, 1984; etc.), there is genetic, immunological, and ethological evidence (Dubost, 1965; Todd, 1975) that distinguish Recent tragulids from other ruminants and indicate

their primitive characters. Some plesiomorphies are shared with the Suiformes. For example, *Tragulus javanicus* shares more muscle antigens with the Suiformes than with ruminants (Duwe, 1969). However, the stomach of Recent tragulids already has a true ruminant reticulum and other ruminant characters (Boas, 1890) which are not present in the Suiformes.

The main purposes of this work are (1) to clarify the evolutionary trends and relationships of tragulines using cranial, dental, and postcranial characters; and (2) to revise the phylogeny and classification of the tragulines. Special emphasis is made on the investigation of character polarities and on the estimation of the taxonomic level of features.

This research is based on abundant fossil material from China and Mongolia that is housed in the Paleontological Institute of the Russian Academy of Sciences (PIN); on fossil tragulines from Europe, Asia, America, and Africa; and on Recent tragulines from Asia and Africa. These specimens are from the American Museum of Natural History (AMNH); Museum of Natural History, London (BMNH); University of Kansas; Zoological Institute of the Russian Academy of Sciences; University of Hanoi; and the University of Montpellier.

Scanning electron microscopy of the enamel ultrastructure of traguline molars and X-ray study were performed at the Paleontological Institute of the Russian Academy of Sciences.

The anatomy, behavior, and habitats of Recent chevrotains were studied during a biological expedition to Vietnam.

In addition to the traguline material, the rich collections of ancient ungulates in the American Museum of Natural History were also used in this work.

## Chapter 1

## THE MAIN PROBLEMS OF CLASSIFICATION AND PHYLOGENY IN TRAGULINES

The rank determination and composition of the taxon *Tragulina*, proposed by Flower (1883) based on the family *Tragulidae*, as well as the rank determination and composition of some other superspecies of traguline taxa, is still controversial. The *Tragulina* has been regarded as a suborder of the order *Artiodactyla* (Osborn, 1910; Colbert, 1941), an infraorder of the suborder *Ruminantia* (Matthew, 1929; Simpson, 1931, 1945; Viret, 1961; Webb and Taylor, 1980; Scott and Janis, 1992; Sudre, 1995), or a parvorder of the infraorder *Ruminantia* (Geraads *et al.*, 1987). Some researchers regarded all tragulines as one group, *Traguloidea* (Romer, 1966). Matthew (1934) united all extinct and extant specimens into a single family, *Tragulidae*, which he placed in the *Pecora*.

The rank determination of higher taxa is a recurrent problem in taxonomy and a very difficult process depending on the knowledge of comparative morphology and phylogeny. The existence not only of species and genera but also of higher taxa, confirmed, in particular, by their taxonomic structure (Chernykh, 1986) and exponential character of survivorship (survival) curves (Markov and Naimark, 1994) testify that natural classification is also real. Such classification should not be a "decision-making process" and not "the most useful generalization" (Mayr, 1982), but a reconstruction of the real hierarchy of taxa according to the level of affinity. This requires an understanding of the processes of evolutionary transmission of heredity (inheritance) and the evolutionary development of adaptations. If extinct species of tragulines, like modern ones, are distinguished mainly by initial ecological and ethological adaptations that are exhibited in some initial features of specialization, extinct genera differ in more profound adaptations exposed in morphological and behavioral characters. The morphological criteria of the higher taxa reflect an even more profound affinity and fundamental adaptation of the component units ranging according to their levels.

The most important criteria for the determination of taxonomic rank are as follows:

(1) The principle of subordination of taxa, meaning that the hierarchy of taxa is determined according to the profundity of similarity between the taxa.

(2) The principle of morphological isolation, meaning that the more peculiar a taxon is, the higher its rank. From lower to higher taxa, a gradual accumulation of adaptive features of wider significance occurs (Schmalhausen, 1939).

(3) The principle of equivalent ranks in related taxa, meaning that the group distinguished as a definite taxon

must possess a set of characters which makes it equivalent in rank to the acknowledged related taxa.

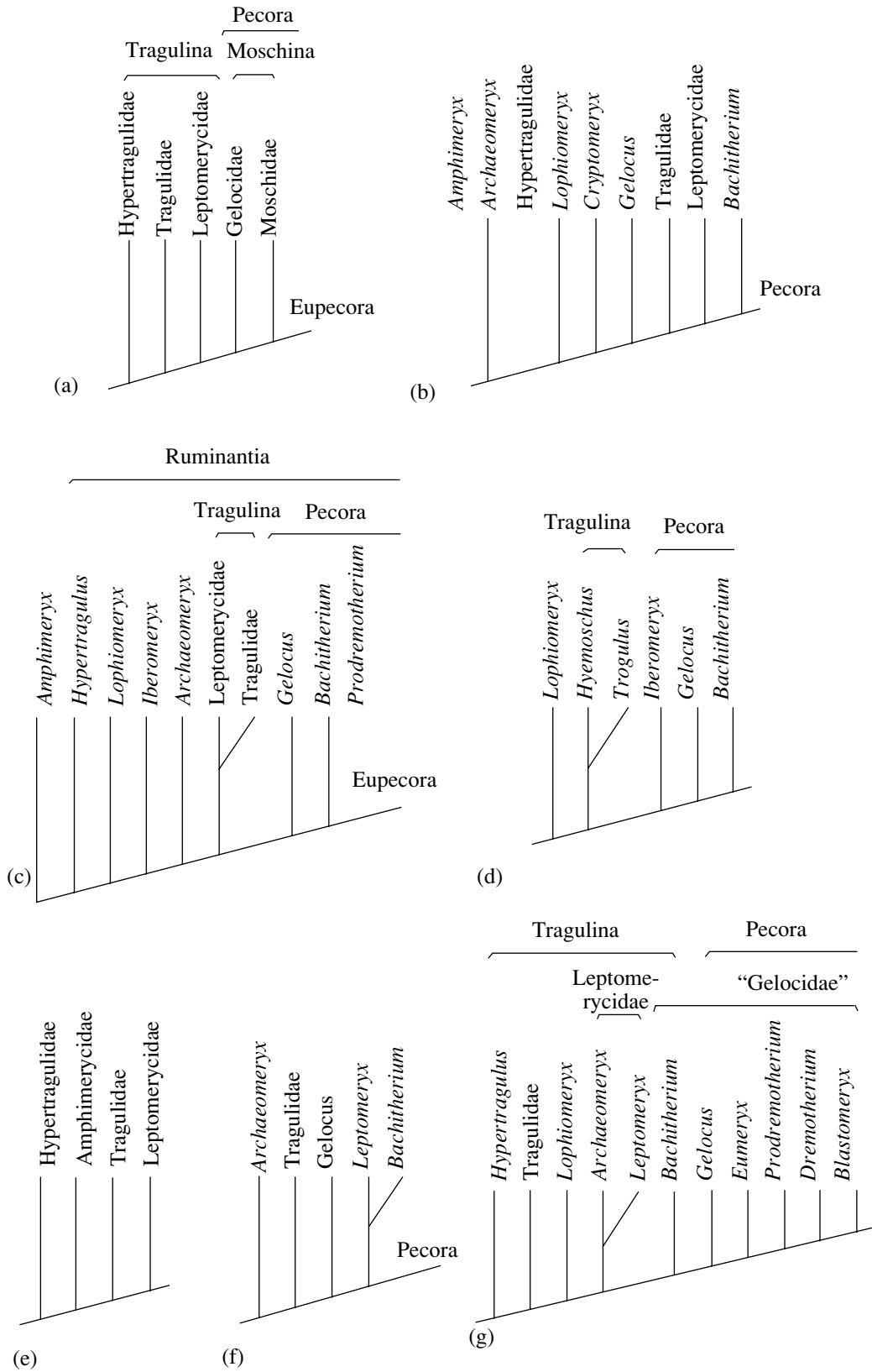
The objective renovation of phylogeny and taxonomy must be based on the revelation of the basal structures and main evolutionary trends (transmission of heredity and main adaptation trends). Both processes must be far from a formal estimation of the character polarities, but also must follow the data on evolutionary morphology.

Following Colbert (1941), the *Tragulina* was divided for a long time into three superfamilies: *Amphimerycoidea*, *Hypertraguloidea*, and *Traguloidea* (Table 1) (Simpson, 1945; Viret, 1961). Colbert (1941) recognized the superfamily *Traguloidea* based on a single family *Tragulidae*, but Simpson (1945) and Viret (1961) added the *Gelocidae* to that superfamily. The superfamily *Hypertraguloidea*, first proposed and placed by Scott (1940) in the *Tylopoda*, comprised two families, *Hypertragulidae* and *Protoceratidae*. The superfamily *Amphimerycoidea*, introduced by Colbert (1941) with a single family *Amphimerycidae*, was later excluded from the *Tragulina* along with *Protoceratidae*. Most researchers referred amphimerycids to the *Tylopoda* (Lavocat, 1951; Viret, 1961; Patton and Taylor, 1973). However, they are more likely to belong to the *Bunoselenodontia* (Müller, 1970).

Beginning in the 1980s, a number of cladistic analyses were performed to revise the taxonomic position and composition of separate groups and the relationships among primitive ruminants. Several cladograms were produced and a number of contradictory versions of relationships were proposed based mainly on the combination of variously interpreted dental and distal limb bone characters (Fig. 1) (Webb and Taylor, 1980; Bouvrain and Geraads, 1985; Bouvrain *et al.*, 1986; Geraads *et al.*, 1987; Janis, 1987; Janis and Scott, 1988; Scott and Janis, 1992; Gentry and Hooker, 1988; Moyá-Solá, 1988; Webb, 1998).

The composition and phylogenetic pattern of the *Tragulina* underwent some important changes. The names *Traguloidea* and *Hypertraguloidea* were almost abandoned. Moreover, the monophyly of the *Tragulina* was thrown into doubt because of great differences among various genera. It seemed that some genera should be removed from the *Tragulina* or even from the *Ruminantia*.

There was no consensus of opinion among researchers regarding the taxonomic position of almost any known group (except for the *Tragulidae* and *Leptomerycidae*) and the foundation of their relationships.



**Fig. 1.** Cladograms of primitive ruminants. (a) Webb and Taylor (1980); (b) Bouvrain and Geraads (1985); (c) Geraads *et al.* (1987); (d) Moyá-Solá (1988); (e, f) Gentry and Hooker (1988); and (g) Scott and Janis (1992).

**Table 1.** The major classifications of the Tragulina

<p>1. Osborn (1910) Order Artiodactyla Suborder Tragulina Family Gelocidae Family Hypertragulidae Family Tragulidae</p>	<p>4. Webb, Taylor (1980) Suborder Ruminantia Infraorder Tragulina Family Hypertragulidae Family Tragulidae Family Leptomerycidae Infraorder Pecora Division Moschina Family Gelocidae Family Moschidae Division Eupecora</p>	<p>7. McKenna, Bell (1998) Suborder Ruminantia Family Amphimerycidae Family Hypertragulidae Subfamily Hypertragulinae <i>Hypertragulus</i> <i>Patvitragus</i> <i>Nanotragulus</i> <i>Andegameryx</i> Subfamily Hypisodontinae <i>Hypisodus</i> Family Tragulidae <i>Dorcatherium</i> <i>Dorcabune</i> <i>Siamotragulus</i> <i>Yunnanotherium</i> <i>Tragulus</i> <i>Hyemoschus</i></p>
<p>2. Colbert (1941) Order Artiodactyla Suborder Tragulina Superfamily Amphimerycoidea Family Amphimerycidae Superfamily Hypertraguloidea Family Hypertragulidae Subfamily Hypertragulinae Subfamily Hypisodontinae Superfamily Protoceratidae Superfamily Traguloidea Family Tragulidae Subfamily Tragulinae Subfamily Gelocinae</p>	<p>5. Geraads <i>et al.</i> (1987) Infraorder Ruminantia Plesion <i>Amphimeryx</i> Plesion Hypertragulidae Plesion <i>Lophiomeryx</i> Plesion <i>Iberomeryx</i> Plesion <i>Archaeomeryx</i> Parvorder Tragulina Plesion Leptomerycidae Family Tragulidae Parvorder Pecora Plesion <i>Gelocus</i> Plesion <i>Bachitherium</i> Plesion <i>Prodremotherium</i> Sous-parvorder Eupecora</p>	<p>Family Leptomerycidae Subfamily Archaeomerycinae <i>Archaeomeryx</i> <i>Indomeryx</i> <i>Xijiangmeryx</i> <i>Miomeryx</i> Subfamily Leptomerycinae <i>Leptomeryx</i> <i>Pronodens</i> <i>Pseudoparablastomeryx</i> Family Bachitheriidae <i>Bachithetium</i> Family Lophiomerycidae <i>Cryptomeryx</i> <i>Iberomeryx</i> <i>Lophiomeryx</i></p>
<p>3. Simpson (1945), Viret (1961) Order Artiodactyla Suborder Ruminantia Infraorder Tragulina Superfamily Amphimerycoidea Family Amphimerycidae Superfamily Hypertraguloidea Family Hypertragulidae Subfamily Archaeomerycinae Subfamily Hypertragulinae Tribe Leptotragulini Tribe Hypertragulini Tribe Leptomerycini Tribe Hypisodontini Family Protoceratidae Superfamily Traguloidea Family Gelocidae Family Tragulidae</p>	<p>6. Scott, Janis (1987, 1992) Infraorder Tragulina Family Hypertragulidae Family Tragulidae Family Leptomerycidae Infraorder Pecora Family "Gelocidae"</p>	<p>Family Leptomerycidae Subfamily Archaeomerycinae <i>Archaeomeryx</i> <i>Indomeryx</i> <i>Xijiangmeryx</i> <i>Miomeryx</i> Subfamily Leptomerycinae <i>Leptomeryx</i> <i>Pronodens</i> <i>Pseudoparablastomeryx</i> Family Bachitheriidae <i>Bachithetium</i> Family Lophiomerycidae <i>Cryptomeryx</i> <i>Iberomeryx</i> <i>Lophiomeryx</i> Family Gelocidae <i>Gelocus</i> <i>Notomeryx</i> <i>Gobiomeryx</i> <i>Prodremotherium</i> <i>Phaneromeryx</i> <i>Pseudogelocus</i> <i>Pseudomeryx</i> <i>Paragelocus</i> <i>Pseudoceras</i></p>

**Table 2.** Revised Classification of Tragulines

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 Infraorder Tragulina Flower, 1883

## Superfamily Traguloidea Gill, 1872

## Family Tragulidae Milne-Edwards, 1864

*Tragulus* Brisson, 1762*Dorcatherium* Kaup, 1833*Hyemoschus* Gray, 1845*Siamotragulus* Thomas, Ginsburg, Hintong, et Suteethorm, 1990*Krabimeryx* Ducrocq, 1992

## Family Gelocidae Schlosser, 1886

*Phaneromeryx* Schlosser, 1886*Gelocus* Aymard, 1855*Prodremotherium* Filhol, 1877*Paragelocus* Schlosser, 1902*Pseudogelocus* Schlosser, 1902*Pseudoceras* Frick, 1937*Gobiomeryx* Trofimov, 1957*Pseudomeryx* Trofimov, 1957

## Family Leptomerycidae Zittel, 1893

*Leptomeryx* Leidy, 1853*Pseudoparablastomeryx* Frick, 1937*Pronodens* Koerner, 1940*Hendryomeryx* Black, 1978

## Family Archaeomerycidae Simpson, 1945, rank nov.

*Archaeomeryx* Matthew et Granger, 1925*Miomeryx* Matthew et Granger, 1925*Notomeryx* Qiu, 1978*Xinjiangmeryx* Zeng, 1978

## Family Lophiomerycidae Janis, 1987

*Lophiomeryx* Pomel, 1853*Indomeryx* Pilgrim, 1928*Iberomeryx* Gabunia, 1964

## Family Bachitheriidae Janis, 1987

*Bachitherium* Filhol, 1882

## Superfamily Hypertraguloidea Scott, 1940

## Family Hypertragulidae Cope, 1879

*Hypertragulus* Cope, 1873*Nanotragulus* Lull, 1922

## Family Hypisodontidae Cope, 1887, rank nov.

*Hypisodus* Cope, 1873

## Family Praetragulidae, fam. nov.

*Praetragulus* Vislobokova, 1998*Simimeryx* Stock, 1934*Parvitrugulus* Stock, 1978



The principle differences of opinion concerned the positions of the Hypertragulidae and *Archaeomeryx*. The inclusion of the Gelocidae and Bachitheriidae (*Bachitherium*) in the Pecora was also disputed.

Nevertheless, many interesting data on the morphology of primitive ruminants were obtained and many disputed issues of their relationships were highlighted.

Apart from insufficient morphological data and the use of homoplastic characters (convergent, parallel, or reversible), there are two main causes of difficulties of using cladistics for the reconstruction of the phylogeny of the group.

The first (objective) is related to the mosaic nature of the evolution. Because of this, the morphological resemblance of various tragulines may not reflect their close affinity, but rather is the result of adaptation to similar habitats, persistence of characters of remote ancestors, similar mechanisms of morphogenesis, different evolutionary rates in separate groups, and different evolutionary rates of some features. Particularly numerous examples of parallel evolution are expressed in the details of dental structure and in common trends of the development of dentition and limbs, such as the tendencies towards the inclusion of the lower canine in the incisor row, the loss of the first premolars, and the fusion of some bones of the autopodium. These characters are usually taken for cladistic analyses of primitive ruminants. Such characters should not be used for the determination of branching in higher taxa (families and above). They may only provide evidence for evolutionary polarities in well defined groups usually of lower ranks.

The second (subjective) cause of unreliable cladistic data obtained for primitive ruminants is a result of incorrect comparisons between taxa of different ranks. A comparison must be adequate and made between the taxa of the same taxonomic level in the frame of the same higher level taxa to reveal the natural phylogenetic relationships. Moreover, the evolutionary history of the families was often not taken into account. The interfamily relationships must be analyzed based not on generic or species-specific characters but on the fundamental characters of families, such as a set of cranial characters and the more general characters of dentition and postcranial skeleton, which reflect basic family-level adaptations.

The most adequate cladistic analysis of primitive ruminants was made by Webb and Taylor (1980) on the basis of an excellent morphological study, including several very important cranial characters (condition of the mastoid, foramen ovale, postglenoid process and foramen, tensor tympani fossa, etc.), and a comparison of cranial, dental, and postcranial characters of the type genera. Webb and Taylor (1980) referred three "paraphyletically related" families, Hypertragulidae, Tragul-

idae, and Leptomerycidae, to the infraorder Tragulina, which was assigned to the suborder Ruminantia, and combined the Gelocidae with the Pecora. Only two defining features were given for the Tragulina: (1) fusion of the cuboid and navicular, and (2) three-chambered stomach with a reticulum. For the Tragulidae, the defining characters were as follows: (1) posterior extension of the palatine bone, (2) reduction of the postglenoid process or its overriding by an expanded bulla, (3) posterior restriction of the tensor tympani chamber, (4) *Dorcatherium* fold, and (5) concave malleolar articulation of the calcaneum.

According to Webb and Taylor (1980), the phylogenetic progression within the Tragulina proceeded from the Hypertragulidae through Tragulidae to Leptomerycidae. In their opinion, many plesiomorphies confirm that tragulids appeared due to one of the earliest adaptive radiations of the group and occupied a lower branch than *Archaeomeryx* and the Leptomerycidae. The position of Hypertragulidae at the base of the Ruminantia was determined by the fusion of the cuboid and the navicular, shared with all other ruminants, and by the possession of many primitive characters (such as an open orbit, the retention of P1, and a complete fibula). The Leptomerycidae were considered to be advanced over the Hypertragulidae and Tragulidae because they shared with the Gelocidae and higher ruminants some important derived cranial, dental, and podial characters, such as the closed postorbital bar, posterior restriction of the mastoid bones, lingual elaboration of the lower premolars, and a concavoconvex articulation between the calcaneum and the malleolar bone.

This concept proposed by Webb and Taylor (1980) was supported by some researchers (Sudre, 1984; Janis, 1987; Janis and Scott, 1988; Scott and Janis, 1992). Trying to use nonhomoplastic characters in PAUP analysis, Scott and Janis (1992) obtained results similar to those of Webb and Taylor (1980), but with *Lophiomeryx* placed between tragulids and leptomerycids and with the "gelocid" sequence (including *Bachitherium*, *Prodremotherium*, and some cervid genera).

Other cladograms differ from these schemes in some aspects. Certain character polarities are problematic, because the morphology of most tragulines and the main trends of their evolution require a more detailed investigation than those studied extensively. Because of this, comparative and developmental morphology may contribute more to a better understanding of the real history of this group and to the recognition and delimitation of the natural taxa than cladistic analysis does. Higher level taxonomic features of the type species of the type genera continue to be the basis of classification of higher taxa.

The most essential differences concern the composition and position of the Tragulina and the positions of the Hypertragulidae and certain other groups.

Geraads *et al.* (1987) restricted the parvorder Tragulina to two groups: the family Tragulidae and “plesion” Leptomerycidae placed between *Archaeomeryx* and the Pecora. Tragulids and leptomerycids were supposed to be more progressive than the lower branches (occupied by the branching sequence from *Hypertragulus* through *Lophiomeryx* to *Iberomeryx* and *Archaeomeryx*) in the loss of the upper incisors, some peculiarities of milk premolars, reduced metatarsals II and V, and incompletely fused metatarsals III and IV. Both groups were linked together by the *Tragulus* fold, the labial direction of the posterior wing of the protocone, a p4 with parallel crests, and confluent optic foramina.

Based on the morphology of the lower molars of some selected genera, Moyá-Solá (1988) retained only the Tragulidae (including *Tragulus*, *Hyemoschus*, *Dorcatherium*, and, possibly, *Dorcabune* and *Yunnanotherium*) in the Tragulina and excluded *Archaeomeryx*, leptomerycids, and hypertragulids from the Ruminantia. This point of view conflicts with the opinion of most other researchers.

Regarding the position of the Hypertragulidae, almost all modern researchers, except Sudre (1984) and Moyá-Solá (1988), concluded that *Hypertragulus* was the most primitive member of the Ruminantia. But, while some followed Webb and Taylor (1980) in placing the Hypertragulidae in the Tragulina (Scott and Janis, 1988, 1992), others regarded *Hypertragulus* only as the second most primitive ruminant after *Amphimeryx* (Geraads *et al.*, 1987) or, controversially, preceding the Amphimerycidae (Gentry and Hooker, 1988). In the cladogram of Geraads *et al.* (1987), *Hypertragulus* shared a reduction or loss of the paraconule with other ruminants. The lower position of *Hypertragulus* (as compared to the next level occupied by *Lophiomeryx*) was determined by the following features: (1) low anterior articular surface of the axis, (2) the absence of the *Dorcatherium* fold, (3) unseparated hypoconid, (4) the presence of the trapezium and metacarpal I, and (5) unfused magnum and trapezoid. Sudre (1984) and Moyá-Solá (1988) believed that hypertragulids, a rather specialized group, could not be at the base of ruminants.

Recent discovery of an ancient hypertraguloid *Praetragulus* in Mongolia confirmed the position of hypertragulids among primitive groups of tragulines (Vislobokova, 1998) and gave new evidence on the phylogeny and classification of hypertraguloids.

The position of *Archaeomeryx* was also not quite clear. This genus was first placed in the family Hypertragulidae (Matthew and Granger, 1925b; Colbert,

1941; Simpson, 1945); however, after the work of Webb and Taylor (1980), it was included in the family Leptomerycidae (Sudre, 1984; Janis and Scott, 1988) or was placed in a separate plesion (Geraads *et al.*, 1987). In most cladograms, *Archaeomeryx* is separated from leptomerycids and occupies a position below the Tragulidae and Leptomerycidae (Bouvrain and Geraads, 1985; Geraads *et al.*, 1987). The low position of *Archaeomeryx* was determined by the presence of upper incisors and p1, a non-incisiform lower canine, unclosed anterior lobe of the lower molars, low anterior articular facet on the axis, the presence of the trapezium and metacarpal I, and unfused metatarsals III and IV (Bouvrain and Geraads, 1985). In addition, some milk teeth characters, such as the absence of T2 (paraconid crescent) and T4 (metaconid crescent) on dp4, the “plagioconule” on the crescent of DP3 (Geraads *et al.*, 1987), or the primitive backward position of the metaconid on the lower molars and separate metatarsals III and IV (Gentry and Hooker, 1988) also aided in this determination.

New cranial and postcranial evidence allowed us to establish a new family, Archaeomerycidae, one of the most primitive families within the Tragulina (Vislobokova and Trofimov, 2000a) (Table 2).

New data on the morphology of *Archaeomeryx* based on the study of a series of excellent skeletons from China (including undescribed skeletons excavated by the Soviet–Chinese Paleontological Expedition in the 1950s) are very important for a better understanding of early ruminant evolution and the early evolutionary stages of the order Artiodactyla.

One of the most problematic primitive ruminants, *Lophiomeryx*, has been regarded as a hypertragulid (Matthew and Granger, 1925a), a gelocid (Simpson, 1945; Viret, 1961; Sudre, 1984; etc.), a separate plesion of the Ruminantia (Geraads *et al.*, 1987), or as a separate family (Janis, 1987; Sudre, 1995). According to the cladograms, this genus is placed just after *Hypertragulus* (Bouvrain and Geraads, 1985; Geraads *et al.*, 1987), at the base of ruminants (Moyá-Solá, 1988), just below gelocids, or between tragulids and leptomerycids (Scott and Janis, 1992).

*Lophiomeryx* shares with *Archaeomeryx*, tragulids, leptomerycids, and pecorans the loss of the metacarpal I and trapezium; fusion of the trapezoid and magnum; and the characters of the malleolar bone, e.g., (smaller proximoanterior surface of the malleolar bone in comparison with its proximoposterior surface) (Geraads *et al.*, 1987).

*Lophiomeryx* clearly differs from other primitive ruminants by elongated and pointed premolars (Bouvrain and Geraads, 1985; Geraads *et al.*, 1987) and by the configuration of the lingual parts of the lower

molars, which resembles a figure eight. The latter feature allowed Janis (1987) to assign *Lophiomyx* to a separate nonruminant family.

Actually, the new data on the cranial morphology of *Lophiomyx* (based on the first skull of this genus found in Mongolia by the Joint Soviet–Mongolian Paleontological Expedition) confirm the rank determination given by Janis (1987) but attest to the close relationship of *Lophiomyx* and other traguloids.

There are two controversial positions of the Gelocidae and Bachitheriidae produced by cladistic analyses. Most cladograms show that the Gelocidae was a basal group of the Pecora (Webb and Taylor, 1980; Sudre, 1984; Geraads *et al.*, 1987; Janis and Scott, 1988; Moyá-Solá, 1988; Scott and Janis, 1992). However, according to other cladograms, these groups were placed among primitive ruminants (Bouvrain and Geraads, 1985; Gentry and Hooker, 1988). The gelocids were included in the Pecora based on apomorphic characters shared by both groups, such as: (1) loss of the stapedia artery, (2) reduction of the subarcuate fossa, (3) bifurcated paraconid composing the fourth lingual crest on the lower molars, (4) long forelimbs that are nearly equal to the hindlimbs in length, (5) short astragalus with parallel trochleae, and (6) the absence of the trapezium (Webb and Taylor, 1980). In addition, *Gelocus* was considered to be more advanced than tragulines in several other characters shared with *Bachitherium*, *Prodremotherium*, and higher ruminants (Eupecora), such as a complex talonid on dp3, the development of the “telocrete” (entoconid crescent) on the lower premolars, and incomplete or lost lateral metacarpals (Geraads *et al.*, 1987).

In some cladograms, *Gelocus* was placed below tragulids and leptomerycids (Bouvrain and Geraads, 1985) or below *Leptomeryx* (Gentry and Hooker, 1988). The first position was determined by several tooth characters, such as more bunodont tubercles, more shallow valleys; and a short posterior wing of the protocone that is not labially stretched (Bouvrain and Geraads, 1985). The second position was based on some dental characters (the presence of the entostyle on the upper molars, the *Palaeomyx* fold on the lower molars, and others) and on the separate metatarsals III and IV (Gentry and Hooker, 1988). Almost all of the chosen apomorphic characters, probably except for the loss of the stapedia artery, do not reflect the peculiar pecoran, but the common ruminant characters in their progressive advance. The condition of these characters in gelocids may be connected with their faster evolution in comparison with some other tragulines and with their better adaptation to coarse plant feed and to running.

Undoubtedly, the solution to the problem of the systematic position of gelocids necessitates new evidence on skull and postcranial morphology. The study of undescribed materials on gelocids from Mongolia, housed in the PIN and new cranial data on *Prodremotherium* were very useful for that purpose.

The data on the cranial structure of *Prodremotherim* given in the next chapter support the placing of Gelocidae in the Tragulina.

*Bachitherium* has been regarded as a gelocid (Simpson, 1945), a hypertragulid (Viret, 1961), a leptomerycid (Sudre, 1986), a primitive pecoran (Geraads *et al.*, 1987), or placed in a separate family within the Tragulina (Janis, 1987; Sudre, 1995). In cladograms, *Bachitherium* was linked with *Leptomeryx* (Gentry and Hooker, 1988); placed between the Leptomerycidae and *Prodremotherium* (Bouvrain and Geraads, 1985); below *Gelocus* outside the Pecora (Scott and Janis, 1992, fig. 20.6); or below *Prodremotherium* within the Pecora (Geraads *et al.*, 1987). *Bachitherium* was assumed to be more advanced than the Leptomerycidae in a more crescentic lingual tubercle of the upper molars (Bouvrain and Geraads, 1985), in the presence of the antorbital vacuity, in the fused metacarpals, and in the lost lateral digits (Scott and Janis, 1992). This genus strongly resembles the Pecora in many other derived features, such as a complex talonid on dp3, the presence of the “telocrete” (entoconid) on the lower premolars, a more developed endocone (protocone) on P2 and P3, a lingual cingulum on DP3, a labially directed posterior wing of the protocone, an elongated mandibular diastema, a tendency of metacarpals to fuse, and the reduction of the lateral metacarpals (Geraads *et al.*, 1987). Despite these features, *Bachitherium* preserves many basic features which prevent the assignment of this genus to the Pecora.

Thus, it is evident that the solution of the problems of classification and phylogeny of primitive ruminants requires a well rounded, detailed study of the type genera, as well as investigations of comparative morphology and evolution.

The study of fossil tragulines in Central Asia—the plausible center of origin of group has particular interest in the understanding of the early steps of traguline evolution. The comparisons between the European, Asiatic, American, and African forms help reveal the significant peculiarities of traguline evolution and the key times of dispersal.

Chapter 2  
COMPARATIVE MORPHOLOGY

## SKULL

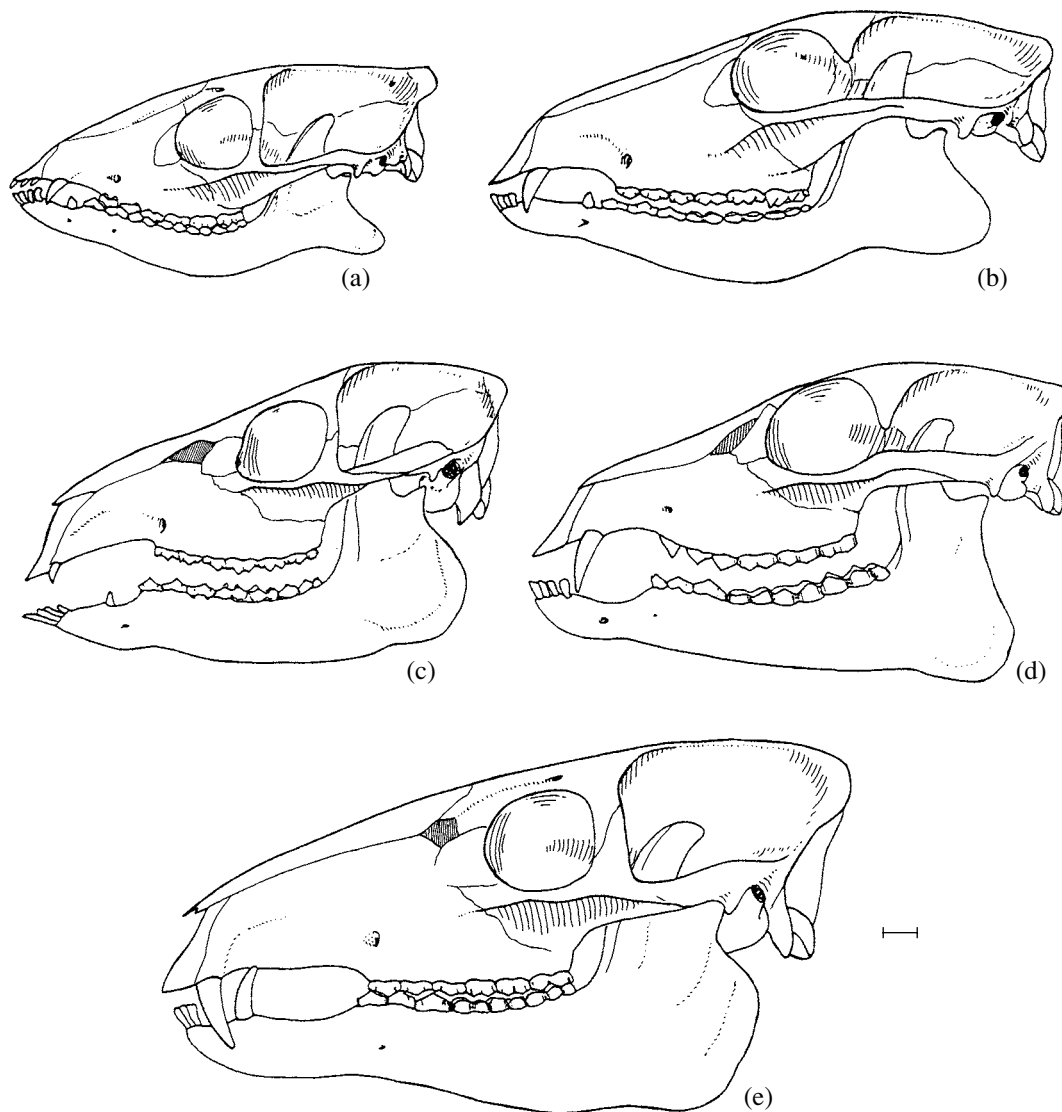
## Skull Shape and Proportions

A brachycephalic skull with a short and tapering snout is the primitive state within the Tragulina. In the course of evolution, both elongation and an increase in the height of the braincase and snout occurred, leading to changes in the skull proportions and to the transformation of major features.

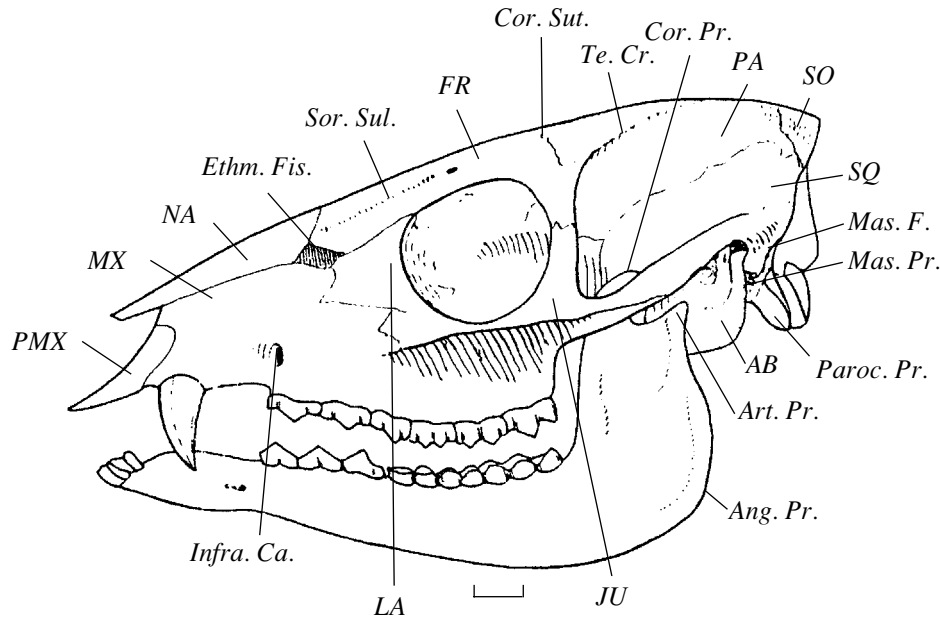
*Archaeomeryx* possesses the shortest snout and the length of its braincase is almost equal to that of the

facial part. The braincase length index (ratio of the braincase length to the basal skull length) is about 0.58. The snout remains shorter than the braincase in juvenile *Hyemoschus*, although the reverse occurs in adults. Within the Tragulina, the most elongated braincase is typical of *Lophiomeryx*, *Hypertragulus*, *Tragulus*, and *Prodremotherium*.

The most primitive braincase is preserved in *Archaeomeryx*, *Lophiomeryx*, *Prodremotherium*, and, possibly, in *Bachitherium*. In dorsal view, the braincase in these genera is very weakly expanded approximately



**Fig. 2.** Lateral views of skulls. (a) *Archaeomeryx optatus*, PIN, no. 2198/149; (b) *Lophiomeryx angarae*, reconstructed from PIN, no. 3110/964; (c) *Leptomeryx* sp., AMNH, no. 11870; (d) *Praetragulus electus*, reconstructed from PIN, no. 3110/731; (e) *Bachitherium insigne* (Geraads *et al.*, 1987). Scale bar, 1 cm.



**Fig. 3.** Lateral view of the skull of *Hyemoschus aquaticus*, Recent. Designations: (AB) auditory bulla; (Ang. Pr.) angular process; (Art. Pr.) articular process; (Cor. Pr.) coronoid process; (Cor. Sut.) coronal suture; (Ethm. Fis.) ethmoidal fissure; (FR) frontal; (Infra. Ca.) infraorbital canal; (JU) jugal; (LA) lacrimal; (Mas. F.) mastoid foramen; (Mas. Pr.) mastoid process; (MX) maxilla; (NA) nasal; (PA) parietal; (Paroc. Pr.) paroccipital process; (PMX) premaxilla; (SO) supraoccipital; (Sor. Sul.) supraorbital sulcus; (SQ) squamosal; and (Te. Cr.) temporal crest. Scale bar, 1 cm.

at the level of the zygomatic processes of the squamosals and strongly narrowed behind the processes owing to the rather small posterior part of the cerebrum and to the very narrow cerebellum. The braincase has a more spherical shape in *Leptomeryx*, *Hypertragulus*, *Tragulus*, and *Hyemoschus*. The shape of the braincase clearly reflects the structure of brain.

The olfactory bulbs were relatively long in *Archaeomeryx*, *Hypertragulus*, and *Lophiomeryx*, representing a primitive eutherian state. The length of the olfactory bulbs in these genera was a little shorter than in Recent tragulids. In the latter, it is about 25% of the length of the cerebral hemispheres.

The cerebral hemispheres of *Archaeomeryx* and *Lophiomeryx* were relatively narrow and low, compared to the more developed hemispheres of other tragulines. The most developed hemispheres occur in tragulids. It is interesting that there is a long, narrow triangular exposure of the midbrain between the cerebral hemispheres of *Tragulus* and *Hyemoschus* (Milne-Edwards, 1864). This character is regarded as a primitive eutherian trait (Edinger, 1964) and appears to be present in other tragulines.

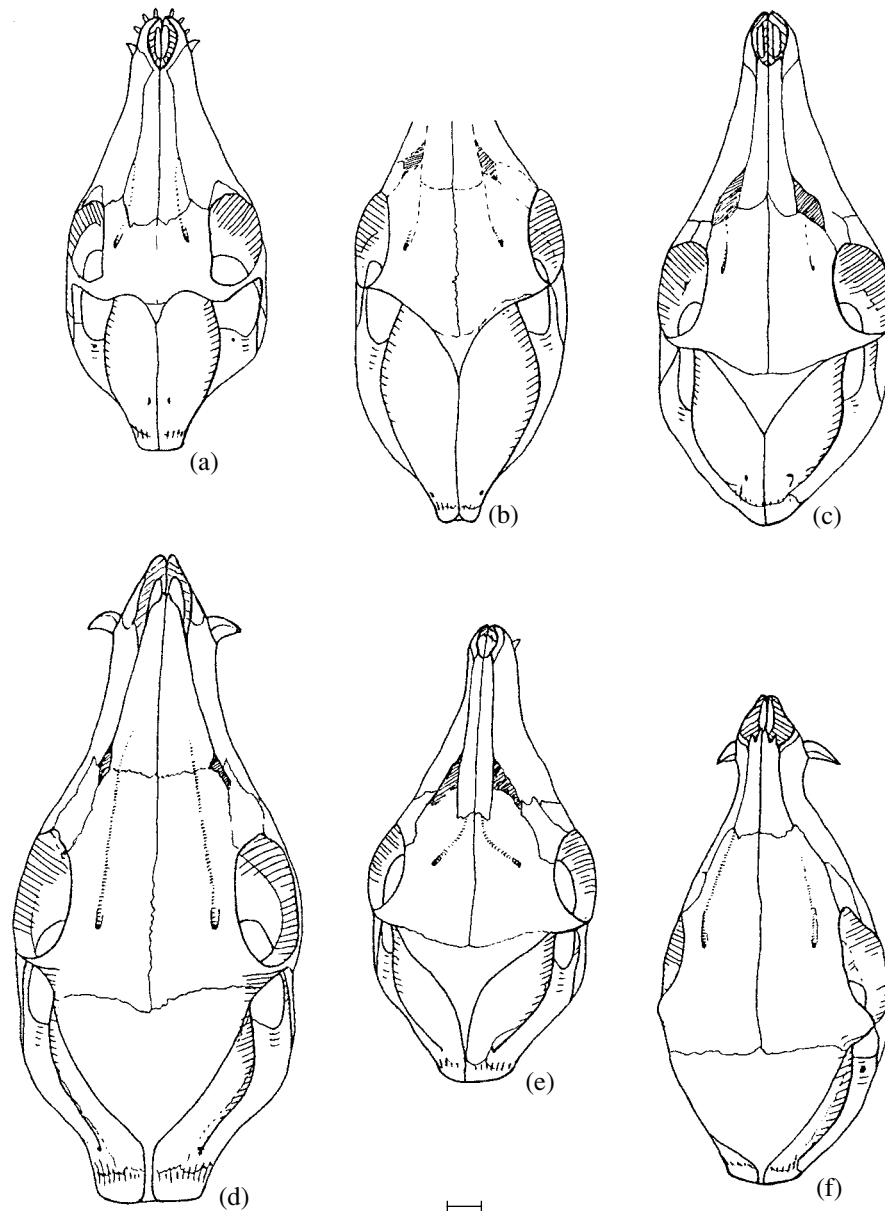
Another primitive condition is the very low cerebellum seen in *Archaeomeryx* and *Lophiomeryx*. The top of the cerebellum in these genera and in *Hypertragulus* was situated lower than the neopallium, similar to those in primitive eutherians. In *Leptomeryx* and Recent tragulids, the cerebellum was higher and better developed.

In lateral view, the roof of the braincase is weakly convex anteriorly and strongly concave posteriorly in *Archaeomeryx* and *Lophiomeryx*. The roof is weakly convex in *Bachitherium* and strongly convex anteriorly in *Leptomeryx*, *Prodremotherium*, *Dorcatherium*, and Recent tragulids. It is almost flat in *Hypertragulus* (Figs. 2 and 3). The most elevated point of the roof is located in front of the medial point of the coronal suture (bregma) in *Hypertragulus* and approximately in the middle of the braincase length in others. At the boundary between the braincase and snout (in the interorbital), the skull roof is almost flat in *Bachitherium* and tragulids and slightly concave in *Hypertragulus* and *Prodremotherium*.

The occiput in the primitive state is concave with a very marked, posteriorly projecting occipital crest. This state is observed in *Archaeomeryx*. The occiput is almost flat in *Hypertragulus*, *Leptomeryx*, and *Prodremotherium*, and flat or convex in *Tragulus*.

The angle between the occiput and the skull roof is approximately 90° in *Hyemoschus*, approximately 100° in *Archaeomeryx* and *Tragulus*, and 108° in *Leptomeryx*.

In dorsal view, the primitive occiput has a long, narrow posteromedial flaring due to a very strong development of the occipital crest. Such a structure is typical of *Archaeomeryx* (Fig. 4). A weaker projection, sometimes with a medial curvature, is preserved in *Prodremotherium* and *Hyemoschus*. In *Hypertragulus*, *Leptomeryx*, and *Tragulus*, the line of the occiput is convex.



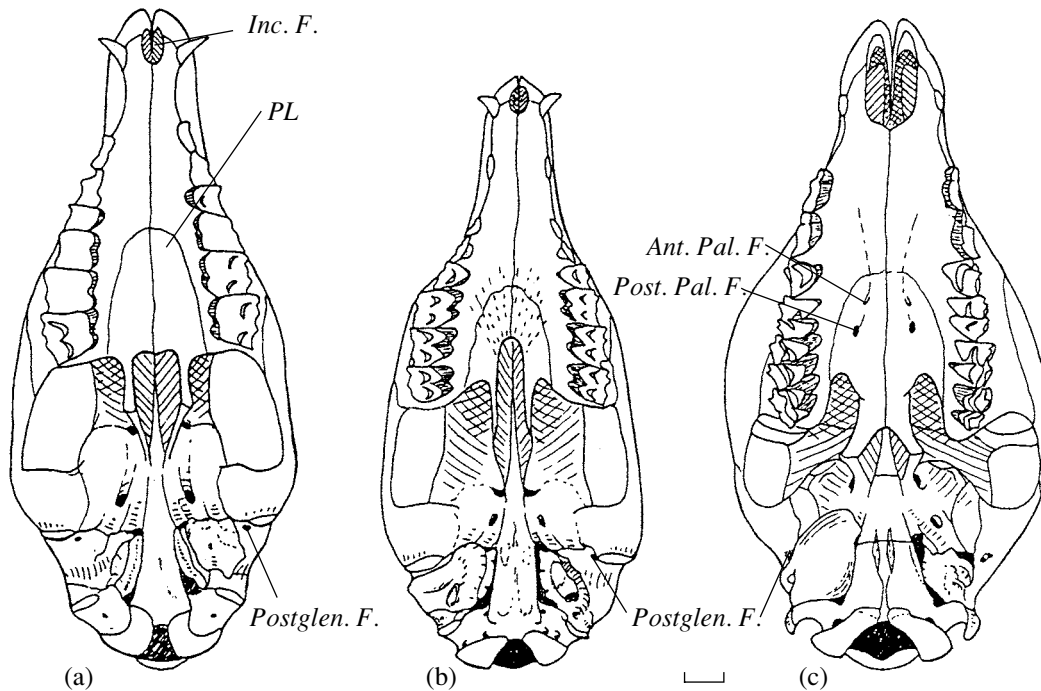
**Fig. 4.** Dorsal views of skulls: (a) *Archaeomeryx optatus*, PIN, no. 2198/154; (b) *Prodremotherium* sp. (Jehenne, 1997, pl. 1, fig. A); (c) *Leptomeryx* sp., AMNH, no. 11870; (d) *Hyemoschus aquaticus*, Recent; (e) *Hypertragulus hesperius*, AMNH, no. 7918; and (f) *Tragulus kanchil*, Recent. Scale bar, 1 cm.

In ventral view, the basicranium in the primitive condition has a relatively long posterior part behind the auditory bulla. This feature is present in *Archaeomeryx*, *Hypertragulus*, and *Lophiomeryx* (Fig. 5). The anterior part of the braincase in front of the external acoustic foramen is only slightly longer than the posterior part in *Archaeomeryx* and increases in length in all others. In the derived state, the posterior part of the basicranium is short.

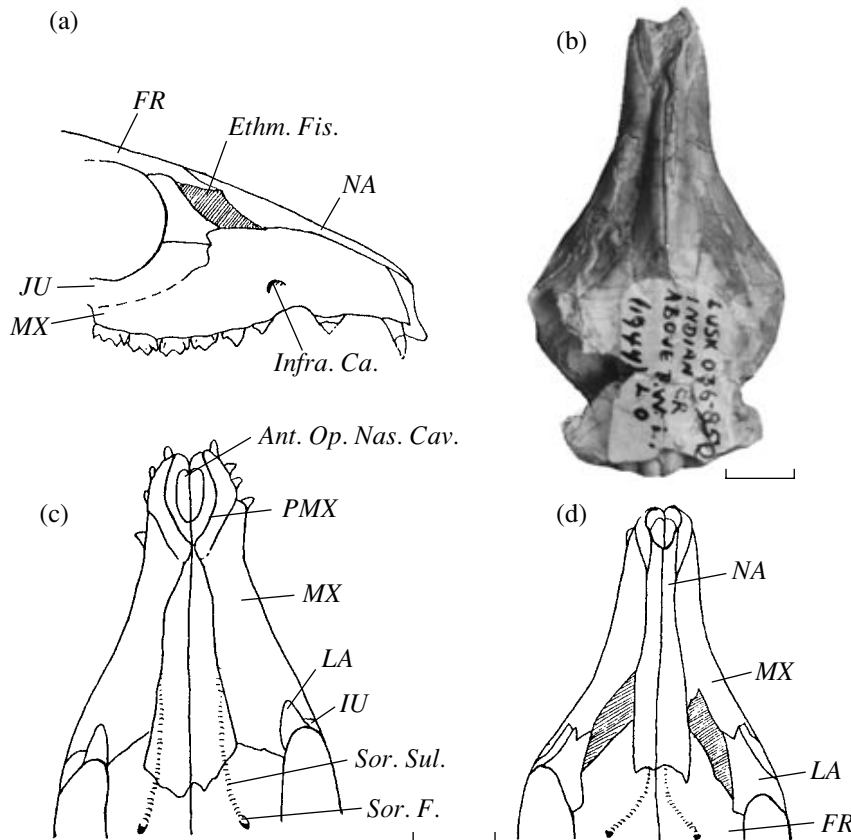
The lowest snout is observed in *Archaeomeryx*. The highest snouts are in *Prodremotherium* and *Bachitherium*.

The facial part is very short in *Archaeomeryx* and probably in *Lophiomeryx*. It is most elongated in *Gelocus*. In other tragulines, there are different stages of snout elongation. The indices of snout length (relative to the basal length) range from 0.54 in *Archaeomeryx* to 0.68 in *Bachitherium* and *Tragulus*.

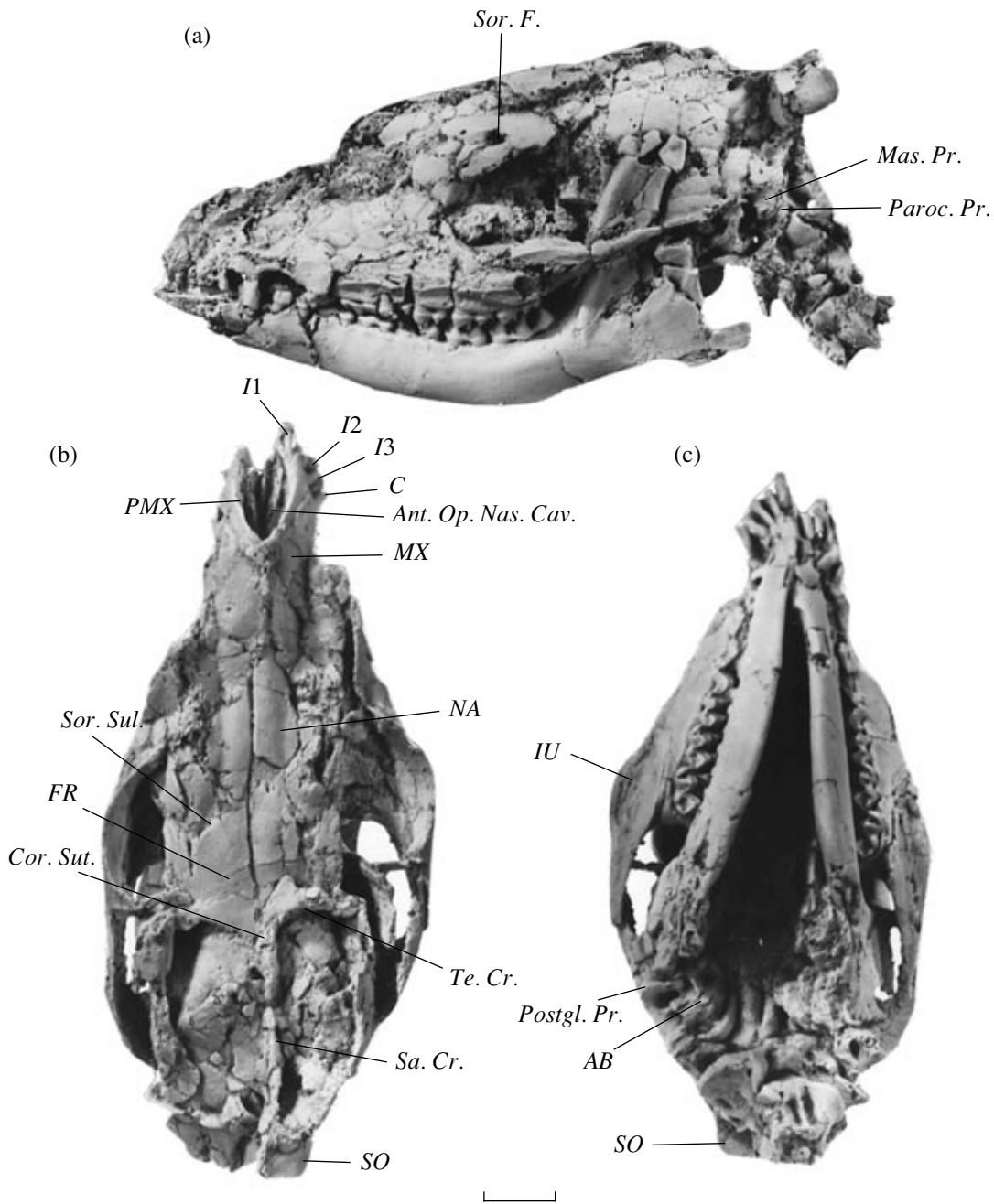
In dorsal view, the snout is strongly narrowed in *Archaeomeryx* (PIN, no. 2198/154), *Hypertragulus* (AMNH, no. 53 865), *Leptomeryx*, and *Tragulus*, and much less narrowed in *Hyemoschus*. In the primitive condition, the snout almost does not increase in width at the level of the upper canines in *Archaeomeryx*,



**Fig. 5.** Ventral views of skulls: (a) *Lophimeryx angarae*, reconstructed based on PIN, no. 3110/964; (b) *Hypertragulus calcaratus*, reconstructed based on AMNH, no. 53 802; and (c) *Tragulus meminna*, Recent. Designations: (*Ant. Pal. F.*) anterior palatine foramen; (*Inc. F.*) incisive foramen; (*PL*) palatine; (*Postglen. F.*) postglenoid foramen; and (*Post. Pal. F.*) posterior palatine foramen. Scale bar, 1 cm.



**Fig. 6.** Facial part of skulls: *Hypertragulus*, reconstructed based on AMNH, no. 53865, in (a) lateral and (b, d) dorsal views and (c) *Archaeomeryx optatus*, reconstructed based on PIN, no. 2198/154, dorsal view. Designations: (*Ant. Op. Nas. Cav.*) anterior opening of nasal cavity; (*Ethm. Fis.*) ethmoidal fissure; (*FR*) frontal; (*Infra. Ca.*) infraorbital canal; (*JU*) jugal; (*LA*) lacrimal; (*MX*) maxilla; (*NA*) nasal; (*PMX*) premaxilla; (*Sor. F.*) supraorbital foramen; and (*Sor. Sul.*) supraorbital sulcus. Scale bar, 1 cm.



**Fig. 7.** Skulls of *Archaeomeryx optatus*, Middle Eocene, Ula-Usu, China: (a) PIN, no. 2198/149, lateral view and (b, c) PIN, no. 2198/154, (b) dorsal and (c) ventral views. Designations: (AB) auditory bulla; (Ant. Op. Nas. Cav.) anterior opening of nasal cavity; (Cor. Sut.) coronal suture; (FR) frontal; (JU) jugal; (Mas. Pr.) mastoid process; (MX) maxilla; (NA) nasal; (Paroc. Pr.) paraoccipital process; (Postgl. Pr.) postglenoid process; (PMX) premaxilla; (Sa. Cr.) sagittal crest; (SO) supraoccipital; (Sor. F.) supraorbital foramen; (Sor. Sul.) supraorbital sulcus; and (Te. Cr.) temporal crest. Scale bar, 1 cm.

*Hypertragulus*, and *Leptomeryx*. The snout is widened in male tragulids that possess large upper canines.

A considerable transformation of the structure of the anterior opening of the nasal cavity occurred in the course of traguline evolution. The most primitive state is represented in *Archaeomeryx*. In dorsal view, the anterior opening of the nasal cavity of *Archaeomeryx* (PIN, no. 2198/154) is short, ovoid in outline, and

slightly narrowed posteriorly. The premaxillae dorsally overlap the nasals, and the latter do not overhang the opening. In *Hypertragulus* (AMNH, no. 53 865), the opening has a more advanced structure. It is short, pear-shaped, and covered dorsally by the nasals. In the more advanced state, seen in other tragulines, the anterior opening of the nasal cavity is much longer, and the elongated anterior processes of the nasals protrude.



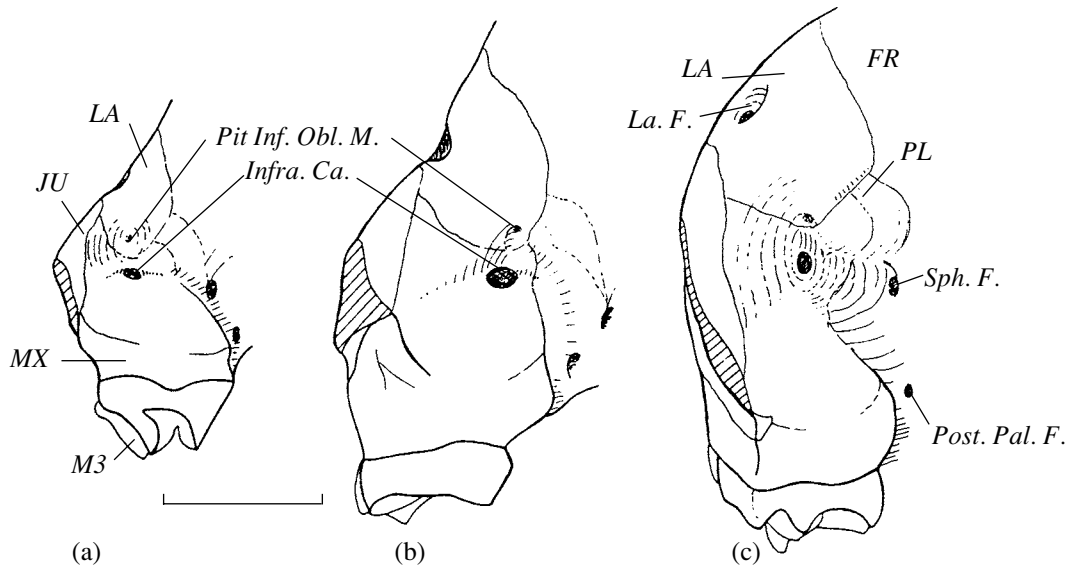
**Table 3.** Comparisons of the main cranial features of tragulines

Feature	Primitive condition	Derived condition
1. Sagittal crest	long (Ar, Ba, Pro)	shorter (Hy, Le, tragulids)
2. Temporal crests	diverging slightly posteriorly to orbits (Ar, Ba, Pro)	(a) diverging strongly posteriorly to orbits at mid-length of braincase (Hy, Le); (b) diverging closely to lambdoidal suture (tragulids)
3. Size of orbits	equal or smaller than M1-M3 (Ar, Lo, Ba)	longer than M1-M3 (Hypi, Hy, Le, Pro, Do, Tra, Hye)
4. Postorbital bar	<u>open posteriorly</u> (Hy, Prae, ?Lo)	closed posteriorly: (a) mostly of frontal (Ar, ?Pro); (b) mostly of jugal (Ba, Tra, pecorans); (c) half of frontal and half of jugal (Le)
5. Ethmoidal fissure	absent or very small (Ar, Lo, tragulids, some pecorans)	better developed (Ba, Hy, Le, Pro, most pecorans)
6. Anterior opening of nasal cavity, dorsal view	<u>short, ovoid</u> (Ar)	(a) peariform (Hy); (b) elongated, with strong anterior protrusion of nasals (Pro, Ba, tragulids, pecorans)
7. Infraorbital canal	lowly situated, small and medium caliber (Ar, Si, Hy, Lo, Ba, Prae)	higher situated, larger caliber (Pro, tragulids, pecorans)
8. Position of posterior opening of infraorbital canal	<u>higher than sphenopalatine foramen</u> (Ar, Pro, Lo, Hy) <u>in maxilla</u> (Ar, Lo, Pro)	opposite or lower than sphenopalatine foramen (Le, tragulids, pecorans) (a) at junction of lacrimal and maxilla (Hy); (b) at junction of lacrimal, maxilla, and palatine (Le, tragulids, pecorans)
9. Median concavity of posterior border of palate	weak (traguloids)	strong (hypertraguloids)
10. Palatine foramina	presence of both anterior and middle palatine foramina (Lo, Tra)	(a) presence of anterior palatine foramen (?Ar); (b) presence of middle palatine foramen (Hy, Le, Pro, Hye)
11. Jugular foramen	<u>not confluent with posterior lacerate foramen</u> (hypertraguloids)	confluent with posterior lacerate foramen (traguloids, pecorans)
12. Basioccipital	<u>elongated, not very expanded posteriorly</u> (Ar, Hy, Lo)	shorter, more expanded posteriorly (Le, tragulids)
13. Basisphenoid	<u>elongated, not very expanded posteriorly, strongly convex ventrally</u> (Ar, Hy)	shorter, more expanded posteriorly and less convex or flat ventrally (?Lo, Le, tragulids)
14. Alisphenoid	<u>almost not rising laterally, with foramen ovale faced ventrally</u> (Ar, Lo, Hy, Le, Prae)	rising laterally, with foramen ovale faced lateroventrally (tragulids)
15. Alisphenoid canal	<u>absent</u> (Ar, Lo, pecorans)	present, anterior opening confluent with foramen orbitotundum (Hy, Prae)
16. Pterygoid canal	<u>absent</u> (Ar, Lo, Hye)	present (Le, some Tra, pecorans)
17. Foramen ovale	<u>small, oval, positioned posteriorly</u> (Ar, Ge, Lo, tragulids)	(a) slitlike, positioned posteriorly (Le); (b) large, oval, positioned posteriorly (Pro); (c) small, oval, positioned approximately in midlength of alisphenoid (Hy, Prae)
18. Optic foramina	<u>separate</u> (Ar, Lo, Hy)	confluent (tragulids) or almost confluent (Le)
19. Pterygoid process	<u>low, with strongly oblique posterior edge</u> (Ar, Hy, Le)	higher, with more weakly oblique posterior edge (tragulids)
20. Promontorium	simple, corresponding to main whorl of cochleae (Ar, Hy, Lo, Prae)	more complex, two last whorls of cochleae almost equal in height (Le, tragulids)

**Table 3.** (Contd.)

Feature	Primitive condition	Derived condition
21. Fenestra vestibuli	small (Ar, Lo, Le, some pecorans)	large (Ge, Prae, Hy, tragulids)
22. Fossa for stapedial muscle	narrow, posteriorly situated (behind fenestrae vestibuli and cochleae) (Ar, Lo, Prae)	displaced anteriorly to level of fenestra vestibuli (Le, Hy, tragulids)
23. Promontory sulcus	<u>absent</u> (Ar, Lo)	present (Hy, Prae, Ge, Le, tragulids)
24. Carotid foramen	separate (Ar, Lo, Tra, Hye)	confluent with posterior lacerate foramen (Hy, Le, pecorans)
25. Lateral wall of epitympanic recess	formed mostly by petrosal (Ar, Hy, Prae)	formed mostly by squamosal (Lo, ?Le, tragulids, pecorans)
26. Mastoid exposure	lateral (Ar, Lo, hypertraguloids, tragulids)	occipital (Le, Ba, Ge, Pro, pecorans)
27. Postglenoid process	absent (tragulids)	present (Ar, Lo, Hy, Pro, Prae, pecorans);
28. Postglenoid foramen	open (Ar, Lo, Tra, Hye, Le)	enclosed by auditory bulla (Ba, Pro, Hy, pecorans)
29. Auditory bulla	small with short external acoustic meatus and longest axis strongly oblique posteriorly (Ar, Lo)	(a) larger, with longer external acoustic meatus, less inclined posteriorly (Le, Ba, Hy, pecorans); (b) large, strongly inflated (tragulids, Hypi)
30. Stylohyoid vagina	shallow, broadly open posteriorly, situated between auditory bulla and tube (Ar, Lo)	(a) bulla deeper, encroached upon, with sharp lateral border (Le); (b) bulla deeper, narrower, encroached upon and enclosed posteriorly (hypertragulids, tragulids)
31. Supraorbital sulcus	curved medially, slightly convergent posterior to nasofrontal suture and continued anterior to this (Ar)	(a) strongly convergent and ended at nasofrontal suture, curved laterally (Hy); (b) ended at posterior border of ethmoidal fissure, parallel (Le) or curved medially (Ba, Pro); (c) parallel or slightly curved laterally, ended at nasofrontal suture (Tra) or slightly anterior to this (Hye)
32. Nasofrontal suture	posterior to antorbital rim (Ar)	opposite or anterior to antorbital rim (Hy, Le, Ba, Pro, tragulids)
33. Nasal	<u>elongated, narrowed anteriorly and posteriorly</u> (Ar, Hy)	(a) shorter, widened posteriorly, narrowed anteriorly (Ba, tragulids); (b) widened posteriorly and anteriorly (Le)
34. Lacrimal	<u>small facial and orbital parts</u> (Ar, Lo)	expanded facial and lacrimal parts (Hy, Le, Ba, tragulids, pecorans) small orbital part (Pro)
35. Jugal	<u>lowly situated, weakly extended anteriorly, with long posterior spine</u> (Ar)	higher situated, more strongly extended anteriorly, with shorter posterior spine (Le, Hy, tragulids, pecorans)
36. Premaxilla	low and short with posterodorsal (nasal) process almost overhanging anterior opening of nasal cavity (Ar)	higher and longer, with wide break between posterodorsal processes: (a) premaxilla–nasal contact present (Hy, Le, Pro, Ba, Tra, most pecorans); (b) premaxilla–nasal contact absent (Hye)
37. Mandibular body	slightly descending anteriorly, with convex ventral border (Ar, Lo, hypertraguloids, tragulids)	strongly descending in front of p2, with almost straight ventral border (Ge)
38. Angular process	not very broad, rounded, strongly projected posteriorly (Ar, Lo)	(a) broader and less strongly projected posteriorly (Le, Hy, pecorans); (b) weakly projected posteriorly (Hye, Tra)
39. Coronoid process	high, with oblique anterior border (Ar, Lo)	lower, with semivertical anterior border (hypertraguloids, tragulids, most pecorans)
40. Articular process	low-situated (Ar, Si, Lo, Hy)	higher situated (Hypi, tragulids, pecorans)

Note: The following acronyms are used: (Ar) *Archaeomeryx*; (Lo) *Lophiomeryx*; (Hy) *Hypertragulus*; (Si) *Simimeryx*; (Prae) *Praetragulus*; (Hypi) *Hypisodus*; (Ba) *Bachitherium*; (Pro) *Prodremotherium*; (Le) *Leptomeryx*; (Do) *Dorcattherium*; (Tra) *Tragus*; (Hye) *Hymoschus*; and (Ge) *Gelocus*. Primitive eutherian characters are underlined.



**Fig. 8.** Posterior view of the anterior orbital wall: (a) *Archaeomeryx optatus*, PIN, no. 2198/162; (b) *Lophiomeryx angarae*, PIN, no. 3110/964; and (c) *Prodremotherium* sp., PIN, no. 2737/412. Designations: (FR) frontal; (Infra. Ca.) infraorbital canal; (JU) jugal; (LA) lacrimal; (La. F.) lacrimal foramen; (MX) maxilla; (Pit Inf. Obl. M.) pit for inferior oblique muscle; (PL) palatine; (Post. Pal. F.) posterior palatine foramen; and (Sph. F.) sphenopalatine foramen. Scale bar, 1 cm.

These processes extend beyond the contact with the premaxilla and cover part of the opening, as in most ungulates (Figs. 4, 6, and 7).

In lateral view, the axis of the braincase base is almost parallel to the axis of the tooth row in the primitive state. The angle between the axes increases in advanced genera. The basicranioalveolar angle is only a few degrees in *Archaeomeryx* and *Hypertragulus*, and reaches  $9^\circ$  in *Lophiomeryx*,  $12^\circ$  in *Leptomeryx*,  $13\text{--}15^\circ$  in *Tragulus*, and  $21^\circ$  in *Prodremotherium*. The flexure of the cranial axis at the interorbital also increased in the course of evolution.

The flexure is very small in *Archaeomeryx* and *Hypertragulus*. The angle between the braincase and facial axes is  $130^\circ$  in *Archaeomeryx*,  $124^\circ$  in *Leptomeryx*,  $116^\circ$  in *Tragulus*,  $120^\circ$  in *Bachitherium*, and probably not less than  $120^\circ$  in *Prodremotherium*.

### Sagittal and Temporal Crests

A long, high sagittal crest and well developed temporal crests are plesiomorphic characters within the Tragulina (Table 3). In the most primitive state (preserved in *Archaeomeryx*), the temporal crests diverge very close to the bregma. They curve strongly anteriorly and extend almost perpendicular to the sagittal plane in their anterior parts owing to the strong development of the temporal muscles and the great length of the sagittal crest. Very primitive structures are also present in *Prodremotherium* and *Bachitherium*. The length of the sagittal crest is about half of the braincase length in these genera. The sagittal crest becomes somewhat shorter in *Hypertragulus* and *Leptomeryx*, and much shorter in tragulids. Sometimes in *Hyemos-*

*chus* the sagittal crest is transformed into two weak parasagittal crests with a flat and rather broad plane between them. In *Hypertragulus* and *Leptomeryx*, the temporal crests diverge more gradually and posteriorly than in *Archaeomeryx* due to a smaller and more posterior and lateral placement of the anterior attachment of the temporal muscle. However, both genera preserve a primitive anterior direction of the curvature of the temporal crests typical of *Archaeomeryx*. A wider and more posterior divergence of the temporal crests is observed in the Tragulidae. They diverge very far from the bregma near the lambdoidal suture and curve posteriorly. This structure is associated with a greater decrease in the size of the temporal muscle.

### Orbital Region

Primitively, the orbit is small, open posteriorly, low and anteriorly positioned.

The orbits are unclosed posteriorly in *Hypertragulus* and probably in *Praetragulus* and *Lophiomeryx angarae*.

In most tragulines, there is the postorbital bar, which is formed mostly by the frontal in *Archaeomeryx*. In Recent tragulids and *Bachitherium*, the postorbital bar consists mostly of the jugal.

Small orbits, the length of which does not exceed the length of M1–M3, are found in *Archaeomeryx*, *Lophiomeryx*, and *Bachitherium*. Large orbits, the length of which exceed the M1–M3 length, are found in *Hypisodus*, *Hypertragulus*, *Leptomeryx*, *Prodremotherium*, and *Dorcatherium*, as well as in *Tragulus* and *Hyemoschus*, which lead a mainly nocturnal mode of

life. In *Hypertragulus*, the orbits are prominent and resemble those of pecorans inhabiting open landscapes.

A low position of the orbits is preserved in *Archaeomeryx*, *Lophiomeryx*, and *Prodremotherium* (PIN, no. 2737/412), whereas a higher position of orbits is typical of *Bachitherium*, tragulids, and hypertraguloids.

The primitive anterior position of orbits is changed to a more posterior position due to the elongation of the facial part of the skull and modification of the masticatory apparatus. However, the enlargement of the orbits makes this process less evident. The anterior border of the orbit lies at the level of M1 in *Archaeomeryx*, *Leptomeryx evansi*, *Lophiomeryx*, *Prodremotherium* (PIN, no. 2737/412), *Praetragulus*, and *Gelocus*, and at the level of M2 in *Hypertragulus*, *Bachitherium*, and *Prodremotherium elongatum*. However, in *Tragulus* with larger orbits, it is at the level of P4. In *Hyemoschus*, the anterior orbital rim is above M1, as in primitive forms possessing smaller orbits.

In lateral view, most of the orbital wall in tragulines is formed by the orbital exposure of the frontal that extends for nearly half the height of the orbital wall and contacts anteriorly with the lacrimal and palatine, inferiorly with the orbitosphenoid and alisphenoid, and posteriorly with the parietal.

The transformation of the orbital region was accompanied by certain changes of the orbital mosaic, including the size and relationships of bones and the position and sizes of the posterior opening of the infraorbital canal and sphenopalatine foramen.

Important primitive traits of the anterior orbital wall are the relatively small lacrimal and jugal exposures, an extensive expansion of the maxilla, posterior opening of the infraorbital canal (for the infraorbital nerve, artery, and vein) in the maxilla, and a higher position of this opening relative to the sphenopalatine foramen.

In the primitive state, preserved in *Archaeomeryx*, *Lophiomeryx*, and *Prodremotherium* (PIN, no. 2737/412), a well developed orbital exposure of the maxilla occupies the anteroinferior and inferior parts of the wall, and the jugal portion is very narrow (Fig. 8). In these genera, the posterior opening of the infraorbital canal is located in the maxilla in a well-outlined pit.

The same structure of the anterior orbital wall is typical of leptictids, some insectivores, and primates (Novacek, 1986), and appears to be a primitive eutherian state. In a more advanced state, seen in *Hypertragulus*, *Leptomeryx*, and tragulids, the portion of the maxilla in the orbit is restricted owing to the enlargement of the lacrimal and expansion of the jugal and palatine. In this state, the posterior opening of the infraorbital canal is displaced to the incisure on the medioinferior border of the lacrimal.

The posterior opening of the infraorbital canal lies primitively higher than the sphenopalatine foramen (providing passage for the sphenopalatine nerve, artery, and vein to the nasal cavity) in *Archaeomeryx*, *Prodremotherium*, *Lophiomeryx*, and *Hypertragulus*.

The most primitive state and very low position of the infraorbital canal are observed in *Archaeomeryx*. In *Lophiomeryx* and *Prodremotherium*, the portions of the lacrimal and maxilla are approximately equal in height, and the posterior opening of the infraorbital canal lies approximately at half the height of the anterior wall of the orbits.

In *Hypertragulus* (AMNH, Doug 30-1163), the orbital wing of the maxilla remains low, but the orbital process of the lacrimal is enlarged. As a consequence, the posterior opening of the infraorbital canal is displaced to the lower half of the anterior wall of the orbits and lies only slightly higher than the sphenopalatine foramen.

In *Leptomeryx* and Recent tragulids, the orbital process of the lacrimal is more enlarged and both openings are located at approximately the same level.

In *Dorcatherium* (BMNH, no. 40632), the orbital process of the lacrimal is strongly enlarged, and the posterior opening of the infraorbital canal occupies a lower level, as in pecorans.

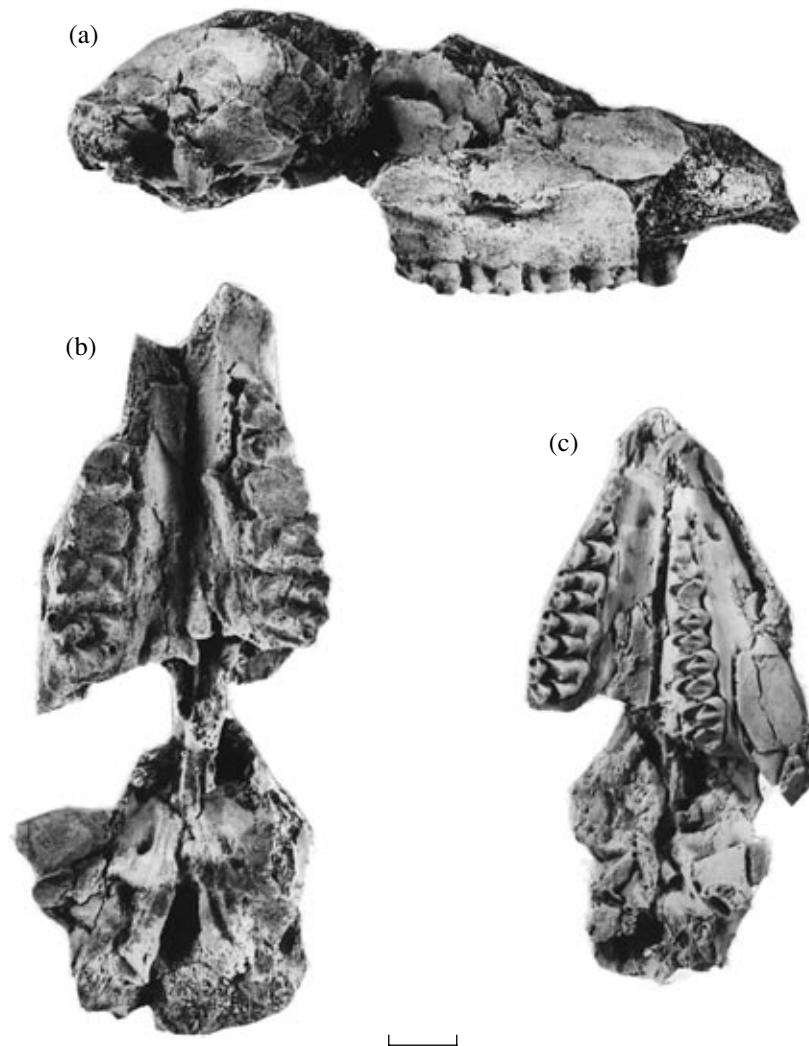
The posterior opening of the infraorbital canal and sphenopalatine foramen are primitively small and equal in size in *Archaeomeryx*. The posterior opening of the infraorbital canal remains rather small in most tragulines. The infraorbital canal has a larger caliber in *Prodremotherium*, tragulids, and pecorans. In *Lophiomeryx* and *Prodremotherium*, the sphenopalatine foramen is smaller than the posterior opening of the infraorbital canal. In *Hypertragulus*, *Leptomeryx*, and tragulids, the sphenopalatine foramen becomes as large as in pecorans. The longest axis of this foramen is almost vertical in *Tragulus*, weakly inclined inside in *Leptomeryx* and *Prodremotherium*, and strongly inclined inside in *Hypertragulus* and *Hyemoschus*.

The orbital exposure of the frontal probably reaches the sphenopalatine foramen in *Lophiomeryx* but does not reach it in tragulids. According to Novacek (1986), the large orbital wing of the frontal, confining the orbitosphenoid and palatine, is primitive.

Posteroventral to the sphenopalatine foramen, there is a small posterior opening of the palatine canal (for the palatine nerves and arteries). In some individuals of *Hyemoschus*, it is double.

In the orbital exposure of the frontal, there are two openings, a more dorsal supraorbital foramen (for the supraorbital artery and vein), and the ethmoidal foramen (for the ethmoidal artery and vein) just above the orbitosphenoid. In *Archaeomeryx*, the ethmoidal foramen is posterior to the palate, as in primitive eutherians. In *Leptomeryx* (AMNH, no. 688) and Recent tragulids, the ethmoidal foramen occupies a more anterior position, similar to that in pecorans.

At the base of the orbital exposure of the alisphenoid, there is a semicircular foramen orbitorotundum through which the ophthalmic and maxillary division of the trigeminal (V), oculomotor (III), trochlear (IV), and abducent (VI) nerves and ophthalmic (transverse) vein pass in the orbital region; it is large in tragulines.



**Fig. 9.** Skulls of traguloids: (a, b) *Lophiomeryx angarae*, PIN, no. 3110/964, Khoer-Dzan, Mongolia; Early Oligocene: (a) lateral and (b) ventral views; and (c) *Archaeomeryx optatus*, PIN, no. 2198/162, Ula-Usu, China; Middle Eocene, ventral view. Scale bar, 1 cm.

Anterior to the foramen orbitorotundum, at the base of the orbitosphenoid, there is the optic foramen, which is moderately large and separate in most tragulines. The optic foramina are almost confluent in *Leptomeryx* and entirely confluent in Recent tragulids due to the enlargement of the orbits.

#### Ethmoidal Fissure

The ethmoidal fissure (or antorbital vacuity) is absent or very small in the primitive state and more developed in the advanced state. Apparently, the ethmoidal fissure is absent in *Archaeomeryx* and *Lophiomeryx*. Other tragulines demonstrate various stages of its development.

In *Leptomeryx*, the ethmoidal fissure is short and irregular rhomboid with a larger part located between the nasal and the maxilla. In *Hypertragulus*, it is long and reaches the level of the anterior opening of the infraorbital canal anteriorly and wedges at equal dis-

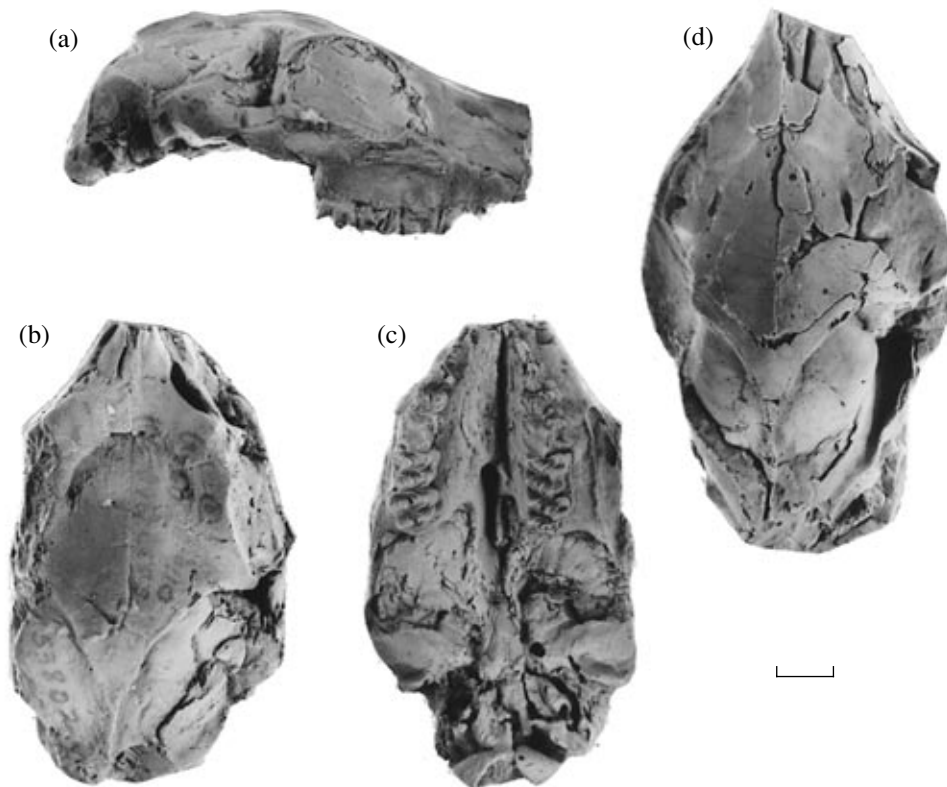
tances between the frontal and lacrimal posteriorly and between the nasal and maxilla anteriorly. The ethmoidal fissures of *Bachitherium* are shorter but wider (Geraads *et al.*, 1987, text-fig. 1); in *Prodremotherium*, it is rather large. In tragulids, the ethmoidal fissure is weakly developed or absent.

The data on the ontogeny of Recent tragulids confirm these evolutionary polarities. The ethmoidal fissure is small, short, and triangular in young *Hyemoschus*, and becomes more developed and rhomboid in adults. In embryo *Tragulus meminna*, it is absent (Carlsson, 1926), and in adults, it is small, short, and triangular or absent.

#### Palate

(Figs. 5, 9, and 10)

A primitive state among the Tragulina is a rather short and narrow palate with almost straight and slightly posteriorly divergent sides. This state is



**Fig. 10.** Skulls of *Hypertragulus*: (a)–(c) AMNH, no. 53802, Orellan of South Dakota, (a) lateral, (b) dorsal, and (c) ventral views; and (d) AMNH, no. Lusko 99-880, dorsal view. Scale bar, 1 cm.

observed in *Archaeomeryx*, *Simimeryx*, *Lophiomeryx*, and *Dorcatherium*. In all of them, the palate is almost flat between the cheek teeth, similar to those of Recent tragulids and pecorans. The palate is concave in *Hypertragulus*, and the same is observed in the anterior part in *Lophiomeryx*. In contrast to other tragulines, the anterior part of the palate is much narrower in front of P2 in *Hypertragulus* and *Leptomeryx* and in front of P3 in *Hypisodus*. The palate is wider in *Archaeomeryx* and *Lophiomeryx* and rather broad in tragulids.

The other primitive character of the palate is the absence of lateral concavities in the posterior border, clearly seen in *Lophiomeryx* and *Praetragulus*. In all other tragulines, lateral concavities are present. They reach the level of the posterior border of M3 in *Archaeomeryx*, *Leptomeryx*, and *Prodremotherium*; the level of the middle of M3 in *Hypertragulus*; and the level of the middle of M3 or the anterior part of M2 in Recent tragulids.

The elongation of the palate occurred mainly through the elongation of the anterior part of the snout on account of the development of the diastemata characteristic of all tragulines and, to a lesser degree, owing to the elongation of the palate posteriorly over the choanae. The latter is most expressed in tragulids.

In tragulines, the C–P2 diastema is usually rather short in the primitive state, as seen in *Archaeomeryx*, where it is much shorter than the premolar row. The

longest diastema, approximately 1.5 times longer than the premolar row, is in *Gelocus*.

In *Hypertragulus* and *Nanotragulus* retaining P1, there are two diastemata approximately equal in length between C and P1 and between P1 and P2.

An essential difference between traguloids and hypertraguloids concerns the characters of the posterior median emargination of the palate. There is a strong median concavity of the posterior edge of the palate opposite M2 in hypertraguloids. In traguloids, the median concavity is weak, as in the primitive state, seen in *Archaeomeryx* and *Lophiomeryx*, or displaced posteriorly in a more advanced state, as seen in Recent tragulids.

A primitive state for the Tragulina is a very small and short incisive foramina (for nerves and vessels extending to the incisive canals) formed by the palatine process of the premaxilla and the maxilla and not extending behind the canine level. This state is exposed in *Archaeomeryx* possessing a very short incisor part of the premaxilla.

In *Lophiomeryx*, the posterior edges of the foramina lie only slightly behind the canine alveoli, similar to that in *Tragulus*. In *Hyemoschus*, the foramina are elongated, and their posterior edges occupy a more posterior position.

The incisive foramina are incompletely divided posteriorly. A narrow triangular posteromedial cut is present in *Hypertragulus*, *Leptomeryx*, *Hyemoschus*, and possibly in *Lophiomeryx*. In most species of the

genus *Tragulus*, this cut is absent. However, in juvenile *Tragulus kanchil*, a small medial cut is observed.

### Occipitals

The supraoccipital, exoccipitals, and basioccipital fused very early in individual age. The supraoccipital occupies the greater part of the occiput and a narrow part of the skull roof, where it adjoins the parietal, squamosal, and mastoid.

A broad exposure of the supraoccipital on the skull roof is primitive and preserved in *Archaeomeryx* (PIN, no. 2198/149) and, to a lesser extent, in tragulids.

In side view, the supraoccipital has the most primitive structure in *Archaeomeryx*, in which it is strongly inclined anteriorly and has a well developed occipital crest considerably projecting posteriorly. A similar structure appears to be typical of *Lophiomeryx* and *Bachitherium*.

In *Leptomeryx*, hypertraguloids, and tragulids, the supraoccipital is virtually not inclined or only slightly inclined posteriorly.

Although there is certain variation in the posterior protrusion of the occipital crest among other tragulines, the crest is weak in most of them.

The exoccipitals surrounding the foramen magnum dorsally and laterally dorsally reach the level of the mastoid foramen (for a vein draining the nuchal muscles) in juvenile *Tragulus*.

The paraoccipital processes are small and very short in the primitive state as seen in *Archaeomeryx*. They remain short in *Lophiomeryx* and *Bachitherium* and become more developed in *Hypertragulus*, *Leptomeryx*, and tragulids. In *Leptomeryx*, the paraoccipital processes project more ventrally than the occipital condyles.

In all tragulines, the foramen magnum faces posteriorly. In *Hypertragulus*, it is more rounded than in *Leptomeryx*. In the latter, the foramen magnum resembles that in *Hyemoschus* in its proportions. In *Tragulus*, a marked medial emargination of the dorsal border of the foramen magnum is present.

The occipital condyles are rather narrow and possess a convex dorsal lobe in the primitive state typical of *Archaeomeryx* and *Lophiomeryx*. In lateral view, the dorsal lobe of the occipital condyles is strongly inclined in these genera, less inclined in *Leptomeryx* and *Tragulus*, and very weakly inclined in *Hypertragulus*.

In *Archaeomeryx* and *Hypertragulus*, the condylar foramen leading to the condylar canal is medium-sized; it is sometimes doubled in *Hypertragulus* and located in a deep and clearly outlined condylar fossa. In *Lophiomeryx*, the condylar foramen is small and placed in a very shallow condylar fossa. In *Leptomeryx* and tragulids, the foramen is large and also located in a shallow condylar fossa.

The hypoglossal foramen, located anteriorly and medially to the condylar foramen, is large in *Archae-*

*omeryx*; *Hypertragulus*; and tragulids; and very small in *Leptomeryx*.

In tragulines, the jugular foramen is usually confluent with the posterior lacerate foramen and a small jugular notch is present at the anteroventral border of the exoccipital. Only in *Hypertragulus* and *Leptomeryx* is the jugular foramen independent and opens behind the posterior lacerate foramen and medial to the stylomastoid foramen (Webb and Taylor, 1980).

The basioccipital is primitively thick, elongated, only slightly expanded posteriorly, and has almost parallel sides; it bears a pair of shallow fossae (for the recti capiti muscles) and a pair of elongated thick muscular tubercles (for the longi capiti muscles). This state is shared by *Archaeomeryx* and *Hypertragulus*. There are some differences between these genera in the structure of the basioccipital. In *Hypertragulus*, the ventral surface of the basioccipital is less convex with a better developed median crest, weaker muscular tubercles, and better developed muscular fossae, like those in most tragulines.

In most tragulines, the basioccipital is less elongated and wider posteriorly, with relatively thinner muscular tubercles. The lateral sides of the basioccipital are divergent posteriorly and concave in *Leptomeryx* and certain members of *Tragulus*, and divergent posteriorly and straight in *Dorcatherium* and *Hyemoschus*. The ventral surface of the basioccipital is convex in *Dorcatherium*, as in *Archaeomeryx*, and almost flat in all other specimens in which the basioccipital is preserved. The characters of the basioccipital in *Lophiomeryx*, *Bachitherium*, and *Gelocus* are unknown. However, in *Lophiomeryx* (PIN, no. 3110/964), the basioccipital appears to be primitively elongated and narrow.

### Sphenoid

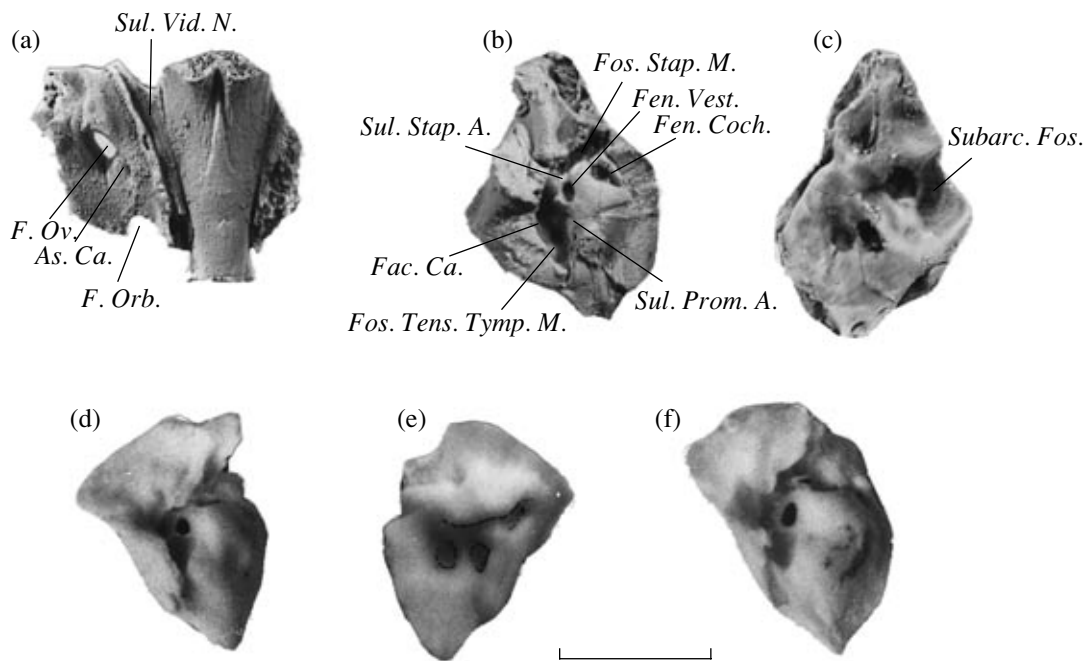
The basisphenoid in the primitive state is elongated and slightly expanded posteriorly. This shape of the basisphenoid is typical of *Archaeomeryx* and *Lophiomeryx*.

The basisphenoid is elongated and strongly expanded posteriorly in hypertragulids and tragulids.

In the primitive state, the ventral surface of the basisphenoid is prominent, very convex ventrally, and has thick muscular tubercles that continue posteriorly to the basioccipital and give the posterior section of the basisphenoid a trapezoidal shape (Fig. 11).

This structure of the basisphenoid is preserved in *Archaeomeryx* and *Hypertragulus*. The ventral surface of the basisphenoid is less prominent in tragulids and almost flat in *Leptomeryx*.

Essential differences between various tragulines are seen in the structure of the alisphenoid, such as the position of the alisphenoid and the peculiarities of particular elements, including the characters of canals, grooves for vessel and nerves, and crests for muscle attachment.



**Fig. 11.** (a) Alisphenoid and (b, c) petrosal of *Praetragulid gobiae*, PIN, no. 3109/248, Ergilin-Dzo locality, Mongolia; Late Eocene; (d, e) petrosal of *Tragulid javanicus*, Recent; and (f) petrosal of *Hyemoschus aquaticus*, Recent. (a, b, d, f) ventral and (c, e) endocranial views. Designations: (As. Ca.) alisphenoid canal; (F. Orb.) foramen orbitotundum; (F. Ov.) foramen ovale; (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; (Subarc. Fos.) subarcuate fossa; (Sul. Stap. A.) sulcus for stapedial artery; (Sul. Prom. A.) sulcus for promontory artery; and (Sul. Vid. N.) sulcus for Vidian nerve. Scale bar, 1 cm.

One of the primitive characters of the alisphenoid, seen in *Archaeomeryx* and *Lophiomeryx*, is its divergence in the plane of the basisphenoid.

The ventral surface of the alisphenoid slopes upwards markedly above the ventral surface of the basisphenoid (it does not rise laterally) only in *Hypertragulid* and *Praetragulid*. In all other tragulines, except for *Tragulid*, the alisphenoid is primitively almost horizontal, in contrast to those of pecorans.

A primitive broad and high frontal–alisphenoid contact remains in *Archaeomeryx*, *Lophiomeryx*, and *Praetragulid*. In *Tragulid* and *Hyemoschus*, this contact is usually absent or very narrow and positioned lower.

The groove for the Vidian nerve located at the base of the alisphenoid and extending along the contact with the basisphenoid is very narrow in *Hypertragulid* and *Lophiomeryx* and better developed in *Leptomeryx* and tragulids.

A crest located lateral to the Eustachian canal is very weak in *Hypertragulid* and *Leptomeryx* and prominent in *Lophiomeryx* and tragulids. This crest begins from the posterior edge of the foramen ovale in *Leptomeryx* near the lateral edge of the foramen ovale in *Lophiomeryx* and *Tragulid* and is placed at the posterolateral corner of the alisphenoid in *Hypertragulid*.

At the boundary of the basicranial and orbital exposures of the alisphenoid, there is a pronounced pterygoid crest (for the external pterygoid muscle).

The pterygoid processes in a primitive state (preserved in *Hypertragulid* and *Leptomeryx*) are low with

strongly oblique posterior borders beginning approximately in the middle of the lateral sides of the sulci for the Vidian nerves. In a more advanced state, seen in tragulids, the pterygoid processes are higher with less sloping posterior borders and they begin more anteriorly.

The alisphenoid contains several foramina varying in shape and position within tragulines.

A small and oval foramen ovale (for the mandibular branch of the trigeminal nerve) is primitively positioned posteriorly (closer to the posterior border of the alisphenoid) and has the long axis parallel to the lateral side of the basisphenoid. This state is seen in *Archaeomeryx*, *Lophiomeryx*, *Gelocus*, and tragulids (Figs. 4 and 11).

In *Prodremotherium*, the foramen ovale occupies the same position, but it is larger. In *Praetragulid* and *Hypertragulid*, the foramen ovale is fairly displaced anteriorly and lies approximately in the midlength of the alisphenoid (Figs. 11 and 12).

In *Leptomeryx*, the foramen ovale is extremely peculiar in shape, e.g., narrow, elongated, and slitlike, and it is primitively posterior in position. Webb and Taylor (1980) correctly presumed the elongation of the foramen ovale to be a derived feature, but mistakenly proposed that such a shape was also typical of *Archaeomeryx*.

In all tragulines, except for *Tragulid*, the foramen ovale faces ventrally. In *Tragulid*, in which the alisphenoid rises dorsolaterally, it faces more laterally.

A very small, circular foramen is located at the anterior extremity of the depression in front of the foramen



ovale in *Praetragulus*, *Hypertragulus*, *Leptomeryx*, and certain members of *Tragulus*. In hypertragulids, this foramen is the posterior opening of the alisphenoid canal (for the internal maxillary artery and vein). The confluence of the anterior opening of the alisphenoid canal with the sphenorbital fissure is typical of primitive eutherians and occurred at very early stages in mammalian evolution (Novacek, 1986). In *Leptomeryx* and *Tragulus*, the foramen leads to the pterygoid canal, the anterior opening of which lies at the base of the pterygoid process. The alisphenoid and pterygoid canals are absent in *Archaeomeryx* and *Lophiomeryx*; i.e., the latter are more primitive in these characters. Webb and Taylor (1980) indicated the presence of the pterygoid foramen not only in *Leptomeryx* but also in *Archaeomeryx*. However, in the skulls of *Archaeomeryx* housed at PIN and AMNH, this foramen is not observed.

### Temporal

The primitive short and broad petrosal with a very weakly pointed apex that reaches the level of the basioccipital is preserved in *Archaeomeryx*, *Lophiomeryx*, and hypertraguloids. In *Leptomeryx*, the medial border of the petrosal lies higher than the ventral surface of the basioccipital. In *Gelocus* and tragulids, the petrosal is elongated and has a relatively narrow cerebral surface.

Furthermore, the petrosal of tragulines (Figs. 11 and 12) displays many other primitive characters. These characters, in comparison with more advanced states, are as follows:

(1) A primitive, weak, low, and simple promontorium that occupies a considerable part of the ventral surface of the petrosal and almost entirely corresponds to the main whorl of the cochlea, is observed in *Archaeomeryx*, *Hypertragulus*, *Lophiomeryx*, and ancient pecorans. In contrast, the promontorium of *Leptomeryx* and tragulids is enlarged and complicated with two marked posterior whorls (almost equal in height).

(2) A very thick promontorium is present in *Archaeomeryx* and *Lophiomeryx*. It is thin in a more advanced state, as seen in *Leptomeryx* and tragulids.

(3) A medium-sized, circular fenestra cochleae (fenestra rotundum, for the membrane tympanica secunda) faces posterolaterally and is widely exposed ventrally in *Archaeomeryx*, similar to those in the Late Cretaceous ferungulate variant (*?Protungulatum*) of the trisulcate petrosal (MacIntyre, 1972) and in *Hyopsodus* (Cifelli, 1982). In Recent tragulids, the fenestra cochleae is less exposed ventrally.

(4) A small and oval fenestra vestibuli (fenestra ovalis, which was filled in the animal's lifetime by the footplate of the stapes) is observed in *Archaeomeryx*, *Leptomeryx*, and *Lophiomeryx* and was possibly inherited by ancient pecorans. The fenestra vestibuli is larger in a more advanced state, seen in *Praetragulus*, *Hypertragulus*, *Gelocus*, and tragulids, as in *?Protungulatum* (MacIntyre, 1972).

(5) The primitive posterior position (behind the fenestrae vestibuli and cochleae) and narrowness of the stapedia muscle fossa (fossa muscularis minor) are preserved in *Archaeomeryx* and *Lophiomeryx*. This fossa remains in the posterior position in *Gelocus* and *Praetragulus*; however, it is broad in the former and narrow and sinuous in the latter. In other tragulines, including *Leptomeryx* and *Hypertragulus*, the stapedia muscle fossa is displaced somewhat forward to the level of the fenestra vestibuli. The fossa is narrow and sinuous in *Hypertragulus* and subcircular in *Leptomeryx*, *Tragulus*, and *Hyemoschus*.

(6) The small and posteriorly positioned tensor tympani fossa (fossa muscularis major) is pocketed only in the lateral wall. In *Archaeomeryx*, the tensor tympani fossa is located opposite the posterior part of the main whorl. This position and lateral excavation are also preserved in *Gelocus*, although the latter has a broader tensor tympani fossa. In *Hypertragulus*, the tensor tympani fossa is pocketed in both the lateral and medial walls, whereas in tragulids, it is more primitive and pocketed only in the medial wall, where it is encroached upon by the promontorium but placed more anteriorly (Webb and Taylor, 1980).

(7) A thick medial edge of the petrosal is observed in *Archaeomeryx*, *Lophiomeryx*, and *Leptomeryx*. In all others, the medial edge becomes thinner.

(8) A primitively deep and broad subarcuate fossa for the flocculus of the cerebellum is observed in *Archaeomeryx* and most tragulines, except for *Gelocus*, in which the fossa is shallow. In Recent tragulids, it is deep but pocketed. A deep subarcuate fossa is a primitive eutherian character.

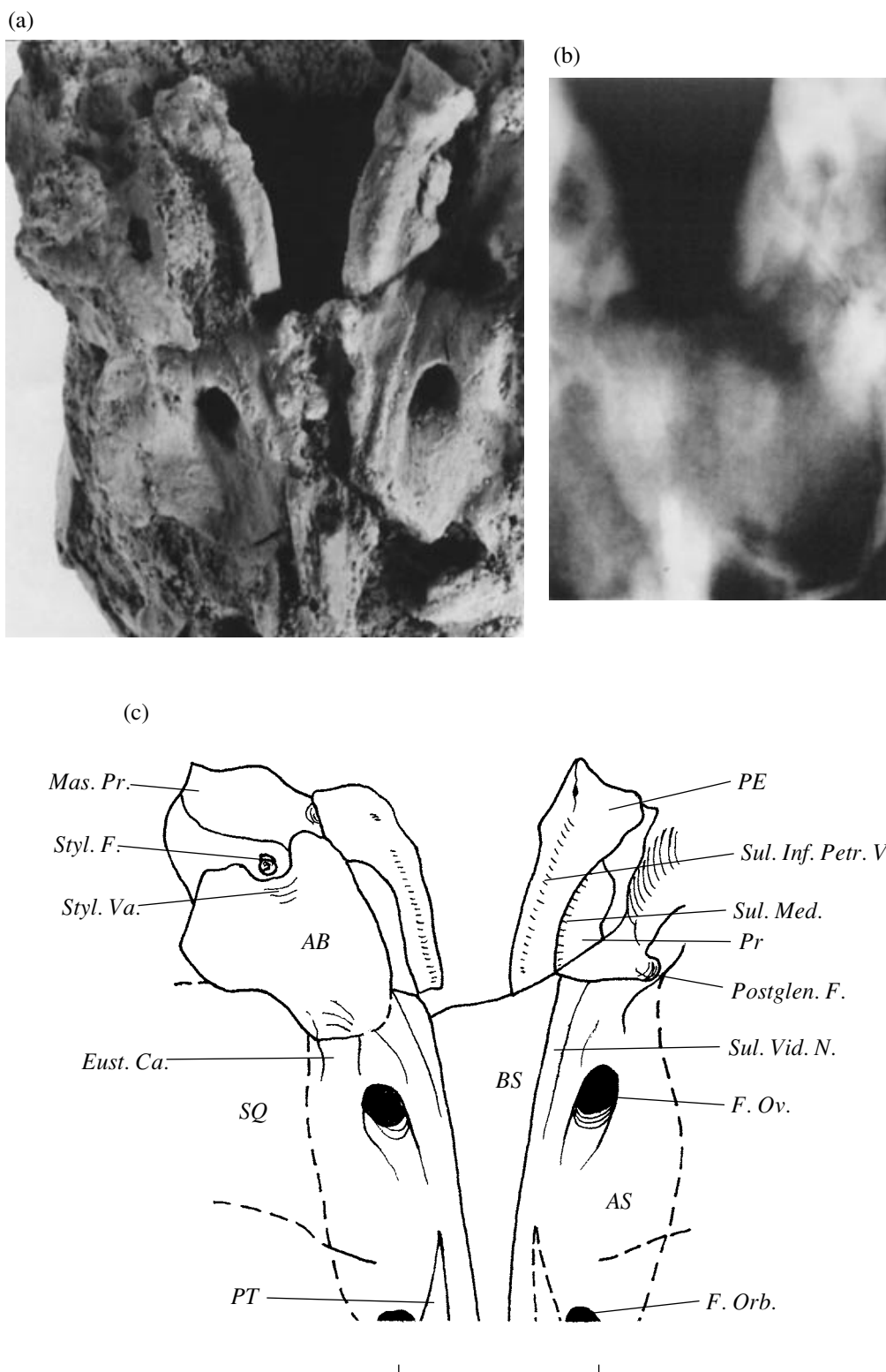
(9) A primitive separate carotid foramen is present in *Archaeomeryx* and *Lophiomeryx*. The confluence of this foramen with the posterior lacerate foramen (foramen jugulare) is a derived state, seen in *Hypertragulus* and *Leptomeryx*. In *Tragulus* and *Hyemoschus*, a separate median carotid foramen notches the wall of the bulla.

(10) The fossa cerebellaris is deep.

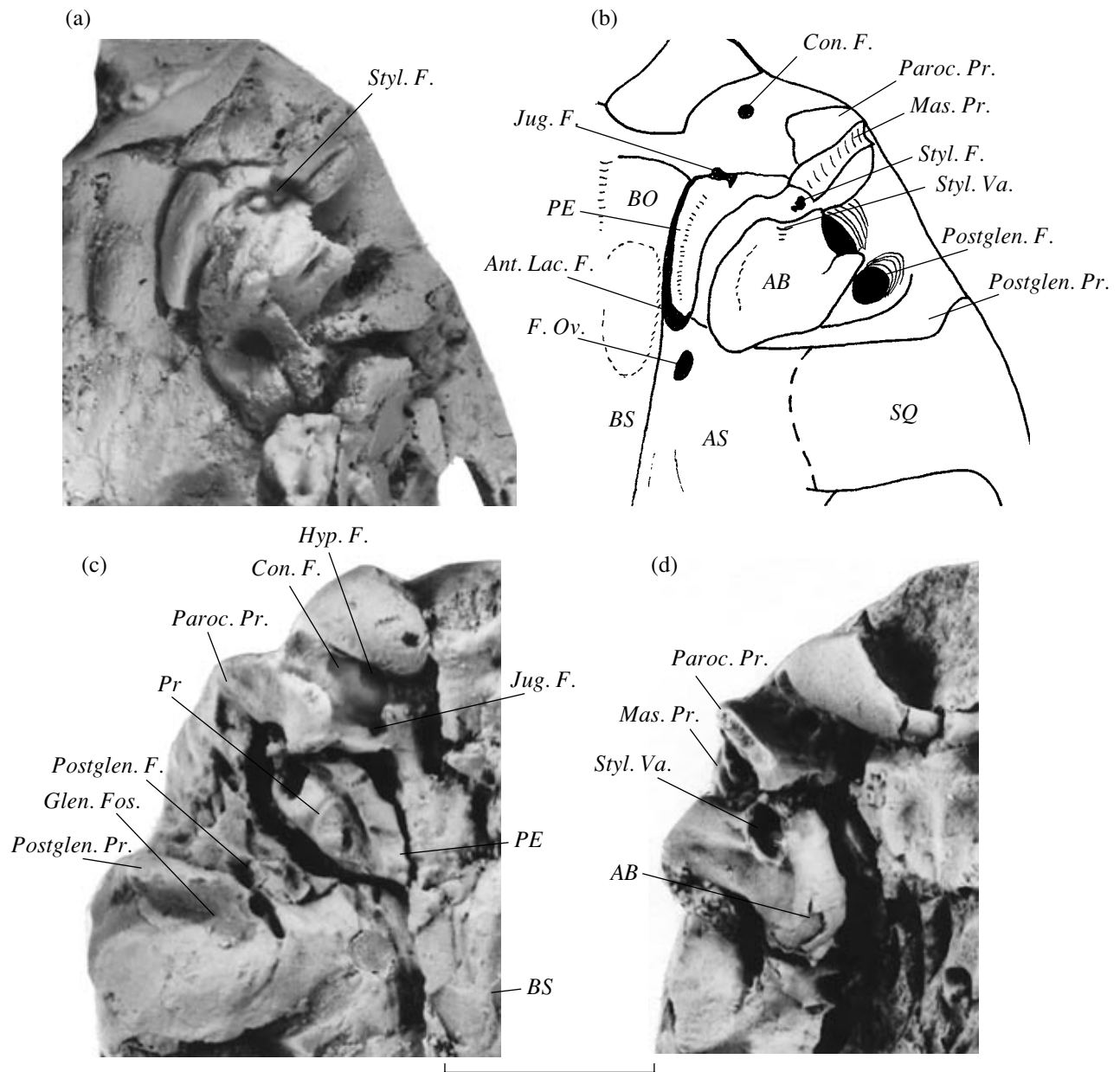
(11) The presence of the foramen stylomastoideum primitivum was reported for *Archaeomeryx* (Webb and Taylor, 1980) and *Prodremotherium* (Jehenne, 1977). It is apparently present in *Lophiomeryx*, as revealed by X-ray photographs.

Important distinct plesiomorphies are revealed in the peculiarities of the major grooves and canals.

The petrosals of *Archaeomeryx* and *Lophiomeryx* resemble the primitive trisulcate petrosal pattern described by MacIntyre (1972) and are characterized by the presence of three grooves (for the facial nerve, stapedia artery, and inferior petrosal vein) and by a distinct medial groove probably providing passage for the medial ramus of the internal carotid artery. In addition, the promontory sulcus is present in *Hypertragulus*, *Leptomeryx*, *Gelocus*, and Recent tragulids and appears



**Fig. 12.** Braincase of *Lophiomeryx angarae*, PIN, no. 3110/964: (a, c) ventral view and (b) ventral view in X ray. Designations: (AB) auditory bulla; (AS) alisphenoid; (BS) basisphenoid; (Eust. Ca.) Eustachian canal; (F. Orb.) foramen orbitorotundum; (F. Ov.) foramen ovale; (Mas. Pr.) mastoid process; (PE) petrosal; (Postglen. F.) postglenoid foramen; (Pr) promontory; (PT) pterygoid; (SQ) squamosal; (Styl. F.) stylomastoid foramen; (Styl. Va.) stylohyoid vagina; (Sul. Inf. Petr. V.) sulcus for inferior petrosal sinus; (Sul. Med.) sulcus for medial ramus of internal carotid artery; and (Sul. Vid. N.) sulcus for Vidian nerve. Scale bar, 1 cm.



**Fig. 13.** Ventral views of tympanic regions: (a, b) *Archaeomeryx optatus*, PIN, no. 2198/154; (c) *Hypertragulus*, AMNH, no. Lusko 99-880; and (d) *Hypertragulus calcaratus*, AMNH no. 53082. Designations: (AB) auditory bulla; (Ant. Lac. F.) anterior lacerate foramen; (AS) alisphenoid; (BO) basioccipital; (BS) basisphenoid; (Con. F.) condylar foramen; (F. Ov.) foramen ovale; (Glen. Fos.) glenoid fossa; (Hyp. F.) hypoglossal foramen; (Jug. F.) jugular foramen; (Mas. Pr.) mastoid process; (Paroc. Pr.) paroccipital process; (PE) petrosal; (Postglen. F.) postglenoid foramen; (Postglen. Pr.) postglenoid process; (Pr) promontory; (SQ) squamosal; (Styl. F.) stylomastoid foramen; and (Styl. Va.) stylohyoid vagina. Scale bar, 1 cm.

to be a derived character. This sulcus is absent in *Archaeomeryx* and *Lophiomeryx*, as in early placentates and marsupials; however, according to Cifelly (1982), it is well developed in *Protungulatum*, *Hyopsodus*, and *Homacodon*. Webb and Taylor (1980) believed that the presence of both promontory and stapedia artery grooves in the petrosal of *Hypertragulus* means that this genus is more primitive than *Archaeomeryx*. However, the promontory artery is not “primitively the mainstream artery” (MacIntyre, 1972, p. 291). It

could represent a laterally displaced internal carotid artery (Presley, 1979). Thus, *Archaeomeryx* is more primitive in the petrosal sulcus pattern than *Hypertragulus*.

The same condition concerns the other character (a more complex path of the facial canal in *Hypertragulus*) regarded by Webb and Taylor (1980) as a primitive character. The smooth path of the facial canal between the foramen stylomastoideum primitivum and the opening of the facial canal, seen in *Archaeomeryx*, *Lepptomeryx*, and, in X-ray photographs, in *Lophiomeryx*, is

evidently a primitive condition that resembles a primitive eutherian state. In *Hypertragulus* and tragulids, the facial canal is more curved (arched) dorsally and posteriorly around the post-tympanic neck and resembles that of *Dacrytherium* (Beaumont, 1963; Webb and Taylor, 1980).

The tympanic process and the tympanohyal are unfused in tragulids, as in primitive eutherians, in which they may form a nearly complete ring around the foramen stylomastoideum primitivum (MacIntyre, 1972).

The tympanohyal is fused with the mastoid portion of the petrosal and forms the processus hyoideus.

The epitympanic recess for the auditory ossicles lies lateral to the facial crista and to the opening of the facial canal and is adjacent to the external auditory meatus. The epitympanic recess is primitively located on the petrosal in *Praetragulus*, *Hypertragulus*, and, possibly, in *Archaeomeryx*. The lateral wall of the epitympanic recess is formed by the squamosal in *Lophiomeryx*, *Leptomeryx*, and tragulids, as in the ferungulate type and pecorans. Judging from the data obtained by Jehenne (1977), the epitympanic recess of *Prodremotherium* is formed by the petrosal and mastoid.

Primitive lateral exposure of the mastoid is preserved in hypertraguloids, *Archaeomeryx*, *Lophiomeryx*, and tragulids.

According to Novacek (1986), extensive occipital exposure of the mastoid is a primitive eutherian state, but this is considered to be a derived character by Simpson (1933).

According to MacIntyre (1972), the mastoid of the species with a primitive trisulcate petrosal has a large lateral expansion.

In juvenile *Tragulus* and *Hyemoschus*, the mastoid occupies a more lateral position and is broader than in adults, in which it becomes narrower and more posterior due to posterior expansion of the squamosal. 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. Among ancient artiodactyls, the lateral position of the mastoid is observed in *Caenotherium*.

In *Leptomeryx*, *Bachitherium*, and *Prodremotherium*, the mastoid lies in the plane of the occiput, similar to that in pecorans. The occipital position of the mastoid, more developed paraoccipital processes, nuchal crest, and lines reflects a derived state of the development of the skull and neck muscles attached to them.

In *Archaeomeryx* and *Lophiomeryx*, in addition to lateral expansion, a primitive extensive ventral portion of the mastoid is observed. In other tragulines, this portion is narrower.

A clear groove for the attachment of the digastric muscle to the ventral portion of the mastoid process, well separated from the weak paraoccipital process, is seen in *Archaeomeryx* and *Lophiomeryx*. This groove is absent in *Hypertragulus*, where it is convex. The deep

groove for the digastric muscle on the mastoid process is a primitive eutherian state (Novacek, 1986). MacIntyre (1972) did not believe that the mastoid process is a place of origin for that muscle. He thought that the process could serve for the attachment of the muscle that moved the head and neck. Although MacIntyre's opinion is apparently correct for species with occipital exposure of the mastoid, this is not suitable for primitive forms, with relatively anteriorly placed mastoid processes bearing large ventral projections.

A large mastoid foramen in the lateral position is primitive for the Tragulina and present in *Archaeomeryx*, *Hypertragulus*, *Lophiomeryx*, and tragulids, in which the mastoid foramen is at the mastoid-squamosal suture. In *Leptomeryx* and *Prodremotherium*, the mastoid foramen occupies the occipital position and opens in the mastoid-occipital suture. In *Prodremotherium*, there are two foramina in the mastoid-occipital suture (Jehenne, 1977).

The absence of the postglenoid process behind the glenoid cavity of the squamosal is possibly a primitive eutherian character that distinguishes tragulids from most ruminants (Carlsson, 1926). Webb and Taylor (1980) proposed that the absence of the postglenoid process in tragulids is a derived character. They connected the disappearance of this process with a very strong enlargement of the auditory bulla.

Among other tragulines, there are two main types of the postglenoid process: (1) very low and long in *Archaeomeryx* and *Leptomeryx* (AMNH Dick 28-934), and (2) moderately high and short in *Hypertragulus* and *Lophiomeryx*. In these genera, the axes of the postglenoid processes diverge posterolaterally, while the posterior edge of the zygomatic process is directed anterolaterally in tragulids.

The structure of the glenoid cavity, as well as the size and position of the postglenoid foramen, is rather diverse in tragulines. In the primitive state, represented in *Archaeomeryx* and *Lophiomeryx*, the glenoid cavity is very shallow, poorly outlined, large, and flat, corresponding to a flattened articular process of the lower jaw. In *Hypertragulus* and *Leptomeryx*, the glenoid cavity is groove-shaped, narrow, and clearly visible.

A primitive, laterally open postglenoid foramen is seen in *Archaeomeryx*, *Lophiomeryx*, and *Leptomeryx* and inherited by some pecorans. In other tragulines and according to Jehenne (1977), the postglenoid foramen becomes completely enclosed in *Prodremotherium*, as in advanced pecorans.

The closing of the postglenoid foramen is mainly attributed to the enlargement of the pars tympanica. This also depends on the size of the squamosal portion behind the postglenoid process and the direction of the posterior edge of the base of the zygomatic process.

A small pars tympanica does not cover the postglenoid process in the primitive state, which is well preserved in *Archaeomeryx* and *Lophiomeryx*. In ventral view, with the auditory bulla removed, the squamosal

portion behind the glenoid process is rather broad in these genera, as in *Hypertragulus*. The posterior ventral portion of the squamosal is narrower in a more advanced state, which is typical of *Leptomeryx* and tragulids.

The postglenoid foramen, placed just behind the postglenoid process, is very small and circular in *Hypertragulus*, and larger and oval in *Archaeomeryx*. In ventral view of the skulls with the auditory bulla in the original position, the postglenoid foramen is not visible in *Bachitherium*, *Prodremotherium*, and *Hypertragulus*, as it is in pecorans. In *Prodremotherium*, it is closed by the auditory bulla. In *Hypertragulus*, the postglenoid foramen is covered by the external acoustic meatus and closely pressed against the postglenoid process. In *Leptomeryx* and Recent tragulids, the postglenoid foramen is very clearly visible between the postglenoid process and the external acoustic meatus.

The supraglenoid foramen is indicated in *Prodremotherium* and *Gelocus*, as in pecorans (Jehenne, 1977; Webb and Taylor, 1980), and absent in *Leptomeryx*, *Bachitherium*, and tragulids.

The auditory bulla is most primitive in *Archaeomeryx* and *Lophiomeryx* (Figs. 12 and 13). It is very small, flask-shaped, unexpanded, positioned posteriorly, and has an extremely short external acoustic meatus. The longitudinal axes of the auditory bulla and external acoustic meatus coincide in this primitive state. In ventral view, the axes are strongly oblique relative to the sagittal plane in both genera, and are located at an angle of about 40° to the latter. In contrast to the auditory bulla of *Archaeomeryx*, that of *Lophiomeryx* seems more strongly pressed to the postglenoid process. In *Hypertragulus* and *Leptomeryx*, the external acoustic meatus is longer and less inclined posteriorly, and the inclination is about 50–55°. In these genera, the longitudinal axes of the auditory bulla and the external acoustic meatus are at acute angles.

Furthermore, the auditory bulla in a primitive state is not pressed against the basioccipital, and the petrosal is visible in the space between these elements. This state is seen in *Lophiomeryx*, *Hypertragulus*, and *Leptomeryx*, and is most strongly manifested in *Archaeomeryx*. In *Bachitherium*, the auditory bulla is pressed to the basioccipital and postglenoid process, and the longest axis of the bulla lies nearly parallel to the transverse plane. In *Hypisodus* and Recent tragulids, the auditory bulla is very strongly inflated. In *Hypisodus*, the bullae meet at the middle line and almost entirely cover the basisphenoid. In *Tragulus* and *Hyemoschus*, they reach anteriorly the middle of the basisphenoid length and cover the foramen ovale in the first form. In tragulids, the inclination of the longitudinal axis of the auditory bulla is relatively strong, approximately 35° in *Hyemoschus* and 40° in *Tragulus*.

The stylohyoid vagina is most primitive in *Archaeomeryx* and *Lophiomeryx*: it is very shallow, widely open posteriorly, and located at the posterolateral side of the bulla. In *Leptomeryx* the stylohyoid vagina is

more advanced; it is deeper, encroaches upon the bulla, and has a sharper lateral border. In *Hypertragulus* the stylohyoid vagina is still more advanced; it is narrower, deeper, well-outlined, encroaches upon the bulla, and enclosed posteriorly. In tragulids, the stylohyoid vagina is also well defined, deep, and enclosed posteriorly. Encroaching upon the bulla, it occupies a posterolateral position owing to a strong enlargement of the bulla in this family.

Thus, the evolutionary trend is from a very shallow and weak stylohyoid vagina that is widely open posteriorly (preserved in *Archaeomeryx*) to a relatively deep, clearly outlined, and posteriorly enclosed vagina at the posterolateral side of the bulla (developed in *Hyemoschus*).

### Parietal

The parietal occupies the skull roof between the frontal, alisphenoid, squamosal, and supraoccipital. There are distinct temporal and sagittal crests for the attachment of the temporal muscles. The form and length of these crests are different in various groups of tragulines, as described above.

The parietal foramina primitively lie close to the sagittal crest in *Archaeomeryx* and are at a great distance from the midline in others. This displacement correlates with the expansion of the braincase and diminishes the place of the temporal muscle attachment. The parietal foramina remain at a relatively short distance from the sagittal crest in leptomerycids.

### Frontal

The frontal is short in the primitive state observed in *Archaeomeryx* and *Hypertragulus*, moderately short in *Bachitherium* and *Prodremotherium*, and longer in *Leptomeryx* and tragulids.

Certain differences are observed in the shape of the coronal suture and the supraorbital sulcus, and the position of the supraorbital foramen. The coronal suture is slightly curved posteriorly in *Archaeomeryx*; strongly curved posteriorly in *Hypertragulus*, *Leptomeryx* (AMNH, Dick 28-934), and *Prodremotherium* (Jehenne, 1977, pl. 1, fig. A); and almost straight or slightly curved posteriorly in *Dorcatherium*, *Tragulus*, and *Hyemoschus*. At the bregma, the curvature forms almost a right angle in *Hypertragulus*, a very wide angle directed posteriorly in *Dorcatherium*, and looks like a very small posterior prominence in some members of the genus *Tragulus*.

In *Archaeomeryx*, the supraorbital sulci cross the nasofrontal suture and continue onto the nasals. They converge slightly at the middle of this suture and diverge slightly in front of it. In contrast, the supraorbital sulci in *Hypertragulus* end at the posterior border of the nasal (the nasofrontal vein appears to go into the nasal cavity, as in *Tragulus*). They are longer and more strongly curved medially.

The supraorbital sulci begin at the level of the anterior part of the orbits in *Hypertragulus*, *Leptomeryx*, and *Hyemoschus*, and approximately at the midlength of the orbit in *Tragulus*. In *Prodremotherium* and *Leptomeryx*, the supraorbital sulci are primitively curved medially. In tragulids, they are slightly curved laterally or almost straight. The sulci terminate at the posterior border of the ethmoidal fissure in *Leptomeryx*, at a short distance anterior to the nasofrontal suture in *Hyemoschus*, and at its lateral end in *Tragulus*.

In *Archaeomeryx* and *Prodremotherium*, the supraorbital foramen primitively occupies the most posterior position and is placed behind the line connecting the orbital centers.

### Nasal

The nasals are primitively long, convex dorsally, increase slightly in width posteriorly at the maxillary–nasal contact, and narrow posteriorly and anteriorly. This state is preserved in *Archaeomeryx* and, to a lesser degree, in *Hypertragulus*.

In *Archaeomeryx* (PIN, no. 2198/154), the nasals are very long; their posterior edges taper and almost reach the line connecting the orbital centers; and the anterior nonprotruding edges border the anterior opening of the nasal cavity.

The nasals of *Hypertragulus* (AMNH, no. 53865) resemble those of *Archaeomeryx*. Although the posterior edges of the nasals are displaced to the level of the anterior part of the orbits, they are long owing to the elongation of the snout (Figs. 4, 6, and 8). In other tragulines, the nasals are shorter and their posterior edges occupy a more anterior position.

The short nasofrontal suture, strongly curved posteriorly and placed at the level of the orbit, is primitive and typical of *Archaeomeryx*, *Hypertragulus*, and, apparently, *Lophiomeryx*.

A broad and almost straight nasofrontal suture, located anteriorly to the orbits, is the derived state typical of tragulids.

The nasofrontal suture lies at the level of the antorbital rim in *Prodremotherium* and in front of the orbits in *Leptomeryx* and *Bachitherium* (both retain rather elongated nasals). In dorsal view, the nasals are expanded posteriorly from the level of the ethmoidal fissure in *Leptomeryx* and expand more gradually in tragulids. In *Leptomeryx*, they are also slightly expanded anteriorly, in contrast to those of other tragulines. In lateral view, the dorsal border of the nasals is almost straight in *Dorcatherium* and convex in others.

The absence of the anterior protrusion of the nasals is an interesting and very primitive character preserved in *Archaeomeryx*. In *Hypertragulus*, the nasals only slightly protrude, even less than in the ancient tylopod *Caenotherium*. Most other tragulines essentially differ from *Archaeomeryx* and *Hypertragulus* by strongly projecting anterior parts of the nasals anterior to the premaxillary–nasal suture. This projection overhangs

most of the anterior opening of the nasal cavity, as in other artiodactyls. The strongest anterior protrusion of the nasals is observed in *Bachitherium*.

The anterior edges of the nasals have a medial concavity in *Archaeomeryx* and *Hypertragulus*. In *Archaeomeryx* the anterior edge of the nasal forms together with the medial edge of the premaxilla the lateral border of the anterior opening of the nasal cavity. In dorsal view, the opening in this genus is ovoid in outline. In *Hypertragulus* (AMNH, Lusk 53865), the lateral edge of this opening is doubly concave and the opening is pear-shaped in dorsal view. In other tragulines, including *Leptomeryx* and *Bachitherium*, the projecting anterior part of the nasal bears a small lateral concavity, as in pecorans.

### Lacrimal

In the primitive state, preserved in *Archaeomeryx* and *Lophiomeryx*, the lacrimal has an extremely short facial process, a small orbital process, and a single lacrimal foramen at the antorbital rim close to the jugal–lacrimal suture. In these genera, the facial process of the lacrimal is triangular, short, and low. In posterior view, the orbital face of the lacrimal is irregularly rhomboid, only slightly expanded inferiorly, and has a small pit for the inferior oblique muscle of the eye at the inferior angle near the maxillary–lacrimal suture just above the posterior opening of the infraorbital canal (Fig. 7). This appears to be a primitive eutherian state and resembles the structure of the lacrimal in leptictids (Novacek, 1986).

The absence of the junction between the lacrimal and the alveolar process of the maxilla that is typical of the orbital region of *Archaeomeryx*, *Lophiomeryx*, *Prodremotherium*, and *Tragulus* is also a primitive character distinguishing these forms and most other tragulines.

In *Leptomeryx*, *Hypertragulus*, *Bachitherium*, *Dorcatherium*, and *Hyemoschus*, the lacrimal is further enlarged. It has a more elongated facial part and strongly expanded laterally and ventrally orbital parts resembling those of pecorans.

In *Hypertragulus* and *Hypisodus*, the facial process of the lacrimal possesses a distinct frontal process, and the frontolacrimal suture is situated high. On the contrary, in traguloids this process is absent, and the position of the frontolacrimal suture is close to the primitive state.

A peculiar character of *Prodremotherium* is the presence of the preorbital fossa. This is typical of some pecorans and other ungulates.

The lacrimal foramen is positioned primitively within the orbit near the antorbital rim in *Archaeomeryx*, *Leptomeryx*, *Prodremotherium* (PIN, no. 2737/412), *Hypertragulus* (AMNH, Doug 30-1163), *Dorcatherium*, and Recent tragulids. Among them, the most primitive state of the lacrimal foramen appears to be in *Archaeomeryx*, *Lophiomeryx*, and *Prodremotherium*, in which the foramen remains in the lower half of the orbital face of the lacrimal.

A primitive low position of the lacrimal foramen, not far from the jugal–lacrimal contact, is observed in juvenile *Hyemoschus* (BMNH, no. 48.1314).

In *Dorcatherium*, the lacrimal foramen lies at a considerable distance from this contact, but in the lower half of the orbital face of the lacrimal.

This foramen is approximately in the middle between the jugal–lacrimal and frontal–lacrimal sutures in Recent tragulids and located closer to the latter in *Hypertragulus* (AMNH, Doug 30-1163) and *Leptomeryx* (AMNH, no. 688).

In *Hypertragulus* and *Tragulus*, the lacrimal foramen is behind a small and rounded lacrimal tubercle at the antorbital rim.

A facial position with the lacrimal foramen located near the fronto-lacrimal suture is rare in tragulines, but occurs in some *Hyemoschus* (BMNH, no. 50.20510).

### Jugal

In the primitive state preserved in *Archaeomeryx*, the jugal is situated low, virtually does not extend anteriorly, and has a long posterior spine. In this genus, the jugal is expanded dorsoventrally under the infraorbital rim almost to M3, and only a very narrow part of the maxilla is present here. In *Archaeomeryx*, a diagonal suture between the jugal and squamosal extends obliquely from the distal edge of the zygomatic arch near the frontal process of the jugal to the ventral edge of the arch near the base of the zygomatic process of the squamosal.

In all others (including *Leptomeryx*, *Hypertragulus*, *Prodremotherium*, *Lophiomeryx*, and tragulids), the inferior border of the jugal is placed much higher, the portions of the jugal and maxilla above M3 are almost equal in height, and the posterior spine is shorter.

Other primitive characters preserved in *Archaeomeryx* and *Lophiomeryx* are the narrowness and shortness of the anterodorsal process of the jugal. The process ends at the antorbital rim and does not reach anteriorly the level of the anterior point of the orbit. The anterior dorsal process of the jugal extends ahead of this point only a little in *Prodremotherium* (PIN, no. 2737/412). In a more advanced state, this process is broader, longer, and expanded more anteriorly. The anterior border of the jugal lies at the level of the anterior border of the lacrimal in *Hypertragulus* and occupies a more posterior position, but is also in front of the antorbital rim in *Leptomeryx* and tragulids.

The frontal process of the jugal is very massive and long in *Bachitherium*, long and more slender in tragulids, and short in all others.

The facial ridge for the masseter muscle at the lateral surface of the jugal is prominent, but not very elongated in *Archaeomeryx*, *Lophiomeryx*, and tragulids. In *Archaeomeryx*, the place of the attachment of the masseter muscle is primitively restricted almost entirely by the lateral surface of a slightly expanded

jugal. Other tragulines differ in the degree of development and extension of the facial ridge at the facial surface of the maxilla. In all tragulines, the facial ridge remains less prominent and long, as in pecorans.

### Maxilla

The primitive state is a low and rather short maxilla with an almost straight ventral border that curves only slightly dorsally between the premolars and the canines, and is inclined ventrally in the anterior part. This condition is typical of *Archaeomeryx* and is preserved in *Tragulus*.

In lateral view, there is a clear flexion located in front of P2 in *Leptomeryx*, *Lophiomeryx*, and *Dorcatherium*, and in front of P3 in *Praetragulus* and *Hypertragulus*. In the latter form, a reduced P2 is located on a strongly inclined surface and appears not to be functional. The anterior part of the maxilla is strongly inclined downward in *Hypertragulus* and *Leptomeryx*.

The facial tuber in front of the anterior border of the jugal above P4 and M1 is very weak in *Archaeomeryx*; hardly marked in *Leptomeryx* and tragulids; and very strong in *Hypertragulus*, in contrast to those of other ruminants. The tuber serves for the attachment of the profound longitudinal layer of the buccal muscle and the tendon of the superficial part of the masseter muscle.

A short, low-situated infraorbital canal of very small caliber that is situated low is primitive in the Tragulina.

The anterior opening of the infraorbital canal above P2 is very small and low in position in *Simimeryx* (?) and *Praetragulus*. It is medium-sized and lies above the posterior part of P2 in *Archaeomeryx*, *Prodremotherium* (PIN, no. 2737/412), and *Hypertragulus*. However, in the latter genus, it is located a little higher than in the first two. The opening is medium-sized and located more anteriorly and higher in *Leptomeryx* and tragulids. The opening is above the anterior part of P2 in the first and in front of it in the second.

### Palatine

The structure of the palatine gives important evidence for the taxonomy of tragulines. In addition to the above noted characters, the major differences are the following:

(1) The anterior edges of the palatines on the palate are positioned differently. The palatines reach the level of P4 in *Archaeomeryx*, *Lophiomeryx*, *Prodremotherium*, *Bachitherium*, *Hypertragulus*, *Hypisodus*, and *Tragulus*. They reach the level of M1 in *Leptomeryx* and *Hyemoschus*. A primitively anterior position of the anterior edge of the palatine is found in *Simimeryx*, which has the anterior palatine foramina between P3 (Stock, 1934).

(2) The shape of the anterior edges of the palatines on the palate varies. The palatines form a narrow, rounded anterior projection between the maxillae in *Archaeomeryx*, *Lophiomeryx*, *Prodremotherium*, *Hypertragulus*, and *Tragulus*. In the derived state char-

acteristic of *Leptomeryx* and *Hyemoschus*, the anterior palatine projection is widened, and the anterior edges of the palatines are almost straight.

(3) The number and position of the palatine foramina on the palate also vary. The smaller anterior palatine foramina and larger middle palatine foramina are present in *Lophiomeryx*; the former are between M1 and the latter are between M2, similar to those in *Tragulus*. The presence of both anterior and middle palatine foramina may be a primitive eutherian state (Novacek, 1986). In *Archaeomeryx*, only foramina between M1 are visible. In *Hypertragulus*, *Leptomeryx*, *Prodremotherium*, and *Hyemoschus*, there is only the middle palatine foramen, which is located between M2. In *Hyemoschus*, there are a number of small vascular openings behind the middle palatine foramen.

### Premaxilla

The primitive state is a low, short premaxilla with a short posterodorsal process almost overhanging the anterior opening of the nasal cavity, as seen in *Archaeomeryx* (PIN, no. 2198/1540). Small premaxillae possessing short posterodorsal (nasal) processes and small incisive foramina may be expected in primitive eutherians (Novacek, 1986).

The posterodorsal processes of the premaxillae are strongly displaced to the side in almost all tragulines due to the enlargement of the anterior opening of the nasal cavity and the anterior elongation of the nasals. A relatively wide anterior gap between the premaxillae, with the anterior protrusion of the nasals is typical of most eutherians and is already present in most ancient tragulines from which this part of the skull is known.

Apart from *Archaeomeryx*, a state similar to the primitive one is observed in *Hypertragulus*.

Another primitive condition is the presence of the premaxilla–nasal contact typical of most Tragulina with the exception of *Hyemoschus*. The premaxilla–nasal contact is relatively long in *Hypertragulus* (AMNH, no. 53865) with a long nasal or posterodorsal process of the premaxilla. The contact remains long in *Tragulus* and *Dorcatherium*. It is absent in the most derived state seen in *Hyemoschus*.

In lateral view, the anterior border of the premaxilla is slightly inclined posteriorly in *Archaeomeryx*, *Hypertragulus*, and *Bachitherium*. The inclination is greater in *Leptomeryx* and tragulids. The degree of inclination depends on the elongation of the premaxilla, enlargement of the canine, and an increase in snout height.

### Mandible

The body of the mandible is primitively low, descends slightly anteriorly, and has a strongly convex inferior border.

These characters are preserved in *Archaeomeryx*, *Lophiomeryx*, hypertragulids, and tragulids. In *Gelo-*

*cus*, the body of the mandible is high beneath the cheek teeth and very low and strongly descending anteriorly in front of p2. The ventral border of the body of the mandible is strongly convex in front of the angular process in *Archaeomeryx*, weakly curved downward and possessing two concavities (in front of the angular process and anterior to p2) in hypertraguloids and tragulids, and almost straight in *Gelocus*.

The mental foramina in the primitive state occupied the posterior position and were displaced anteriorly with the development of the diastemata.

A small anterior mental foramen located beneath p1 is observed in *Archaeomeryx*, a large foramen placed almost at the level of the middle of the c–p2 diastema is in hypertragulids and tragulids, and an extreme anterior position of the foramen is in *Gelocus*. A small posterior mental foramen is located in front of p2 in *Gelocus*; beneath p2 in *Simimeryx*, *Hypertragulus*, and *Praetragulus*; and beneath p3 in *Archaeomeryx*. In *Parvitrugulus* this foramen lies under p3 or p4.

The diastemata are primitively very short. A short c–p1 diastema and a close series of the premolars are observed in *Gobiomeryx dubius* and *Lophiomeryx angarae*.

The next evolutionary stage was associated with the development of a small diastema between p1 and p2, which is seen in *Archaeomeryx optatus*.

As the snout elongated, the first diastema became longer, as in *Lophiomeryx*, or the elongation affected both diastemata, as in *Hypertragulus*.

Most tragulines possess a single diastema separating the lower canine from p2. This is rather short in *Simimeryx*, *Praetragulus*, and tragulids, and very long in *Gelocus*.

Three posterior premolars usually form a close series in all tragulines, except for *Hypertragulus*, *Nanotrugulus*, and *Hypisodus*, in which p2 is separated from p3 by a short diastema similar to that in some tylopods.

The symphysis is long and extends to p2 (in *Archaeomeryx*), to a point anterior to p2 (*Leptomeryx*, *Parvitrugulus*, and *Hyemoschus*), or more anteriorly (*Praetragulus*, *Gelocus*, and *Tragulus*).

The primitive angular process is narrow, rounded, and strongly projects down and backward. The most primitive state is in *Archaeomeryx* and resembles that in *Protungulatum*.

The process is slightly broader but also strongly projects posteroventrally in *Lophiomeryx*, in hypertraguloids (except for *Nanotrugulus*), and in *Pseudoceros*.

There is a particularly widely rounded angular process in *Leptomeryx*. Its posterior border very weakly projects posteriorly in *Hyemoschus* and *Tragulus*.

A well-developed masseteric tuberosity for the pars superficialis m. masseter and well-marked masseteric fossa for the pars profunda m. masseter are present on the lateral surface of the angular process.

The coronoid process is high, strongly narrowed dorsally, and possesses a convex anterior border in *Archaeomeryx* and hypertragulids. The latter is weakly oblique relative to the tooth row axis in *Archaeomeryx*



**Table 4.** Comparisons of the main features of dentition of tragulines

Feature	Primitive condition	Derived condition
1. I1–I3	<u>present</u> (Ar)	absent (Lo, Ge, Ba, Pro, tragulids, hypertraguloids, pecorans)
2. C	<u>small, procumbent</u> (Ar)	(a) weakly enlarged, less procumbent (Hy); (b) strongly enlarged, not procumbent (Lo, Pro, Ba, Prae, tragulids, early cervoids)
3. P1	<u>present</u> (Hy, Na)	absent (Ar, Lo, Ge, Pro, Si, Prae, Hypi, tragulids, pecorans)
4. P2	well developed (all tragulines, except Hypi)	vestigial or absent (Hypi)
5. P2–P4 row	<u>rather long</u> (Ar, Le, Ge, Pro)	(a) more elongated (Lo); (b) shortened (hypertraguloids)
6. M1–M3 crown	<u>strongly expanded labially and narrowed lingually and posteriorly</u> (Ar, Lo)	more symmetrical (Ge, Pro, Ba, tragulids, pecorans)
7. M3 metaconule	very weak (Ar, Lo, Prae, Si, Pro)	better developed (Ge, Ba, tragulids)
8. M1–M3 paraconule	absent (all tragulines, except Si?)	present (Si?)
9. M1–M3 parastyle	<u>large and rounded</u> (Ar, Lo, Prae, Si)	smaller, pressed (hypertraguloids, except Si, Prae)
10. m1–m3 mesostyle	present (all tragulines, except Hy, Na, Parv, Hypi)	absent (hypertraguloids, except Si, Prae)
11. i1–i3	<u>procumbent</u> (Ar, Le)	not procumbent (all tragulines, except Ar, Le)
12. i1	<u>small, with almost symmetrical crown</u> (Ar)	enlarged, with asymmetrical crown: (a) oblique, spatulate (Hy, Ge, some pecorans); (b) fan-shaped (Tra, Hye)
13. c	not completely included in incisor row (Ar, Si, Prae)	completely included in incisor row (tragulids, pecorans)
14. c size	<u>moderate, larger than i1</u> (Ar, Prae)	(a) enlarged (Si, Parv) (b) diminished, smaller than i1 (all other tragulines, pecorans)
15. p1	<u>present</u> (Ar, Hy, Na, Lo, Ge, some Do)	absent (Si, Par, Prae, most tragulids and pecorans)
16. p1 shape	small, conical (Ar, Le, Lo, Na, Go)	(a) enlarged, caniniform (Ba, Hy) (b) enlarged, premolariform (Ge, some Do)
17. p2	present (all except Hypi)	absent (adult Hypi)
18. p2 shape	<u>pointed with anteriorly positioned protocone</u> (hypertraguloids, except Hypi)	less pointed with almost middle position of protocone (traguloids, pecorans)
19. p2–p4 row	<u>rather long</u> (traguloids, pecorans)	short (hypertraguloids)
20. <i>Dorcatherium</i> fold	absent (all tragulines, except tragulids)	present (tragulids)

Designations: (Go) *Gobimeryx*; (Mio) *Miomeryx*; and (Parv) *Parvitragus*; for others, see Table 3.

and approximately perpendicular to it in *Simimeryx*, *Hypertragulus*, and *Praetragulus*. A deep fossa for the temporal muscle is present on the lateral surface of the coronoid process. This fossa is most developed in *Hypisodus*, which has a very high coronoid process.

As the temporal muscle decreased in size, the anterior border of the coronoid process occupied a more vertical position, and the process became relatively lower. The relative length of the coronoid process is minimal in *Tragulus* and *Hyemoschus*.

A low articular process located not very high above the level of the tooth row is a primitive eutherian state preserved in *Archaeomeryx*, *Lophiomeryx*, *Simimeryx*, and *Hypertragulus*. With the development of rumination and masticatory abilities, its position became higher. The same tendency is typical of higher ruminants and other herbivorous mammals. Among tragulines, the highest position of the articular process is observed in Recent tragulids.

## DENTITION

**Dental Formula**

The primitive dental formula for tragulines was apparently 3.1.4.3/3.1.4.3. However, even the most ancient tragulines show different stages of reduction of the dentition due to their specialization. The reduction occurred in several ways with similar evolutionary tendencies, such as the disappearance of the upper incisors and first upper and lower premolars.

An adaptive trend to the early loss of P1 with an attendant reduction of p1 is seen in *Archaeomeryx*, *Lophiomeryx*, *Gelocus*, and *Prodremotherium* (Table 4). The loss of P1 was caused by the weakness of its functioning because of the enlargement of the upper canine and elongation of the snout through the development of the diastema between the premolar row and the upper canine. The next stage of the development in this direction was the loss of p1. This trend was followed by many tragulines, including the hypertraguloids *Simimeryx*, *Parvitrágulus*, and *Praetrágulus*, and was later inherited by pecorans. Some hypertraguloids, *Hypertragulus*, *Nanotragulus*, and *Hypisodus* evolved in other ways. *Hypertragulus* and most likely *Nanotragulus* retained a double-rooted and enlarged P1 and a single-rooted and small p1.

**Incisors and Canines**

The primitive position is strongly reduced and procumbent upper incisors and small, procumbent, and spatulate lower incisors with almost symmetrical crowns and a lingual excavation, seen in *Archaeomeryx*. Slightly procumbent and spatulate crowns of the incisors, almost equal in size and having a weak lingual excavation, were typical of primitive eutherians (Simpson, 1936; Kielan-Jaworowska *et al.*, 1979) and preserved in many tragulines.

Almost all traguline genera, except for *Archaeomeryx* and possibly *Hypertragulus*, *Hypisodus*, and *Leptomeryx* (Matthew, 1902; Scott, 1940), lost their upper incisors. The reduction of these teeth occurred in parallel in various groups of the Ruminantia, as in various groups of tragulines, and was linked to the development of a derived form of food manipulation using a mobile tongue and the lips.

The first lower incisors are only a little larger than the others in *Archaeomeryx* and *Praetrágulus gobiae*. In more advanced genera, the difference in size between them and other incisors is greater. The i1 has a wide cutting edge with the outer angle pulled

outward and the inner angle rounded in *Praetrágulus* and *Hyemoschus*. A rather symmetrical crown of i1 remains in *Gelocus*, but i3 is thin and pointed (Kowalevsky, 1876–1877).

**Canines.** The canines of ancient tragulines resemble a primitive eutherian type in the procumbent position, curvature, and faint excavation on the posterolingual side (Simpson, 1936).

The upper canines are primitively small, procumbent, and gently curved with rounded anterior and sharp posterior edges and convex inner and concave outer surfaces in *Archaeomeryx* and *Hypertragulus*. The canines become very large, less procumbent, and more curved in *Prodremotherium*, *Bachitherium*, *Lophiomeryx*, *Praetrágulus*, and tragulids. The enlargement of the upper canines evolved in parallel in various groups of the Tragulina. In tragulids, the upper canines grew at a right angle to the lower border of the maxilla; in *Dorcatherium*, the upper canines are almost straight; and in *Tragulus* and *Hyemoschus*, they curve strongly outward and backward. Sex-related variation of the canines in ancient tragulines could be similar to that in Recent species. In female *Hyemoschus* and *Tragulus*, canines are smaller, shorter, and less curved than in males.

Incisiform lower canines already occurred in the most ancient tragulines except for *Simimeryx* and *Parvitrágulus*. In *Archaeomeryx*, *Miomeryx*, and *Praetrágulus*, the canines are still larger than i3. In tragulids they are completely included in the incisor row. In *Simimeryx* and *Parvitrágulus*, the lower canines increased but retained the primitive procumbent position.

**Premolars**

In the course of evolution, the premolar row tends to become slightly shorter relative to the molar row. The longest premolar row is observed in *Archaeomeryx*, *Leptomeryx*, and *Lophiomeryx*, and the shortest row is in hypertragulids.

Unicuspid and double-rooted anterior premolars consisting of a single outer cusp followed and preceded by a minute basal shelf or cuspule and very weakly molarized posterior premolars is a primitive state among the Tragulina. The nonmolarized anterior premolars of hypertraguloids *Hypertragulus* and *Simimeryx* resemble those of early eutherian mammals.

In addition, in the lower premolars of hypertraguloids, the tip of the protocone is located anteriorly to the middle of the crown, similar to that in the ancestral type

of primitive eutherians. This peculiarity is very well developed in *Bachitherium* and, to a lesser extent, in *Archaeomeryx*, *Gelocus*, and *Leptomeryx*.

The molarization of premolars occurred independently in various groups of the Tragulina and reached different stages.

A long and narrow DP2, with three sharp cusps (anterior cone, paracone, and metacone) is a relatively primitive state, preserved in *Tragulus* and *Hyemoschus*. In *Hyemoschus*, the posterior part of the tooth is more inflated than in *Tragulus* and bears a low cingulum. In the former, a very small lingual cusp, located posteriorly, is sometimes present.

In the primitive state, DP3 is narrow and elongated and has a long anterior part, lacking lingual cusps, and a very weakly molarized posterior part possessing a short anterior wing of the hypocone. The wing is directed anteriorly and does not enclose the posterior lobe of the tooth.

In the course of evolution, the anterior part of the crown shortened, the labial crests developed, and the posterior lobe was enclosed anteriorly, resembling the posterior lobe of the molars.

In *Lophiomeryx*, there are three labial cusps connected by longitudinal crests and one lingual posterior crest; the posterior lobe, however, is not enclosed anteriorly.

In *Bachitherium*, *Prodremotherium*, and tragulids, the anterior part of the DP3 crown is rather short, with lingual cusps.

In *Bachitherium* and *Prodremotherium*, they form a lingual wall. In tragulids this wall is absent. The posterior lobe of DP3 resembles those in the molars of *Bachitherium* and *Prodremotherium* in which the anterior wing of the hypocone adjoins the paracone–metacone junction.

The mesostyle developed to different degrees in various tragulines.

A wide, rounded anterior lingual cusp (possible analogue of the parastyle) is confluent lingually with the paracone in *Bachitherium* and *Prodremotherium*, similar to the state in pecorans.

A molariform DP4 with a low nonsymmetrical crown that is strongly expanded labially, narrowed posteriorly, and has a very small hypocone and well-developed para- and mesostyles is a primitive state preserved in *Lophiomeryx* and *Praetragulus*.

In *Bachitherium*, *Prodremotherium*, and tragulids, the crowns are more symmetrical. A relatively wide parastyle is preserved in *Bachitherium* and *Hyemoschus*. Hypertraguloids, except for *Simimeryx* and *Pra-*

*etragulus*, possess a weaker parastyle and, with the exception of *Praetragulus*, lack the mesostyle.

In the primitive state preserved in *Lophiomeryx*, *Praetragulus*, *Bachitherium*, *Tragulus*, and *Hyemoschus*, the posterior wing of the protocone is very short and mainly directed posteriorly. In the more advanced state, this wing is longer and directed labially, as in *Prodremotherium*.

DP4 of *Hyemoschus* possesses small folds in the anterior wing of the protocone and the posterior wing of the hypocone and a strong lingual cingulum.

Deciduous premolars dp2 and dp3 are primitively long, relatively simple, three-cusped, bear a distinct protoconid located relatively close to the anterior border of the crown, and have a relatively small paraconid and hypoconid. This state is preserved in *Lophiomeryx*, *Praetragulus*, and *Tragulus*. In addition, dp2 of *Prodremotherium* and *Hyemoschus* possesses a narrow heel composed of two short crests directed backward from the hypoconid. On dp2 of *Prodremotherium* and *Lophiomeryx chalaniati*, the protoconid bears a very weak lingual crest.

The tooth dp3 is a little more elaborate than dp2 and has two or three short crests, including the protoconid crest (metaconid) and two posterior crests. In *Gelocus communis*, dp3 has more elaborate lingual cusps. In a worn dp3 of *G. communis* (BMNH, no. M.1427), the metaconid is confluent with the entoconid, closing a small fossette similar to that in some pecorans. In *Bachitherium*, dp3 differs from those of other tragulines by the more central position of the protoconid with a very long oblique lingual crest that reaches the posterior corner of the crown and is isolated from the entoconid crest by a narrow and deep valley.

In the primitive state, dp4 consists of three lobes with incompletely developed lingual crests, crescent-shaped labial cusps, and a very short longitudinal crest connecting anterior and medial labial cusps. This state is preserved in *Lophiomeryx*. In this genus, the valley between the anterior and medial lingual cusps is widely open labially and the posterior valley is open posterolabially.

In the more advanced state, the labial crests become longer, but the longitudinal direction of the crest between the anterior and medial cusps still remains. The anterior wing of the medial cusp is directed slightly anterolingually only in *Prodremotherium*, *Bachitherium*, and *Gelocus*, which have the most developed crescents and isolated enclosed valleys in worn teeth.

In all tragulines, except for *Bachitherium*, the valleys of the first and second lobes remain confluent even in worn teeth, although a complete lingual wall is formed in some derived genera, such as *Gelocus*.

The presence of a small, nonmolarized, and double-rooted P1 is a primitive character that is retained in

*Hypertragulus* and *Nanotragulus*. In other tragulines, including *Archaeomeryx* and *Simimeryx*, P1 is absent.

P2 is simple and basically primitive in *Simimeryx* and *Hypertragulus*. It is short, laterally compressed, and consists of a high trenchant paracone and a very small posterior cusp aligned anteroposteriorly. A very weak internal cingulum is present at the anterior and posterior ends of the crown. In *Parvitrugulus*, P2 is more complex than in *Hypertragulus* and *Simimeryx* and possesses a small parastyle and strongly pointed protocone. In *Hypisodus*, P2 is sometimes lost in older individuals (Emry, 1978).

By a primitive structure, P2 of *Hypertragulus* and *Simimeryx* substantially differs from those of other tragulines and resembles the anterior premolars of ancient eutherians.

P2 of most traguloids is longer and less compressed laterally. It has a prominent but lower paracone, with sharp crests descending to the anterior and posterior edges of the crown and forming distinct para- and metastyles, respectively. The cingulum is developed lingually at the base of the crown.

This structure of P2 is typical of *Archaeomeryx* and tragulids. A small conic protocone is present in P2 of more advanced genera, such as *Leptomeryx*, *Lophiomeryx*, and *Gelocus*. It becomes crescentic in *Bachitherium* and *Prodremotherium*, in which its anterior and posterior wings adjoin the parastyle and metastyle, respectively.

P3 is triangular in outline and usually slightly larger and more complex than P2. The paracone (the most prominent cusp), the parastyle and the metastyle that are more developed than those of P2, and the protocone is conical or crescent-shaped. The size, structure, and position of the protocone vary in different genera; the same is true of the size and position of other elements. The protocone is small and weakly trenchant in *Hypertragulus*; weakly crescentic in *Lophiomeryx*, *Cryptomeryx*, and *Leptomeryx*; and very strongly crescentic in *Bachitherium* and *Prodremotherium*. A transverse crest connects the protocone to the paracone in *Hypertragulus*, *Parvitrugulus*, *Lophiomeryx*, *Gelocus*, and *Prodremotherium*. The two latter genera have a more molarized P3 with an internal conjunction to the metastyle. The protocone is approximately in the middle of the lingual side of the crown in *Hypertragulus* and *Bachitherium*. In *Archaeomeryx*, *Lophiomeryx*, *Prodremotherium*, and *Gelocus*, this cusp occupies a more posterior position. In *Leptomeryx*, it is in a much more posterior position.

In P3 of *Hypertragulus*, the labial crest is more oblique than those of *Archaeomeryx*, *Lophiomeryx*, etc., including tragulids.

P4 of all tragulines is well molarized. The protocone is substantially larger than that of P3 and usually more crescentic. The anterior wing of the protocone is connected to the parastyle, and the posterior wing of the protocone reaches the metastyle.

The genera differ from each other in the form and height of the crowns and in the sizes of the principal elements. The crowns are strongly expanded labially in *Hypertragulus*, *Lophiomeryx*, *Prodremotherium*, and tragulids and less expanded labially and more symmetric in *Archaeomeryx*, *Leptomeryx*, *Gelocus*, and *Bachitherium*. In *Hypertragulus*, the parastyle is weaker than the metastyle. In others, including *Gelocus*, *Bachitherium*, *Lophiomeryx*, and *Prodremotherium*, the metastyle is weaker. In *Archaeomeryx* and *Leptomeryx*, the parastyle and metastyle are approximately equal in size.

In *Parvitrugulus*, there are two labial cusps, the paracone and metacone. In this genus, the protocone of P4 is substantially larger than that of P3 and is usually more crescentic. The anterior wing of the protocone adjoins the parastyle. The posterior wing of the protocone reaches the metastyle.

The presence of p1 is also a primitive character for the Tragulina. This tooth is lost in advanced species of many genera. A small conical, single-cusped p1 is apparently a plesiomorphic state for the Tragulina that is observed in *Archaeomeryx*, *Nanotragulus*, *Leptomeryx*, *Lophiomeryx*, and *Gobiomeryx*.

More progressive stages imply the enlargement of p1 (this is typical of *Hypertragulus* and *Bachitherium*) or the molarization and enlargement of p1 that are obviously secondary processes, displayed in *Dorcatherium cappuisi* (BMNH, no. M. 21343), *D. nauyi* (BMNH, no. M. 40362), and, according to Webb and Taylor (1980), in some members of the genus *Gelocus*.

Within the Tragulina, there are the following five types of p2: (1) single-cusped in *Hypertragulus*; (2) double-cusped with the protoconid and paraconid in *Pronodens*; (3) three-cusped (a large protoconid and smaller paraconid and hypoconid) in *Archaeomeryx*, *Leptomeryx*, *Prodremotherium*, and *Dorcatherium*; the posterior wing of the metaconid is present in *Archaeomeryx* and *Leptomeryx*; (4) four-cusped with a small heel or hypoconid and entoconid in *Lophiomeryx*, *Gobiomeryx*, *Pseudomeryx*, *Tragulus*, and *Hyemoschus*; and (5) five-cusped with the metaconid in *Gelocus* (Table 5).

There are six types of p3: (1) double-cusped with the protoconid and hypoconid in *Simimeryx* and *Nanotragulus*; (2) three-cusped with the protoconid, entoconid, and hypoconid in *Hypertragulus*; (3) three-cusped with the protoconid, paraconid, and hypoconid in *Lophiomeryx*, *Gobiomeryx*, and *Tragulus*; (4) four-cusped that differs from the third type by the develop-

**Table 5.** Main trends and stages of lower premolar molarization in tragulines

Trend	Stage			
	two-cusped	three-cusped	four-cusped	five-cusped
1. Typical of traguloids	–	prd + pad + hyd (p2 Ar, Le, Pro; p3 Lo, Go, Pse, Tra)	(a) (prd + pad + hyd) + entd (p2 Lo, Go, Pse; Tra; p3 Ar)  (b) (prd + pad + hyd) + med (p3 Ba)	(a) (prd + pad + hyd + entd) + me (p2 Ge; p3 Ge, Le; p4 Ar)  (b) –
2. Typical of hypertraguloids	prd + hyd (p3 Si, Na);	(prd + hyd) + entd (p3 Hy);		(prd + hyd + entd) + pad + med (p4 Hy, Na);
3. Pronodens	prd + pad (p2 Pronodens)			(prd + pad) + med + end + hyd (p3, p4 Pronodens)

Acronyms: (entd) entoconid; (hyd) hypoconid; (med) metaconid; (pad) paraconid; (prd) protoconid; (Na) *Nanotragulus*; and (Pse) *Pseudomeryx*. For other acronyms, see Tables 2 and 3.

ment of the entoconid in *Archaeomeryx*, *Dorcatherium*, and *Hyemoschus*; (5) four-cusped that differs from the third type by the development of the metaconid in *Bachitherium*; and (6) five-cusped with the development of both the entoconid and metaconid in *Leptomeryx* and with the entostylid in *Gelocus*.

There are four types of p4: (1) four-cusped with the paraconid, protoconid, metaconid, and hypoconid in *Dorcatherium*; (2) the same as the latter, also including the entostylid in *Hypertragulus*; (3) five-cusped with the paraconid, protoconid, hypoconid, endoconid, and entostylid in *Tragulus* and *Hyemoschus*; and (4) five-cusped with the paraconid, protoconid, metaconid, hypoconid, and entoconid in *Archaeomeryx* and *Nanotragulus*. More advanced modifications of the latter type include the entostylid (observed in *Hypisodus*), parastylid (*Leptomeryx*), or a closed posterior fossettoid formed by the hypoconid and entoconid (*Gelocus*).

A common trend of lower premolar molarization was from a plesiomorphic single-cusped state with an anteriorly located protoconid that is preserved in p2 of *Hypertragulus* to the derived five-cusped state with the development of the paraconid, metaconid, hypoconid, and endoconid, in addition to the protoconid, which is

typical of p4 *Archaeomeryx*, *Leptomeryx*, *Gelocus*, and *Hypisodus*.

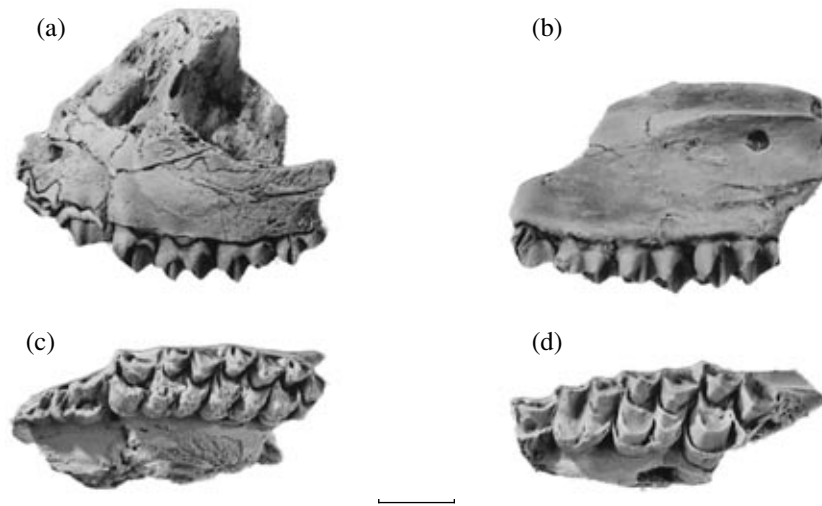
Apparently, at least three different ways of lower premolar molarization occurred in the course of early traguline evolution, as follows:

(1) From a very common stage with a large protoconid and smaller paraconid and hypoconid typical of p2 in *Archaeomeryx*, *Leptomeryx*, *Prodremotherium*, and *Dorcatherium*; and p3 in *Lophiomeryx*, *Gobiomeryx*, *Pseudoceras*, *Dorcatherium navi*, and *Tragulus*; the changes led to the four-cusped stage and, subsequently, to the five-cusped stage.

In this manner, two different trends of the development of the four-cusped stage are observed.

The first trend associated with the development of the entoconid, in addition to three initial cusps, was typical of p2 of *Lophiomeryx*, *Gobiomeryx*, *Pseudomeryx*, *Tragulus*, and *Hyemoschus* and p3 of *Archaeomeryx* and some members of *Dorcatherium*. In this case, the five-cusped stage was reached by the development of the metaconid and is seen in p2 and p3 of *Gelocus*, p3 of *Leptomeryx*, and p4 of *Archaeomeryx*.

The second trend implies that the metaconid developed earlier than the entoconid that is observed in p3 of



**Fig. 14.** Upper jaws: (a, b) *Prodremerium* sp., PIN, no. 2737/412, Early Oligocene Shunkht, Mongolia and (c, d) *Lophiomeryx angarae*, PIN, Late Eocene Ergilin-Dzo, Mongolia. (a, b) buccal and (c, d) occlusal views. Scale bar, 1 cm.

*Bachitherium*. This condition might be also explained by the reduction of the entoconid.

(2) The double-cusped stage, with an anteriorly located protoconid and a smaller hypoconid or heel, is observed in p3 of *Simimeryx* and *Nanotragulus*.

The process of molarization in this way was associated with the development of the entoconid, which is seen in p3 of *Hypertragulus*, and subsequent development of the paraconid and metaconid that is typical of p4 in *Hypertragulus* and *Nanotragulus*.

(3) A relatively rare double-cusped stage, with the anteriorly located protoconid and smaller paraconid, seen in p2 of *Pronodens*.

Thus, the data on the molarization of the lower premolars show that adaptive radiation of tragulines occurred at the initial stage of premolar molarization. There are two main distinguishable directions: (1) leading to traguloids, and (2) leading to hypertraguloids. *Pronodens* occupies a peculiar position.

### Molars

Upper molars that are strongly expanded labially and narrowed posteriorly, and that have an elevated anterior part of the tooth crowns are primitive within the Tragulina, and are remnants of the tribosphenic molars that arose in the Late Cretaceous in primitive mammals. These characters are particularly well-expressed in M3 of Tragulina and well-preserved in

*Lophiomeryx* and hypertraguloids (Fig. 14). They are slightly less evident in *Archaeomeryx*.

The molars of various tragulines differ in the stages of development and in the position of the crescents, styles, cingulum, and the degree of hypsodonty.

In the primitive state, the principal cusps are low, pointed, and lack crescents, as in ancient eutherians.

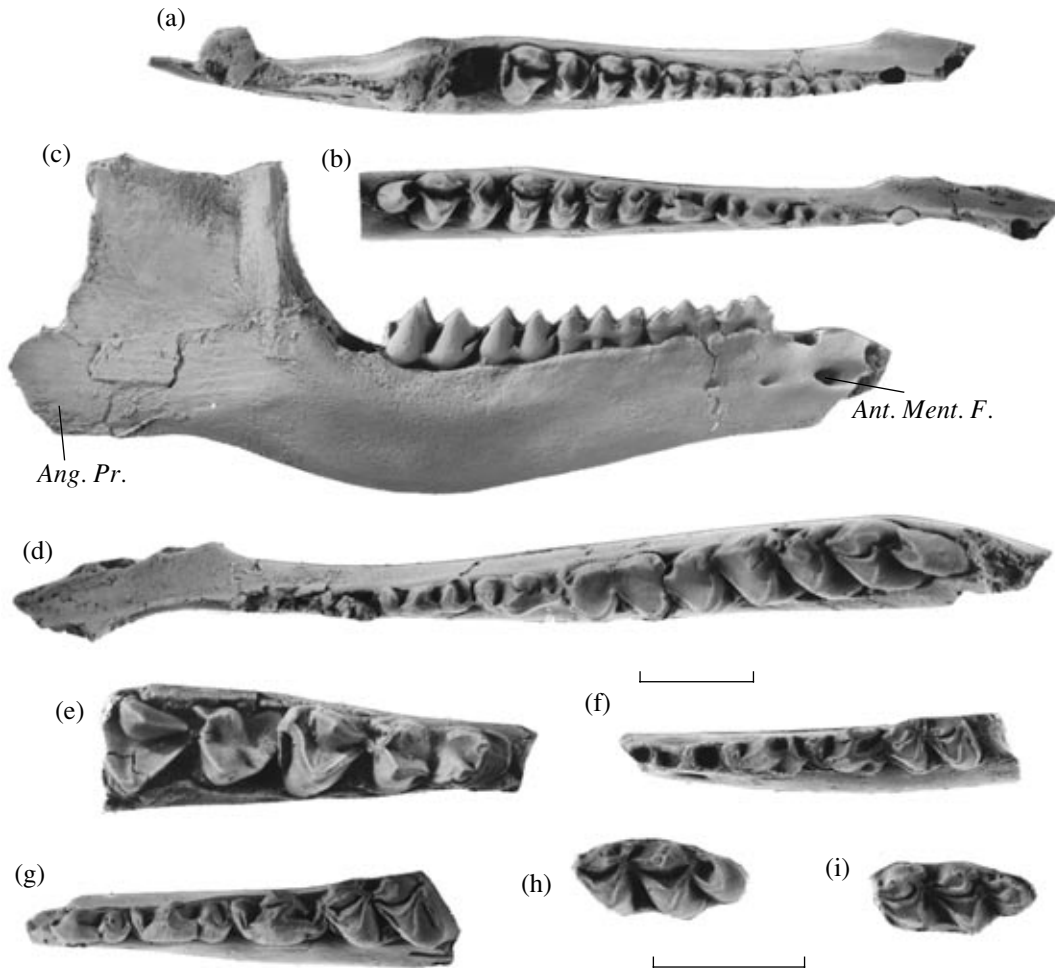
The labial cusps of the upper molars are virtually not crescentic in the primitive state, seen in *Archaeomeryx*. They form short crests in *Indomeryx* and *Lophiomeryx*, and become very crescentic in *Hypertragulus*, *Leptomeryx*, and gelocids. In hypertraguloids, the metacone and paracone lie almost in a straight line, and become confluent very early.

The lingual cusps of the upper molars are not crescentic in the primitive condition, seen in *Indomeryx*, and remain very weakly crescentic in *Archaeomeryx*, *Lophiomeryx*, *Simimeryx*, and *Praetragulus*.

The posterolingual cusp in the upper molars of most artiodactyls (including tragulids) is not homologous to the hypocone, but rather to the metaconule of the original tribosphenic molar (Matthew, 1929).

The metaconule was very small and not crescentic even in strongly worn teeth of *Simimeryx*, *Praetragulus*, and ancient *Lophiomeryx*. The weak development of the metaconule is related to the tribosphenic molars of early eutherians.

An increase in metaconule size occurred independently in various groups of tragulines. According to Simpson (1936), its appearance in many mammals is



**Fig. 15.** Lower jaws and teeth: (a–c) *Miomeryx altaicus*, Early Oligocene Khoer-Dzan, Mongolia, PIN, no. 3110/1225: (a) occlusal and (c) buccal views and (b) PIN, no. 3110/1226, occlusal view; (d) *Lophiomeryx angarae*, PIN, no. 3109/249, Late Eocene Ergilin-Dzo, Mongolia; (e) *L. cf. mouchelini*, PIN, no. 475/4804, Early Oligocene Tatal-Gol, Mongolia; (f) *Pseudomeryx gobiensis*, PIN, no. 475-1793, Early Oligocene Tatal-Gol, Mongolia; and (g–i) *Gobiomeryx dubius*: (g) PIN, no. 475-4805, (h) PIN, no. 475-4806, and (i) PIN, no. 475-4807, Early Oligocene Tatal-Gol, Mongolia. (d–i) occlusal views. Designations: (*Ang. Pr.*) angular process and (*Ant. Ment. F.*) anterior mental foramen. Scale bar, 1 cm.

associated with the absence or weak development of the paraconid.

At the early stages of the development of selenodonty, the posterior wings of the protocone and metaconule appeared. However, they remained rather short and directed posteriorly and slightly labially, as in *Archaeomeryx*, *Lophiomeryx*, and *Praetragulus*.

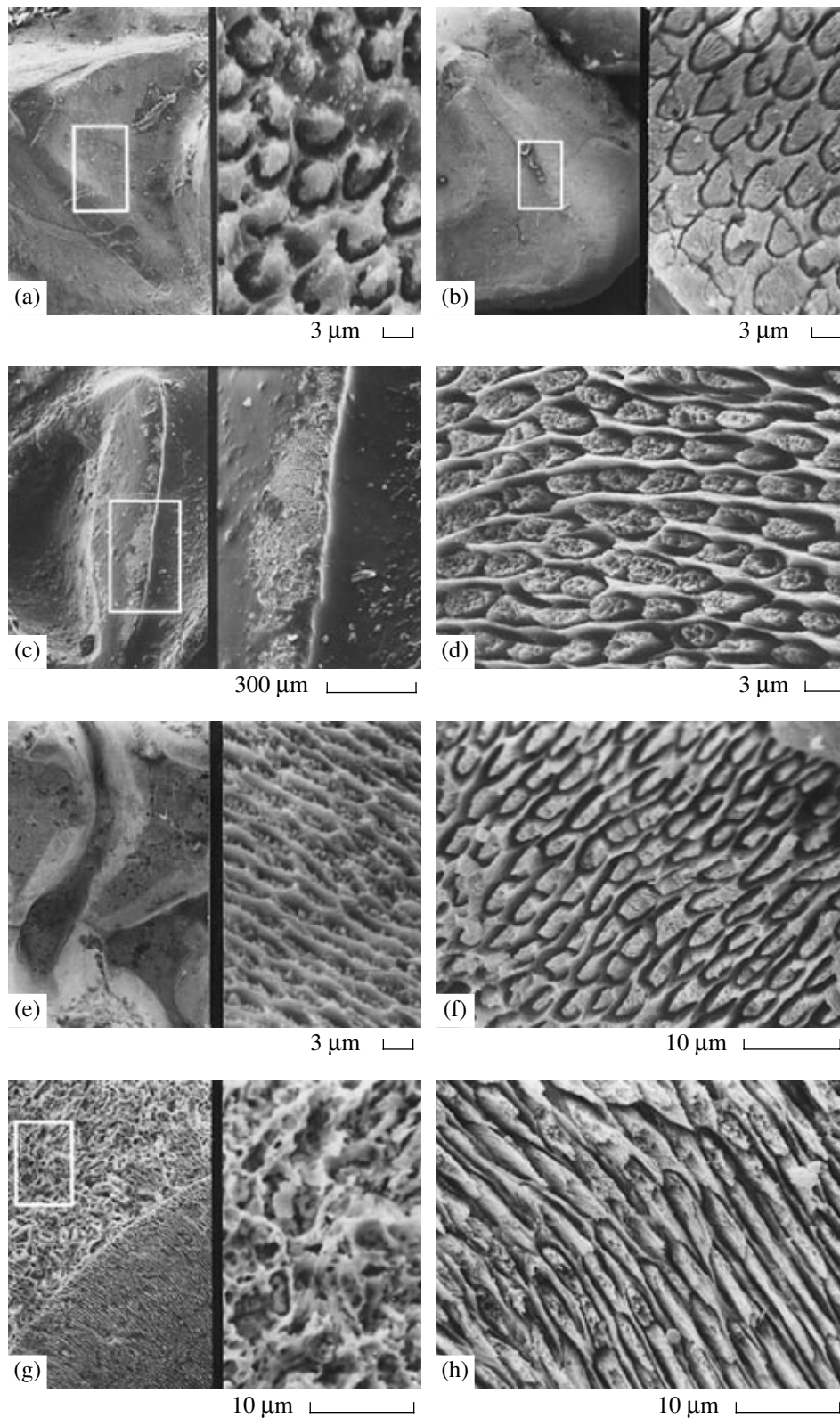
In these genera, the anterior wing of the metaconule is also short and does not reach the paracone–metacone junction. In the species possessing more selenodont molars, these wings became very long, directed labially, and very often confluent with the labial crescents, as in *Hypertragulus*.

The primitive state appears to be the presence of three labial styles (parastyle, mesostyle, and endostyle). These are strongly developed in *Archaeomeryx*

and expressed to a lesser extent in *Lophiomeryx* and *Praetragulus*. In all known hypertraguloids, except for *Praetragulus*, the mesostyle is absent.

In *Archaeomeryx* and *Lophiomeryx*, the labial styles are rounded and project labially, as in ancient eutherians, whereas in most hypertraguloids, they are compressed and stretch anteroposteriorly. Only in *Simimeryx*, is the parastyle widely rounded, as in ancient traguloids. It seems evident that a strong parastyle is a primitive ancestral state that is retained in *Archaeomeryx* and *Simimeryx*.

Only in *Simimeryx* is there a small anterior intermediate cusp in the upper molars, which is regarded as the protoconule (paraconule) by Stock (1934). However, it is not improbable that the cusp is an element (fold) on



**Fig. 16.** Enamel ultrastructure in M1 in occlusal view: (a) *Archaeomeryx optatus*, PIN, Middle Eocene of China; (b) *Miomeryx altaicus*, PIN, Early Oligocene of Mongolia; (c, d) *Leptomeryx* sp., AMNH, Orellan-Whitneyan of South Dakota; (e) *Dorcatherium* sp., BMNH, Early Miocene of Africa; (f) *Lophiomeryx* cf. *angarae*, PIN, Early Oligocene of Mongolia; and (g, h) *L.* cf. *mouchelini*, PIN, Early Oligocene of Mongolia.



the anterior wing of the protocone, because it looks quite different from a true paraconule of other selenodont artiodactyls and ancient ungulates.

On the lower molars, the lingual crescents are very weakly developed at the early stage of selenodonty (Fig. 15). The posterior wing of the entoconid remains distinct (isolated) from that of the hypoconid in *Simimeryx*, *Archaeomeryx*, *Miomeryx*, *Praetragulus*, *Lophiomeryx*, etc.

The main tendency from brachyodonty to hypsodonty occurred independently in various families and genera of Tragulina. The lowest crowns are in *Indomeryx* and *Archaeomeryx*. The most hypsodont molars are developed in *Hypisodus*.

### Enamel Durability

An increase in the enamel durability of molars is associated with an increase of the resistance of dental tissue to wear. This occurs through an increase in the enamel thickness or through a more effective arrangement and orientation of crystallites from the prisms to interprismatic regions.

The main directions in the development of the enamel ultrastructure due to chewing pressure can be summarized as follows.

(1) A complication of the prism arrangement, i.e., a simple radial structure of prisms transforms first into chains or simple bands, and subsequently forms a decussate structure known as Hunter–Schreger bands.

(2) An increase in prism inclination. In the primitive state, the prisms are almost perpendicular to the wear surface, whereas in a more advanced state they are inclined to the latter.

(3) The arrangement of the interprismatic crystallites in parallel planes.

(4) A decrease in the thickness of prisms and interprismatic planes.

(5) An increase in the thickness of enamel.

In tragulines, the most primitive enamel ultrastructure, with large arc-shaped prisms that are rather short, almost parallel to each other, radially oriented, and surrounded by well-developed interprismatic crystallites, is typical of *Archaeomeryx* and *Miomeryx* and resembles the enamel ultrastructure of multituberculates investigated by Carlson and Krause (1985). In *Archaeomeryx* and *Miomeryx*, the prisms are approximately perpendicular to the wear surface. This structure appears to be inherited from ancient eutherians and is the basis of all other enamel structures found in tragulines (Figs. 16 and 17).

Apart from a primitive type of enamel structure, seen in *Archaeomeryx* and *Miomeryx*, the three following ultrastructural patterns occur:

(1) The prisms are inclined to the wear surface and often form chains that are almost perpendicular to the enamel–dentine junction. Various genera of gelocids and hypertraguloids differ in the degree of inclination and enamel thickness and density. The inclination is rather weak in *Pseudomeryx* and *Hypisodus*; stronger in *Hypertragulus*; and even stronger in *Nanotragulus*, which possesses thicker and denser enamel.

(2) The prisms remain almost perpendicular to the wear surface but are arranged in simple bands that are confined to the parallel planes of interprismatic crystallites in leptomerycids and some tragulids. In Early Miocene African *Dorcatherium*, this structure is thinner than in Oligocene American *Leptomeryx*.

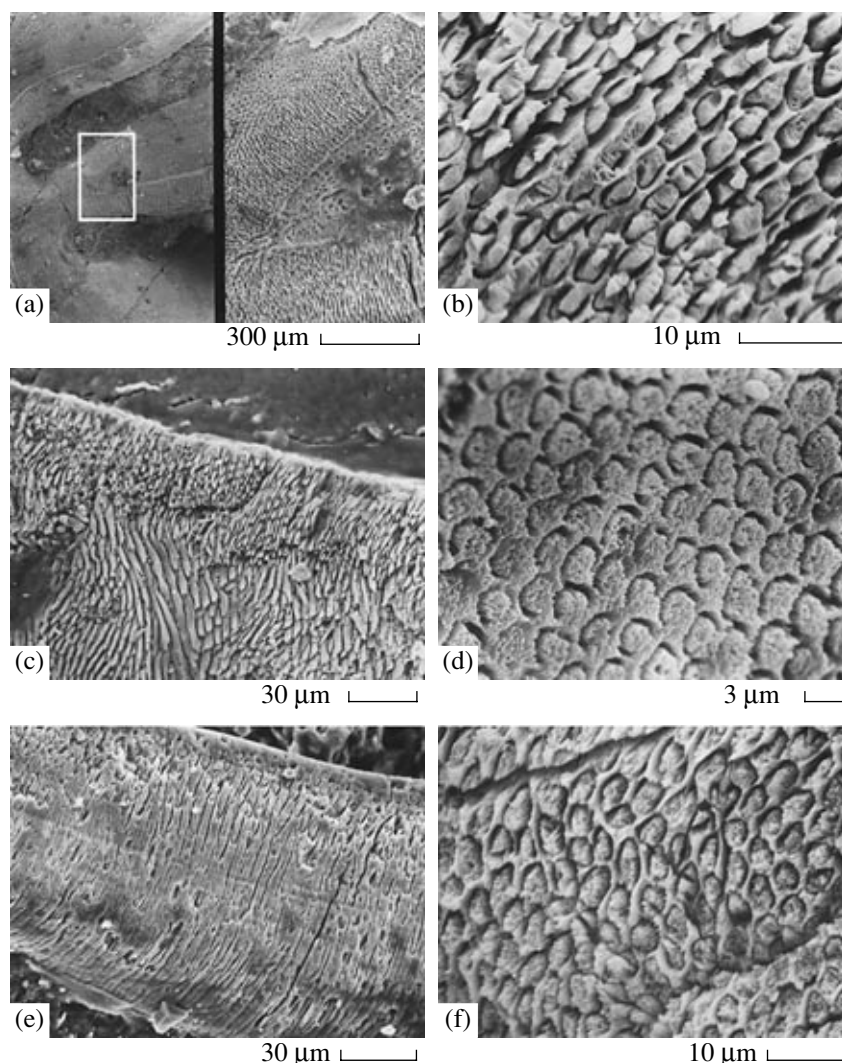
(3) The prisms and interprismatic material are arranged in rather primitive short Hunter–Schreger bands in some gelocids. At the enamel–dentine junction, the prisms form lines that are confined to vertically oriented planes of the interprismatic crystallites. The Hunter–Schreger bands are located at a distance from the enamel–dentin junction. This pattern is marked in *Gobiomeryx* and resembles the enamel structure of Early Paleocene arctocyonids (Koenigswald *et al.*, 1987). In most Paleocene arctocyonids and Oligocene pecorans, the Hunter–Schreger bands were better developed. Within eutherians, these bands are absent in insectivores and chiropterans, as well as in the Late Cretaceous arctocyonid *Protungulatum* (Koenigswald *et al.*, 1987).

The absence of Hunter–Schreger bands in most tragulines confirms their low level of specialization to herbivory.

### LIMB BONES

Most tragulines demonstrate a very low stage of paraxony development and limb simplification, although transformation in these directions embraces all limbs and limb articulations and is particularly clearly seen in the tarsal joints.

Tragulines retain many characters of the generalized pentadactyl limbs that are not typical of higher ruminants. Among these characters, there is a greater degree of mobility of certain articulations that does not provide a strict forward–backward movement of the legs. Even Recent *Tragulus*, possessing the most advanced skeleton within tragulines, clearly differs from other rumi-



**Fig. 17.** Enamel ultrastructure in M1 in occlusal view: (a, b) *Pseudomeryx gobiensis*, PIN, Early Oligocene of Mongolia; (c, d) *Gobiomeryx dubius*, PIN, Early Oligocene of Mongolia; (e) *Hypertragulus calcaratus*, AMNH, Orellan of Colorado; and (f) *Hyposodus* sp., AMNH, Chadronian of Nebraska.

nants in its well-developed abductors and muscles providing pronation (Carlsson, 1926).

Tragulines show great variety in the elongation and massiveness of limb bones, the degree of fusion or elimination of some of them, the combination of limb characters, and in the relative lengths of limb segments (Tables 6–8). The difference between the lengths of the fore and hind legs is negligible in *Gelocus*, almost so in *Hypertragulus*, very marked in *Hyemoschus*, and intermediate in *Archaeomeryx*.

### Scapula and Humerus

In ancient tragulines, the following features are indicators of greater mobility of the humeral articulation than in other ruminants:

- (1) the hemispherical head of the humerus;
- (2) a high, long scapular spine for the attachment of a powerful deltoid muscle (mainly a flexor but also a pronator and supinator of the joint);
- (3) a large infraspinous fossa (for the strong abductor of the joint);
- (4) a broad supraspinous fossa (for the extensor and abductor of the joint); and
- (5) a well-developed tuber and clearly expressed coracoid process of the scapula for the coracobrachial muscle (extensor and abductor of the joint), as seen in *Archaeomeryx*, *Praetragulus*, and *Gelocus*.

The other primitive characters of the scapula are an almost median position of the spine and widely

**Table 6.** Comparisons of the main postcranial features of tragulines

Feature	Primitive condition	Derived condition
1. Fore limb length	<u>much shorter than hind limb</u> (Ar)	elongated, almost equal to fore limb (gelocids)
2. Radius and ulna	<u>separate</u> (traguloids)	partly fused (hypertraguloids)
3. Facet for triquetrum on distal articular surface of radius	<u>absent</u> (Ar, Hy, Le, Prae)	present (Ge, Hypi, Hye, pecorans)
4. Manus	<u>pentadactyl</u> (Ar, Hy)	tetradactyl (Ge, Lo, Ba, Le, tragulids)
5. Trapezoid and magnum	<u>separate</u> (hypertraguloids)	fused (traguloids)
6. Trapezium	present (Ar, Lo, Hy, Hye)	absent (Le, Tra, pecorans)
7. Metacarpals III and IV	<u>separate</u> (all tragulines, except Pro)	partially fused (Pro)
8. Metacarpals II and V	almost not reduced (Ar, Hy)	strongly reduced (Pro, Le, Ge, tragulids, pecorans)
9. Metacarpal I	present (Ar, Hy)	absent (Le, Ge, tragulids, pecorans)
10. Tibia and fibula	separate (Ar, Le, Prae, Hye)	partially fused (Hy, Hypi, Tra)
11. Fibula	complete (Ar, Hy)	incomplete (Ge, Ba, tragulids, pecorans)
12. Malleolar bone	undeveloped (Ar, Hy)	developed: (a) separate from tibia (Lo, Ge, Ba, Le, Hye, pecorans); (b) fused with tibia (Tra)
13. Cuneiform II and III	<u>separate</u> (Ar, Lo)	fused (Ge, Pseu, tragulids, hypertraguloids, pecorans)
14. Cuneiform II + III and scaphocuboideum	separate (Ge, Pseu, Do, hypertraguloids, pecorans)	fused (Tra, Hye)
15. Astragalus	three-pulley (Ar, Mio)	double-pulley (Lo, Hy, Prae, tragulids, gelocids, pecorans)
16. Astragalus trochleae	nonparallel (Ar, Mio, Hy, Prae)	almost parallel (Lo, Le, Ba, tragulids)
17. Metatarsals III and IV	<u>separate</u> (Ar, Hy, Prae, Lo)	fused (Ba, Pro, Le, tragulids)
18. Metatarsals II and V	<u>complete</u> (Ar)	incomplete (Le, gelocids, tragulids, pecorans)
	<u>separate</u> (Ar, Hy)	partly fused with metatarsals III + IV (Le, Ge, Ba)

**Table 7.** Relative length of forelimb segments

Species	h/r	mc/mt	h + r + mc/f + t + mt	mc/h + r + mc
<i>Archaeomeryx optatus</i>	1.108	0.648	0.702	0.203
<i>Hypertragulus calcaratus</i>	1.172	0.644	0.756	0.187
<i>Praetragulus electus</i>		0.75		
<i>Leptomeryx</i> sp.	1.233	0.58	0.669	0.21
<i>Bachitherium curtum</i>	1.144	0.657	0.699	0.263
<i>Bachitherium</i> cf. <i>insigne</i>	1.035	0.768	0.731	0.31
<i>Lophiomeryx chalaniati</i>		0.97		
<i>Gelocus communis</i>	1.253	0.84	0.766	0.279
<i>Tragulus meminna</i>	1.197	0.64	0.674	0.221
<i>Tragulus javanicus</i>	1.133	0.68	0.686	0.239
<i>Hyemoschus aquaticus</i>	1.27	0.512	0.637	0.279

**Table 8.** Relative lengths of hindlimb segments

Species	mt/f + t + mt	f/f + t + mt	t/f + t + mt	mtIII/f
<i>Archaeomeryx optatus</i>	0.22	0.367	0.412	0.599
<i>Hypertragulus calcaratus</i>	0.22	0.39	0.39	0.564
<i>Leptomeryx</i>	0.24	0.346	0.412	0.69
<i>Bachitherium curtum</i>	0.28	0.32	0.4	0.875
<i>Bachitherium</i> cf. <i>insigne</i>	0.26	0.339	0.398	0.65
<i>Lophiomeryx chalaniati</i>	0.97			
<i>Gelocus communis</i>	0.254	0.366	0.38	0.65
<i>Tragulus meminna</i>	0.233	0.363	0.404	0.64
<i>Tragulus javanicus</i>	0.242	0.364	0.394	0.66
<i>Hyemoschus aquaticus</i>	0.186	0.407	0.407	0.47

rounded anterior and posterior angles. They are present in *Praetragulus* and *Gelocus*.

An increase in the range of fore-and-aft motion of the humeral articulation is reflected in the anteroposterior elongation of the head and the diminishing of the coracoid process. The longest axis of the head first occupies an oblique position relative to the distal trochlea, as in *Leptomeryx*, and subsequently becomes almost perpendicular to this trochlea, as in *Hypertragulus*. Other derived transformations of the scapula are its narrowing, a more cranial displacement of the scapular spine, and a relative decrease in the size of the supraspinous fossa, as seen in tragulids.

In the primitive state preserved in *Archaeomeryx*, the humerus is slender and relatively short with a hemispherical head and a narrow distal trochlea that possesses a weakly inflated medial part. Furthermore, the major lateral tubercle for the supraspinous and infraspinous muscles is rather low and the intertubercular sulcus for the tendon of the broccoli biceps muscle (extensor of the humeral joint) is shallow.

In a more advanced state, the longest axis of the head becomes almost perpendicular to that of the distal trochlea, the major tubercle is higher, the intertubercular sulcus is broader, and the distal trochlea develops a more inflated medial part.

The most slender humeri with the narrowest heads are found in *Hypertragulus* and *Hypisodus*. They combine a very advanced structure of the proximal epiphysis with a very narrow head (the longest axis of which is perpendicular to that of the distal trochlea) with the primitive state of the distal epiphysis, which has a narrow and weak trochlea. A peculiar character of the distal trochlea in *Hypisodus* is its strongly oblique position relative to the diaphysis.

A short and massive humerus with well-developed epiphyses is present in *Hyemoschus*.

### Radius and Ulna

The radius is a little shorter than the humerus and slender in the primitive state, as in *Archaeomeryx*.

In the more advanced state, it is long and slender, as in *Hypertragulus*, *Leptomeryx*, and *Tragulus*, or very short and massive, as in *Hyemoschus*.

In *Gelocus* and *Hyemoschus*, the radius is much shorter than the humerus. In others (including *Tragulus*), the difference in length between these bones is less marked and is almost imperceptible in *Archaeomeryx*,

some *Leptomeryx* (AMNH, no. 35711), and *Bachitherium* cf. *insigne* (Geraads *et al.*, 1987).

In *Archaeomeryx*, *Leptomeryx*, and hypertragulids, the proximal articular surface for the trochlea of the humerus has lateral and medial concavities that are almost equal in size and a wide, but not particularly deep, groove between them. In tragulids, the difference in size between both concavities is greater and the groove is deeper.

The distal articular surface consists of two facets for the scaphoid and lunar in a primitive state, which are preserved in *Archaeomeryx*, hypertragulids, *Leptomeryx*, and *Tragulus meminna*. In the more progressive state, seen in *Gelocus*, *Hypisodus*, and *Hyemoschus*, a lateral facet for the triquetrum [cuneiform in Webb and Taylor (1980)] is present, as in pecorans. At the early stage of limb development, this facet was completely placed on the distal epiphysis of the ulna.

In all tragulines, except hypertraguloids, the ulna is usually isolated from the radius. A derived partial ossification of the ulna and radius is in *Praetragulus* and complete fusion is typical of other hypertraguloids.

### Manus

*Archaeomeryx* and *Hypertragulus* have a primitive pentadactyl manus; however, the former is more advanced in the co-ossification of the trapezoid and magnum and the latter is more advanced in the absence of contact between the scaphoid and trapezium owing to a strong palmar displacement of digit I.

Palmar displacement of digits I and V differentiates the ungulate manus from the five-toed generalized type of the primitive eutherian manus.

A striking difference in the structure of the manus of *Archaeomeryx* and *Hypertragulus* concerns the degree of its curvature. In *Archaeomeryx*, the curvature is strong and side bones (metacarpals I, II, and V and corresponding carpal bones) are displaced behind the central bones (metacarpals III and IV and corresponding carpal bones), whereas in *Hypertragulus*, the curvature is very weak and side bones lie almost aside of central bones.

The first, more compact arrangement of the manus apparently reflects a more energetically profitable transformation of the foot towards a single tube and belongs to the adaptive direction of ruminant evolution. Owing to this arrangement, the fusion of the magnum and trapezoid in *Archaeomeryx* occurred rather early.

In an almost aligned manus of *Hypertragulus*, these bones remained primitively separate.

All tragulines have a nonserial (or alternating) basipodium. Such an arrangement of the basipodium appears to be the primitive eutherian state (Matthew, 1937) and is typical of most artiodactyls, as well as arcocyonids and hyopsodontids (Schaeffer, 1947).

Unlike other parts of the traguline autopodium, the carpal and tarsal bones are primitively elongated proximodistally and become shorter with the progressive development of feet because of a decrease in the inclination to the ground, strengthening of the fulcrum function, and the changes in weight distribution.

In the most primitive state preserved in *Archaeomeryx* and *Hypertragulus*, the manus remains mainly mesaxonic but still is not truly paraxonic. This character of *Hypertragulus* was first marked by Scott (1940).

The presence of all carpal bones and a primitively unfused trapezoid and magnum is discovered only in hypertraguloids. In *Hypertragulus*, the magnum overlaps metacarpals II and III, and a separate trapezoid rests on metacarpal II.

In traguloids, the trapezoid and magnum fused at an early evolutionary stage. The trapezoidomagnum lies on metacarpals II and III and partly on metacarpal I in *Archaeomeryx*, mainly on metacarpal III in *Leptomeryx* and *Gelocus*, and on metacarpals II and III in *Hyemoschus*.

A separate trapezium is found in *Archaeomeryx*, *Lophiomeryx*, and *Hyemoschus* and is possibly lost in all other tragulines, as it is in pecorans. In *Hyemoschus*, this bone rests on metacarpal II.

The manus of many tragulines is asymmetrical and metacarpal III is longer than metacarpal IV. The central metacarpals are elongated and isolated in *Archaeomeryx*, *Leptomeryx*, *Hypertragulus*, *Gelocus*, *Lophiomeryx*, *Miomeryx*, *Praetragulus*, tragulids (including younger individual *Hyemoschus*), and, possibly, in *Gobiomeryx*. In all tragulines, metacarpal III in addition to the facet for the magnum possesses a small oblique facet for the unciform, which disappears when metacarpals III and IV become completely fused.

The different stages of reduction of metacarpals I, II, and V are represented among tragulines. By the structure of the metacarpus, the most derived genus appears to be *Prodremotherium*, which demonstrates an incomplete fusion of metacarpals II and IV with the cannon bone and a considerable reduction of the side metacarpals. The loss of metacarpal I and the reduction of metacarpals II and V are also typical of *Leptomeryx*,

*Gelocus*, and tragulids. However, in *Gelocus* the reduction is greater and only proximal and distal parts of metacarpals II and V are present (Kowalevsky, 1876–1877).

The other primitive feature of traguline metacarpals is a hemispherical rather than semicylindrical distal trochlea with an incomplete, only palmar, development of the distal keel for the first phalanx.

### Pelvis and Femur

A wider range of rotation in the hip joint of most ancient tragulines compared to other ruminants is indicated by the following features:

(1) The hemispherical head of the femur, which is found in *Archaeomeryx* and *Hypertragulus*, whereas most advanced ruminants possess a more semicylindrical head of the femur;

(2) a considerable elongation of the ramus of the ischium and the medial border of the obturator foramen (origin of the external and internal obturator muscles, the rotators of the joint);

(3) a clearly smaller ischiadic notch for the passage of the internal obturator muscle and a well-developed trochanteric fossa, where both obturator muscles are attached;

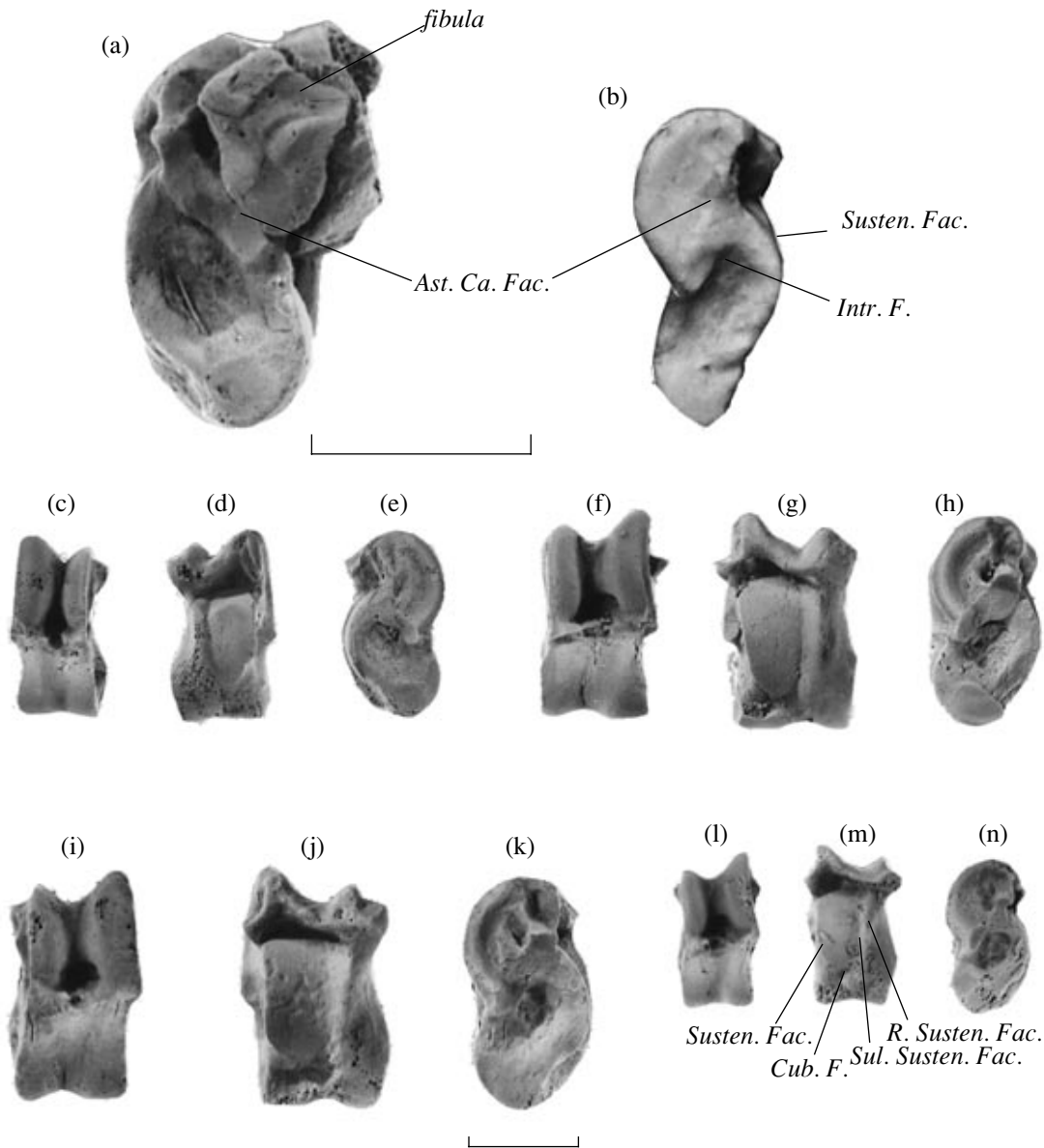
(4) the presence of the neck of the femur, a primitive artiodactyl character (Carlsson, 1926) seen in *Archaeomeryx* and *Hypertragulus*.

A femoral neck permits a greater range of lateral movement, which is very limited in ruminants (Kowalevsky, 1876–1877). The femoral neck is absent in *Gelocus* and *Hypisodus*, as in pecorans, which are characterized by more perfect fore-and-aft movement in the hip joint.

The other primitive feature of the hip joint is the acetabulum facing more ventrally in ancient tragulines in contrast to it facing more laterally in other ruminants.

A great flexibility of this joint in ancient tragulines is also confirmed by a large alar portion of the ilium for the powerful iliopsoas muscle attached to the trochanter minor of the femur, a large and laterally expanded tuberosity of the ischium (for the extensors of the hip joint), and by an elongated symphysis (for the adductors of this joint). In Recent tragulids, these characters are less developed.

In the femur, the primitive features are as follows: the absence of the anteroposterior elongation of the patellar groove, a marked difference in size between the larger medial condyle and the smaller lateral condyle of



**Fig. 18.** Astragalus in tragulines. (a) *Praetragulus gobiae*, astragalus in connection with tibia and fibula, PIN, no. 3110/1232, Late Eocene of Khoer-Dzan, Mongolia; (b) *Archaeomeryx optatus*, AMNH, no. 20322, Middle Eocene of Ula-Ussu, China; (c–e) *Miomeryx altaicus*, PIN, no. 3110/1230, Early Oligocene of Khoer-Dzan, Mongolia. (f–h) *Praetragulus electus*, PIN, no. 3110/1229, Early Oligocene of Khoer-Dzan, Mongolia; (j–k) *Lophiomeryx angarae*, PIN, no. 3110/1228, Early Oligocene of Khoer-Dzan, Mongolia; (l–n) *Pseudomeryx gobiensis*, PIN, no. 3110/1231, Early Oligocene of Khoer-Dzan, Mongolia. (c, f, i, l) dorsal, (d, g, j, m) ventral, and (a, b, e, h, k, n) lateral views. Designations: (*Ast. Ca. Fac.*) astragalocalcaneal facet; (*Cub. F.*) cuboid fossa; (*Intr. F.*) intrarticular fossa; (*R. Susten. Fac.*) ridge of sustentacular facet; (*Susten. Fac.*) sustentacular facet; and (*Sul. Susten. Fac.*) sulcus of sustentacular facet. Scale bar, 1 cm.

the distal epiphysis, seen in *Archaeomeryx* and *Hypertragulus*, and a weak plantar projection of the condyles. The well-developed trochanter major and trochanter minor are derived characters.

### Tibia and Fibula

The shortness of the traguline tibia in comparison with the femur is a primitive artiodactyl feature that is

well preserved in *Hyemoschus*. Although the tibia is longer than the femur in almost all tragulines except for *Hypertragulus* and *Hyemoschus* (Table 8), its elongation remains much weaker than in many other members of the Ruminantia.

In *Hypertragulus calcaratus*, the femur and tibia are almost equal in length. The most elongated tibia is in *Bachitherium curtum* and *Hypisodus minimus*, which are characterized by the highest tibiofemoral (crural)

index. In *Bachitherium curtum*, the index is 1.25 and corresponds to those of *Gazella subgutturosa* and *Capreolus capreolus*. The crural index of *Hypisodus minimus* is 1.32, i.e., it precedes the mean value in other ruminants, is equal to that in *Ochotona daurica*, and is a little lower than that of *Allactaga*.

In addition to other transformations of the postcranial anatomy, an increase in the crural index allowed the animal to move with greater speed. Because of the marked elongation of the tibia, tragulines have been assumed to possess a hopping gait. This appears to be true for most of them, except for *Hyemoschus*, a relatively heavily built animal with shortened limbs.

Other important primitive characters of the tibia are as follows:

(1) a small anteroposterior diameter of the proximal epiphysis, seen in *Archaeomeryx* and *Hypertragulus*;

(2) a weakly developed tuberosity of the tibia, occurring in *Hypertragulus* and, to a lesser degree, in *Archaeomeryx*;

(3) a very long crest on the tibia, preserved in *Archaeomeryx*, *Leptomeryx*, and *Hyemoschus*;

(4) a well-developed medial malleolus, seen in *Archaeomeryx* and *Hypertragulus*;

(5) a narrow, short, and concave facet for the malleolar bone, retained in *Archaeomeryx*; and

(6) a well-developed sulcus for the tendon of the long flexor of the digits at the medioplantar surface of the distal end.

In the derived state, the proximal epiphysis is elongated anteroposteriorly, the tuberosity of the tibia is greater, the crest of the tibia is shorter, and the facet for the malleolar bone is more complex.

The proximal epiphysis is particularly strongly elongated anteroposteriorly in *Pseudoceras*.

The tuberosity of the tibia projects very strongly anteriorly in *Leptomeryx* and *Pseudoceras*.

The crista of the tibia is one-third as long as the tibia of *Gelocus*, shorter in *Hypertragulus* and *Tragulus*, and very short in *Hypisodus*.

The medial malleolus is small in *Tragulus* and very weak in *Hyemoschus*.

The malleolar facet is small and round in *Hyemoschus*. In almost all other tragulines, the facet bears anterior and posterior concavities and a small fossa between them, similar to those in pecorans.

In most tragulines, the fibula is incomplete, its proximal end is fused with the tibia, and its distal part forms the malleolar bone.

The co-ossification of the distal part of the fibula and tibia, occurring in *Hypertragulus*, *Hypisodus*, and *Tragulus*, is a derived character.

Data on the structure of the tibiofibular articulation in *Praetragulus* and *Hyemoschus* conflict with the viewpoint of some researchers (Webb and Taylor, 1980) on the primary fusion of a complete fibula with the tibia in hypertraguloids and a few traguloids and show that the fusion was followed by a great reduction of the fibula and a decrease in its distal part.

The strengthening of the tibiofibular articulation in tragulines evidently occurred in two ways:

(1) with the preservation of certain mobility of this articulation in traguloids (except *Tragulus*) and

(2) with the consolidation of this articulation in hypertraguloids and *Tragulus*. The first (more adaptive) way provided the joint with a better amortization and was later inherited by pecorans.

Primitive traits of the malleolar bone of tragulines include the following:

(1) a very high malleolar bone, narrowing anteroposteriorly, with proximal and distal facets that are not parallel, which are found in *Archaeomeryx* and *Lophiomeryx*; and

(2) a short medial prominence for the tibia, typical of the malleolar bone of *Archaeomeryx*, *Lophiomeryx*, and *Hyemoschus*.

In the more advanced state, the malleolar bone is lower, both facets are almost parallel to each other and the medial prominence for the tibia is stronger. In *Leptomeryx* and *Hyemoschus*, the malleolar bone is low but the facet for the calcaneum is oblique relative to the facet for the tibia.

### Pes

On the whole, the tarsus of primitive tragulines, which possesses all typical artiodactyl characters, was closer to a primitive ferungulate type and generalized eutherian arrangement than to that of other ruminants and the most ancient diacodexids.

*Archaeomeryx* still possessed a functionally tetradactyl pes with well developed lateral digits and showed more primitive and more flexible tarsal joints than other ruminants.



The structurally tetradactyl pes of many other tragulines was already functionally didactyl. In most of them, articulation structures more effectively prevented supination and restricted motion to the parasagittal plane more efficiently than in *Archaeomeryx*. An important role in these processes is played by the astragalus.

**Astragalus.** The most striking character of *Archaeomeryx* is its essentially three-pulley astragalus with a better developed proximal (tibial or upper ankle) trochlea and distal and plantar (lower ankle) trochleae that are approximately equal in size (Fig. 18).

All other tragulines possess a double-pulley astragalus with proximal and distal trochleae that are nonparallel to each other in the primitive state, as seen in *Archaeomeryx*, hypertraguloids and Recent tragulids, and become almost parallel in the derived state, which is typical of *Bachitherium*, *Gelocus*, *Prodremotherium*, and *Dorcatherium*, and resembles the pecoran condition.

The almost semicylindrical plantar trochlea of *Archaeomeryx* is unusual in ruminants. It apparently permits not only vertical rotation (typical of the ruminant astragalus) but also some inversion–eversion motion, which is well pronounced, according to Schaeffer (1947), in some early Paleocene arctocyonids and hyopsodontids.

Among modern orders, the combination of these motions is present in lagomorphs and rodents (Schaeffer, 1947).

The main axis of the plantar joint passes close to the dorsal surface (like that of *Diacodexis*) immediately above the neck of the astragalus and lies at an angle of roughly 80° to the longitudinal axis of the astragalus.

The astragalus of *Archaeomeryx* also shares several other important primitive characters with *Diacodexis* (AMNH, no. 27787) that are derivable from the structure of the astragalus of Protungulatum. Most of these characters show a strong inclination of the limbs to the ground and a restricted amplitude of dorsiflexion and extension in the ankle and subtalar joints. They are as follows:

(1) a large proximodistal elongation, also observed in *Miomeryx* and *Tragulus*;

(2) incomplete development of the distal trochlea that is lower proximodistally and narrower transversally than the proximal trochlea and, furthermore, has a very narrow lateral side (less than half as narrow as the medial side);

(3) a distinct ridge on the lateral part of the distal trochlea that corresponds to the division between the scaphoid (navicular) and cuboid, is preserved in many

tragulines and pecorans (Martinez and Sudre, 1995) and is similar to that in other artiodactyls (Leinders, 1976);

(4) a narrow, not very elongated sustentacular facet on the surface of the plantar trochlea;

(5) a distinct ridge (medial rest for the sustentaculum tali of the calcaneum) at the medial border of the sustentacular facet and a narrow longitudinal sulcus along it; this character does not coincide with the statement of Leinders (1976) that there is no ridge at the medial border of the sustentacular facet in ruminants;

(6) a considerable plantar hollow under the proximal trochlea (above the sustentacular facet), very deep as well in *Miomeryx*, *Lophiomeryx*, and *Praetragulus*, and more shallow in Recent tragulids (superior stop for the sustentaculum tali of the calcaneum);

(7) a very low position of the facet for the lateral process of the scaphocuboid, typical of most tragulines; and

(8) the presence of an elongated astragalocalcaneal facet with two (anteroinferior and posterosuperior) stops at its ends and a large, deep intrarticular fossa for the fibular condyle of the calcaneum on the lateral side of the proximal trochlea.

The last characteristics (8) are well developed in *Miomeryx*, *Lophiomeryx*, and *Praetragulus*, and are weak in *Hypertragulus*, *Leptomeryx*, and tragulids. The anteroinferior stop also serves as a fulcrum for the fibula. This stop is very prominent laterally in ancient tragulines and particularly strong in *Praetragulus*.

The long axis of the astragalocalcaneal facet of *Archaeomeryx* retains a nonparallel position relative to the sustentacular facet that resembles the primitive ferungulate type rather than that of *Diacodexis*, which has a more vertical position of the facet (Schaeffer, 1947). The astragalocalcaneal facet is almost absent in pecorans.

In *Archaeomeryx*, a relatively small amplitude of the fore-and-aft motion in the tarsal joints is clearly seen in the peculiarities of the development and position of the main stops that limit this motion.

The dorsal surface of the astragalus of *Archaeomeryx* demonstrates high-situated flexion stops for the tibia (intertrochlear fossa and distal lapels of the proximal trochlear ridges) and low-situated flexion stops for

the scaphocuboid (lapels of the proximal border of the distal trochlea).

In superior view, the astragalus of *Archaeomeryx* shows a strong medioplantar projection of the medial ridge and a very short lateral ridge of the proximal trochlea (extensor stops for the tibia).

The amplitude of the fore-and-aft motion in the subtalar joints is also limited by the small height and weak curvature, the very short lateral part of the distal trochlea of the astragalus, the lapels of the proximal edge of the distal trochlea, the low plantar processes of the scaphocuboid, and the low cuboid fossa on the plantar surface of the astragalus.

The strong medial lapel of the cuboid fossa serves as the extensor stop for the sustentaculum tali of the calcaneum.

The considerable development of the above-mentioned stops for the tibia on the dorsal and plantar surfaces of the astragalus in *Archaeomeryx* could be also caused by a strong inclination of the limbs.

In the course of evolution, vertical pressure in the tarsal joints increased and caused anteroinferior shortening of the tarsal elements because of the straightening of the limbs and a decrease in limb inclination to the ground. Moreover, a stronger pressure on the plantar trochlea of the astragalus led to its flattening.

In a more advanced (more vertical) position, the astragalus better transmits body weight from the tibia to the scaphocuboid. The astragalus is shorter and broader, the axes of the proximal and distal trochleae are almost parallel to each other, the trochleae are aligned, and the distal trochlea is higher and broader with a better developed lateral part. The sustentacular facet of the astragalus is more elongated, broader, and less convex dorsally, while its medial ridge is less prominent, and the longitudinal sulcus is displaced somewhat laterally (towards the middle of the facet). In advanced forms, the major part of the facet becomes concave, as in pecorans. These peculiarities of the sustentacular facet provide better contact with the calcaneum.

Thus, the sustentacular facet in ruminants varies in structure and the statement that it is concave (Leinders, 1976) can be applied only to higher ruminants.

An oblique position of the ridges of the proximal trochlea relative to the longitudinal axis of the astragalus is preserved in *Miomeryx*, *Lophiomeryx*, and *Pseudomeryx*, and less well expressed in hypertragulids and tragulids. These ridges are almost parallel to the

sagittal plane in *Gelocus*, *Bachitherium*, and *Prodremotherium*.

The medioplantar projection of the proximal trochlea is also well developed in *Miomeryx*. However, it is weaker in *Lophiomeryx* and not expressed in *Pratragulus*, *Hyemoschus*, and *Tragulus*. The proximal and distal trochleae are approximately equal in width in *Gelocus*, *Lophiomeryx*, *Pseudomeryx*, *Dorcatherium*, and *Tragulus*.

The distal trochlea is better developed and wider than the proximal one in *Hypertragulus*, *Leptomeryx*, and *Hyemoschus*. The distal trochlea remains low in *Lophiomeryx angarae* but is more elongated anteroposteriorly on the lateral side than in *Archaeomeryx*.

In other tragulines, the distal trochlea is almost equal in height to the proximal one and has a more developed lateral part.

In *Prodremotherium* and *Gelocus*, the proximal and distal trochleae are aligned in a similar way to those of pecorans (Martinez and Sudre, 1995).

The sustentacular facet is elongated proximodistally and is mostly concave with a broad and shallow median sulcus in *Gelocus*, *Prodremotherium*, *Bachitherium*, and Recent tragulids, as in pecorans.

Thus, similar to *Archaeomeryx*, the genera *Miomeryx* and *Lophiomeryx* had small amplitudes of fore-and-aft motion in the ankle and subtalar joints. The amplitudes could have been a little larger in *Lophiomeryx* than in *Archaeomeryx*, judging from the more developed lateral part of the distal trochlea and the smaller medioplantar stop for the tibia. Other tragulines resemble higher ruminants in the construction of the astragalus.

Calcaneum. The calcaneum of tragulines plays an important role in the locomotor system transmitting the force of the gastrocnemius muscle (a strong extensor of the ankle joint attached to the calcaneal tuber) to the pes.

The elongation of the tuber in ruminants provides essential leverage and is evident in many ruminants.

The calcaneum of *Archaeomeryx* and *Lophiomeryx* has relatively long tuber and a long lower articular part.

Among more advanced tragulids, the calcaneum of *Hyemoschus* differs in the relatively short lower articular part and a long tuber, whereas the reverse is true of the calcaneum of *Tragulus*.

On the lateral side of the calcaneum of *Archaeomeryx*, *Praetragulus*, and *Hypertragulus*, there is a long, deep groove for the tendon of the peroneus longus muscle, which is apparently a primitive state.

The sustentaculum tali of the calcaneum is prominent in all tragulines, and its articular surface for the astragalus is divided into two parts corresponding to the morphology of the sustentacular facet of the astragalus. In *Archaeomeryx*, the medial part of this facet is very narrow, whereas in *Hyemoschus*, both parts of the facet are almost equal in width.

The dorsal surface of the fibular condyle has a narrow convex facet for the malleolar bone in most tragulines, except tragulids, in which it is concave. In *Hypertragulus* and *Pseudomeryx*, this convexity is simple; in *Archaeomeryx* and *Lophiomeryx*, its distal end is weakly concave and resembles the surface in higher ruminants.

**Scaphocuboid.** The scaphocuboid is high in *Archaeomeryx*, *Miomeryx*, *Hypertragulus*, *Bachitherium*, *Pseudomeryx*, and *Lophiomeryx*, and very low in *Hyemoschus*.

In dorsal view, the facet for the calcaneum is long and broad in *Archaeomeryx*. It is short and broad, and only approaches the anterior edge of the bone in *Hyemoschus* and *Tragulus*.

In ventral view, the posteromedial angle projects only slightly backwards in *Archaeomeryx* and *Hyemoschus*, in contrast to that in *Tragulus*.

The groove for the tendon leading to the peroneus longus muscle between the anterior and posterior metatarsal facets is very weak and almost perpendicular to the sagittal plane in *Archaeomeryx* and *Hyemoschus*, is well developed in *Tragulus* and *Hyemoschus*, and strongly oblique relative to the sagittal plane in *Tragulus*.

The tendon for the peroneus longus muscle attached to cuneiform I causes a slight rotation of metatarsal III by the movement of cuneiform I. This rotation allows certain artiodactyls to change their direction of movement at full speed (Leinders and Sondaars, 1974). This feature is typical of high-speed species.

It seems very likely that the flexible talocrural articulation of tragulines was inherited from ancestors, and was improved only in fast-running pecorans.

Additionally, there is a large, deep concavity on the lateral half of the plantar surface of the scaphocuboid in *Archaeomeryx*, *Leptomeryx*, and *Lophiomeryx*. In *Hypertragulus* the concavity is very weak and restricted to the upper lateral corner of the plantar surface.

Unlike the scaphocuboid of other tragulines, those of adult Recent tragulids fused with the ectomesocuneiform (cuneiform III and II). According to Carlsson (1926), the embryo of *Tragulus napu* possesses two external cuneiforms. A separate ectocuneiform is present in *Archaeomeryx* and probably in *Lophiomeryx angarae*. The retention of an isolated ectomesocuneiform in the tarsus is typical of *Gelocus*, *Pseudomeryx*, hypertraguloids, and *Dorcatherium*. The entocuneiform (cuneiform I) is free in all tragulines, as in most ruminants. In *Gelocus*, it supports the rudiment of metatarsal II and rests on the plantar projection of metatarsal III (Kowalevsky, 1876–1877).

**Metatarsus.** In the primitive state, the metatarsus consists of four separate metatarsals that are preserved only in *Archaeomeryx*.

In the derived state, the central metatarsals are co-ossified, and the side metatarsals are substantially reduced.

The central metatarsals are separate in *Archaeomeryx*, *Lophiomeryx*, and hypertraguloids; and fused in *Gelocus*, *Leptomeryx*, *Bachitherium*, *Prodremotherium*, and tragulids, in which they form the cannon bone.

The central metatarsals are substantially elongated in most tragulines, except for *Hyemoschus*, which shows an apparent secondary shortening of the metapodials.

In *Archaeomeryx* and *Hypertragulus*, the relative length of the metatarsi are approximately equal and slightly smaller than in *Tragulus meminna*.

The most elongated metatarsus was in *Bachitherium* and *Prodremotherium*. A remarkable difference in the length of the central metacarpals and metatarsals is observed in *Leptomeryx* and *Hypertragulus*. The central metapodials in the fore and hindlimbs are almost equal in length in *Lophiomeryx*.

Metatarsals II and V are separate, complete, and bear three phalanges in *Archaeomeryx* and *Hypertragulus*. In *Leptomeryx*, metatarsals II and V are reduced to proximal elements. In *Gelocus* and *Prodremotherium*, the proximal end of metatarsal II is fused with the cannon bone, similar to this feature in some ancient pecorans. In the most advanced state, found in *Leptomeryx* and *Pseudoceras*, the proximal ends of metatarsals II and V are fused with this bone.

## Chapter 3

## EVOLUTION OF TRAGULINES

## ORIGIN

**Basal Traguline Group**

There is an extremely poor fossil record of the early stages of the evolution of the Tragulina and very little evidence of their origin.

Although the most ancient tragulines are known only from the Middle Eocene, this group appears to have had an earlier origin than is usually assumed. Tragulines might have diverged from an unknown artiodactyl group that retained many peculiarities of primitive eutherians and yet also showed the first morphological shifts to the paraxonic foot.

Judging by comparative morphologic data, the following plesiomorphies indicate primitive characters of the basal traguline group:

- (1) brachycephaly;
- (2) a long sagittal crest;
- (3) short temporal crests that diverge at a short distance from the posterior edges of the orbits;
- (4) small, unclosed, and anteriorly located orbits;
- (5) a short, low snout;
- (6) a short and ovoid anterior opening of the nasal cavity;
- (7) a short and lowly positioned infraorbital canal;
- (8) a separate jugular foramen;
- (9) the absence of an alisphenoid canal;
- (10) the posterior position and small size of the foramen ovale;
- (11) a weak and simple promontorium;
- (12) the posterior position of the tympanic aperture of the facial canal;
- (13) the posterior position of the fossae for the stapedial muscle and the tensor tympani;
- (14) a lateral exposure of the mastoid;
- (15) a long premaxillary–nasal contact and medial connection of small rostral processes of the premaxilla;
- (16) a low body of the mandible with a convex inferior border;
- (17) a short symphysis;
- (18) a well-developed coronoid process with a semi-vertical anterior margin;
- (19) a low and flattened articular process;
- (20) a strong angular process;
- (21) complete dentition;
- (22) small, procumbent incisors;
- (23) small, procumbent canines;
- (24) a slightly longer premolar row relative to the molar row;

(25) pointed double-rooted anterior premolars with an anteriorly placed protocone;

(26) brachyodont molars;

(27) strongly expanded labially and narrowed lingually upper molars;

(28) weakness of the metaconule on M3;

(29) the absence of the hypocone;

(30) a strong, wide parastyle;

(31) the presence of the paraconule (protoconule) and the absence of the mesostyle;

(32) short limbs;

(33) separate trapezoid and magnum;

(34) a pentadactyl manus;

(35) separate navicular and cuboid;

(36) a separate ulna;

(37) a rather short tibia;

(38) a complete and separate fibula;

(39) rather high bones of the basipodium, including an elongated, asymmetrical, and relatively narrow three-pulley astragalus;

(40) a separate ectocuneiform in the tarsus;

(41) a rather short autopodium;

(42) separate central and complete side metapodials; and

(43) a long tail.

Almost all of these characters, except for the three-pulley astragalus, correspond to those of ancient eutherians. By possessing some of these characters, tragulines are more primitive than all known Eocene artiodactyls.

In addition to the features listed above, the basal suite of characters should also include certain other primitive eutherian traits stated by Novacek (1986) and present in ancient tragulines, such as (1) a small incisive foramina; (2) a long, oblique, and unfurcated lateral maxilla–jugal contact; (3) the presence of anterior and middle palatine foramina; (4) the confluence of the foramen rotundum with the spheno-orbital fissure; (5) a deep subarcuate fossa; and (6) a posteriorly facing foramen magnum.

Cladistic analysis of selected ungulate higher taxa performed by Prothero *et al.* (1988) postulates that the artiodactyls are “the first of the ungulate groups to diverge, since they lack many of the specializations seen in all other ungulates.”

The artiodactyl characters chosen by these researchers include the following features:

- (1) a very narrow trigonid of the lower molar with the paraconid and metaconid closely appressed;
- (2) the absence of the alisphenoid canal;
- (3) an enlarged facial part of the lacrimal;
- (4) an enlarged orbitosphenoid that separates the frontal from the alisphenoid;
- (5) a paraxonic foot with a double-pulley astragalus; and
- (6) enlarged third and fourth metapodials and symmetrically reduced second and fifth metapodials.

In ancient tragulines, most of these characters are at the very initial stage of development.

In the above cladogram, the next level, occupied by arctocyonids, is determined by the position of the tympanic aperture of the canalis facialis, which is located anteriorly to the fenestra vestibuli, by the addition of the hypocone to the upper molars; and by the enlarged, distally shifted third trochanter of the femur. In all these features, tragulines are more primitive than arctocyonids.

The petrosal of *Archaeomeryx* is similar to that of the oxyclaenine arctocyonid *Protungulatum donnae* from Montana described by MacIntyre (1972) in the position of the fossa for the stapedial muscle behind the fenestra vestibuli. However, it is more primitive in the position of the tympanic aperture of the facial canal opposite this fenestra. In the course of evolution, this aperture was displaced anteriorly, as was the fossa for the stapedial muscle. In *Protungulatum*, the tympanic aperture of the facial canal was already slightly anterior to the fenestra vestibuli.

*Archaeomeryx* and *Protungulatum* also show a very close similarity in the structure of the mandible and premolars, but differ in the structure of the molars, which tend to increase the number of cusps in *Protungulatum*, as in dichobunoids. Although the hypocone is always absent in tragulines (as in ruminants), it is occasionally absent or weakly developed in *P. donnae* (Sloan and Van Valen, 1965).

These plesiomorphies are reflected not only in the cranial and postcranial morphology of ancient tragulines, but also in a primitive molar enamel ultrastructure that resembles the enamel ultrastructure of ancient eutherians and the arctocyonid *Protungulatum*. However, the basal traguline group evidently possessed the derived feature of rumination, giving them a definite energy advantage over other artiodactyl groups.

### Tragulines and Other Primitive Artiodactyl Groups

For a long time, different groups of dichobunids (sensu lato) or groups related to them were considered possible ancestors of tragulines (Schlosser, 1886; Matthew, 1934; Pilgrim, 1941; Gentry and Hooker, 1988;

etc.). Homacodontine dichobunids, such as *Mesomeryx*, were often regarded as possible ancestors of hypertragulids (Stock, 1934; Gazin, 1955; Golz, 1976).

However, new data on Eocene tragulines allows us to reconsider those points of view. Although the most ancient dichobunids closely resemble arctocyonids (Van Valen, 1971; Rose, 1996), they are more advanced, in many respects, than archaic tragulines.

Tragulines and some dichobunoid groups (diacodexids and dichobunids) represent independent (parallel) lineages adapted to a similar environment. These groups show a close resemblance in many plesiomorphic characters and in some initial morphological adaptations to herbivory and paraxony, but they differ very clearly in their specialization, which reflects the peculiarities of their adaptations.

Dichobunoids whose fossil remains were first found in the Early Eocene are more primitive than ancient tragulines in some dental and postcranial characters. However, they are more progressive in certain key adaptations, in particular, in a higher degree of premolar molarization and in more tubercular molars, which possess the hypocone and hypoconulid. They precede the most ancient tragulines in the development of some cursorial adaptations.

One of the most ancient diacodexid dichobunids and the oldest known artiodactyl, *Diacodexis*, from the Early Eocene (Wasatchian) of North America and from the Early–Middle Eocene (MP7–MP11) of Europe actually resembles tragulines in some postcranial adaptations, such as the elongation of the tibia and an increase in the crural index; the double-pulley astragalus; the elongation of the central metapodials; and a decrease in the side metapodials.

However, *Diacodexis* (AMNH, nos. 27787 and 128563) clearly differs from tragulines by the stronger molarized premolars, the presence of the hypocone, and by a well-developed paraconule (protoconule) on the upper molars. This genus shows no tendency towards selenodonty and possesses a number of plesiomorphic postcranial characters (moderately strong ulna, unfused cuboid and navicular, pentadactyl manus, etc.), and was already more cursorial (or perhaps more saltatorial) than tragulines, judging from the higher crural index (Rose, 1982). But the cursorial ability of *Diacodexis* developed differently from that of tragulines. *Diacodexis* differs from tragulines in the combination of a relatively progressive, elongated, and slender tibia with a rather primitive ankle joint with a less developed astragalus.

The astragalus of *Diacodexis* resembles that of *Archaeomeryx* but has a deeper hollow on the lateral surface with stronger anterosuperior and anteroinferior projections (stops for the calcaneum) and a lesser developed distal trochlea.

Moreover, in *Diacodexis*, the distal end of the tibia is narrower and that of the fibula is wider than those of tragulines.

In ancient tragulines, perfection of the ankle joint occurred earlier, or at a higher rate, than in dichobunoids.

The first dichobunoids, probable descendants of diacodexids, are represented in Europe at the end of the Early Eocene (MP10) by *Eurodexis* (Erfurt and Sudre, 1996; Sudre and Erfurt, 1996) and persisted up to the end of the Oligocene (MP29). This form is distinguished from tragulines by a distinct molar pattern inherited from diacodexids.

The dichobunoid *Messelbunodon* from the Middle Eocene of Germany (Franzen, 1981) has elongated hindlimbs and strengthened middle metapodials and, in addition, differs from tragulines by a rather robust skull.

Homacodontine dichobunoids from the Early–Middle Eocene (Bridgerian to the Early Duchesnean) of North America were also too highly specialized to be considered as the ancestors of tragulines.

The skull of *Homacodon* (AMNH, no. 12695) from the Middle Eocene (Late Bridgerian) of Wyoming differs from the skulls of ancient tragulines in the structure of the ear region, which has a more advanced petrosal, and in some other progressive cranial characters: a more posterior position of the anterior edge of the orbits (above the M1 and M2 junction), a larger caliber and a higher position of the infraorbital canal, the lacrimal foramen positioned within the orbit, etc.

*Homacodon* also differs from hypertragulids in the absence of strong medial concavity in the posterior edge of the palatine.

The ear region of *Homacodon* is more progressive than those of early tragulines in a wider tensor tympani and a wider stapedial muscle fossae; in more anterior positions of the tympanic aperture of the facial canal, tensor tympani fossa, and meatus acusticus externus; in a more lateral position of the fossa for the stapedial muscle; in a larger epitympanic recessus; and in a narrower mastoid process.

Tragulines are relatively more conservative in the petrosal anatomy, approaching the petrosal of the Late Cretaceous arctocyonid *Protungulatum*, the oldest known ungulate, and only slightly differing from the trisulcate petrosal pattern of ancient eutherians (Cifelli, 1982; MacIntyre, 1972).

The homacodontine *Mesomeryx* from the Late Eocene of North America has progressive quadrangular molar crowns with a less projecting anterolingual corner and more selenodont cusps than tragulines.

Amphimerycids, considered to be possible ancestors of tragulids, gelocids, and hypertragulids (Matthew, 1929; Colbert, 1941; Simpson, 1945), or only of hypertragulids (Webb and Taylor, 1980), could not be the ancestors of the Tragulina because of peculiar and

high specialization that is quite different from traguline specialization. In particular, amphimerycids are more advanced in the number of molar cusps and selenodonty. They had a crescentic paraconule and hypocone.

The placement of dichobunoids or amphimerycids at the base of the traguline lineage based on tooth structure, which is supported by many researchers, requires the postulation that a simplification of the molar pattern and a reduction of the paraconule and hypocone occurred during the early evolution of tragulines. However, in all traguline groups (as in dichobunoids and amphimerycids), gradual complication of the molar pattern occurred, and this process proceeded from a more primitive stage than the stages typical of ancient dichobunoids, amphimerycids, and probably arctocyonids as well. Additionally, the dichobunoid and amphimerycid concepts of traguline origin assume a barely credible reversion of the cursorial adaptations, including their weakening in many aspects.

The close similarity of ancient tragulines to the most ancient primitive artiodactyls (diacodexids and dichobunoids) only attests to the fact that they have arisen from a common ancestor. The retention of many plesiomorphic characters shared with ancient eutherian mammals and the synapomorphies shared with the most primitive arctocyonids distinguish tragulines from other primitive artiodactyls and suggest a very low evolutionary level of traguline divergence. This supports the hypothesis of the pre-Eocene origin of tragulines and the whole order Artiodactyla.

#### MAIN EVOLUTIONARY TRENDS

The pattern of traguline evolution is rather complex. Besides peculiar defining characters, there are many cranial, dental, and postcranial features that evolved in parallel in various groups of the Tragulina. Most of them were associated with the initial adaptations to an herbivorous mode of life, fast locomotion, and the perfection of the senses and foot paraxony. These morphological changes were directed to maximize the energy profit of the structures.

The first true selenodont tragulines with well-pronounced cursorial adaptations appeared at the end of the Middle Eocene and in the Late Eocene when more open dry wood lands became widespread. They are *Gobiomeryx* in Asia, *Gelocus* in Europe, and *Hypertragulus* and *Leptomeryx* in North America. In the Oligocene, the diversity of such forms abruptly increased because of considerable aridization of the inner regions of Asia, North America, and certain mainland parts of Europe. Although all ancient tragulines, like their having counterparts, were forest-dwelling and mixed feeders, as living tragulids are, the proportion of coarse plant food in their diet first increased in certain Eocene

genera. Being mainly browsers and frugivores, they began to feed on coarser foliage and shoots. The change in mode of feeding was accompanied by fundamental changes in locomotion.

### Herbivorous Adaptations

Common adaptations to herbivory were displayed in an increase in the size of the masseter and pterygoid muscles and a decrease in the size of the temporal and digastric muscles, associated changes in the structure of the palate and muzzle and in dentition.

The main transformations in skull and dentition, shared by various traguline lineages, can be summarized as follows:

(1) Skull transformation caused by the perfection of the masticatory apparatus.

(1.1) Changes caused by an increase in the masseter and pterygoid muscles and horizontal displacement of their attachment sites closer to the jaw joint.

A greater development of the masseter and pterygoid muscles indicated a gradual pass of the function of the main jaw adductor from the temporal muscle to the masseter and very likely reflected the formation of a transverse direction in chewing motion of the jaws in some ancient tragulines.

Increased development of the muscles was expressed in the larger and sharper sites of their attachment. An increase in the mechanical efficiency of the masseter was displayed by an increase in the maxilla height, the elongation of the facial crest, enlargement of the facial tuber and the angular process of the mandible, and by a decrease in the posterior protrusion of this process. The relative anterior displacement of the posterior edge of the angular process also allowed the pterygoid muscles to work more efficiently. The action of the pterygoid group of muscles also became more efficient by the enlargement of the process.

A greater mechanical efficiency of the masseter was also achieved by increasing the height of the jaw joint and by the posterior displacement of the masseter attachments closer to the joint.

These transformations led to an increase in the moment arm for the action of the masseter and pterygoid muscles. The most primitive genera in this respect were *Archaeomeryx* and *Lophiomeryx*. However, the latter was more advanced in a higher position of the jaw joint and a slightly broader angular process. The changes in these directions were well pronounced in *Leptomeryx* and *Bachitherium* and particularly strong

in Recent tragulids. These changes reached the greatest development in pecorans.

(1.2) Changes caused by a decrease in the development of the temporal muscle.

A decrease in the development of the temporal muscle was reflected in a decrease in the temporal area, a shortened sagittal crest, a high position of the coronoid process, and in the diminution in the height of the coronoid.

A decrease in the moment arm of the muscle was compensated by the approach of the resultant force to a more vertical direction and by a decrease in the antero-posterior distance between the coronoid and the articular processes.

The most primitive structure is in *Archaeomeryx*. The genera *Hypertragulus*, *Praeartagulus*, *Leptomeryx*, and *Bachitherium* share a relatively primitive stage of the development of the sagittal crest with an advanced, almost vertical position of the coronoid process. The weakest known sagittal crests and coronoid processes, placed almost vertically and close to the jaw joint, are found in Recent tragulids and approach advanced pecorans in this respect.

(1.3) Weakening of the digastric muscle.

The digastric muscle was apparently well developed in *Archaeomeryx* and *Lophiomeryx*, which have well-pronounced attachment points on the ventral faces of the mastoid and in the middle of the lower part of the horizontal ramus of the mandible. The digastric muscles are very weak in Recent tragulids and pecorans.

(2) The elongation and enlargement of the muzzle.

The elongation and enlargement of the muzzle were adaptations that provided (1) an increase in the volume of food that could be masticated; (2) an increase in the respiratory surface in support of cursorial adaptations (Greaves, 1991); (3) an increase in the masseter size and the facial tuberosity (the area of the muscle origin); and (4) an increase in the tongue length and the mobility of the upper lips for a better manipulation of plant food.

According to the data on pecorans, grazers have a more slender muzzle than browsers (Solounias and Dawson-Saunders, 1988). Among pecorans, the narrowest muzzle is typical of the mixed feeders that inhabited open landscapes.

The narrowest muzzles in tragulines are in *Prodremotherium*, *Hypertragulus*, *Leptomeryx*, and *Hypisodus*, which lived in open woodlands (Flerov, 1938; Webb, 1998); the most elongated muzzle is in *Gelocus*.

Apart from the anterior elongation by the development of the diastemata, there are several other ways of enlargement and elongation of the oral cavity:

(1a) by the elevation of a part of the palate in front of P2 or P3 (in *Hypertragulus*, *Simimeryx*, *Leptomeryx*,

and *Dorcatherium*); or (1b) without this (in all others, including *Archaeomeryx* and *Lophiomeryx*);

(2a) by the posterior elongation of the palate (in traguloids); or (2b) without this (in hypertraguloids);

(3a) by the enlargement of the palate between the tooth rows accompanied by an increase in the curvature of the tooth row (in *Lophiomeryx* and *Hypertragulus*); or (3b) without such curvature (in *Archaeomeryx*, *Simimeryx*, and tragulids); and

(4a) by the appearance of a marked difference in the width between the parts of the palate in front of P2 (or P3) and behind it (in hypertraguloids and leptomerycids, a rather narrow anterior part remains in *Hypertragulus*, *Hypisodus*, and *Leptomeryx*); or (4b) without this (in others).

A marked difference in width between the parts of the palate in front of P2 and behind it might be related to a strong development of rumination and the retention of the ability to eat certain insects.

(3) The perfection of dentition and premaxilla.

Many dental adaptations to herbivory evolved in parallel among the Tragulina. The most important morphological changes are as follows:

(3.1) The reduction and loss of the upper incisors.

The loss of the upper incisors is typical of most tragulines. This correlates with a strengthening of the jaw adductors, strong closure of the jaws, and stress on the anterior (incisor) part of the muzzle. These features are accompanied by an increase in the mobility of the tongue and upper lip.

(3.2) Anterior elongation of the premaxilla and an increase in the downward inclination of its anterior part. These features allowed improved grasp and cutting of coarse plants and were particularly well pronounced in hypertragulids and leptomerycids.

(3.3) An increase in the cutting edge of the lower incisors on account of their enlargement and the inclusion of the lower canines in the incisor row.

Most tragulines, predominantly browsers, preserve the initial type of strongly curved incisor row, but usually with increased central incisors (*Lophiomeryx* and tragulids). The grazer-like forms, rare among tragulines, possessed a more straighter incisor row, and their incisors were almost equal in size (*Praetragulus gobiae* and *Leptomeryx*).

(3.4) The development of the diastemata.

(3.5) The disappearance of the upper and lower first premolars.

(3.6) An increase in selenodonty, including the development of the crescents and molarization of the premolars.

Balanced mixed feeders preserved weakly molarized and only slightly elongated premolars (*Archaeomeryx* and hypertragulids), whereas animals with a larger proportion of plants in the diet had stronger molarized and longer premolars (*Lophiomeryx* and *Gelocus*).

(3.7) An increase in the durability of the cheek teeth (owing to adaptations to coarse food) occurred by (a) an increase in the enamel durability (most developed in hypertraguloids and gelocids) and (b) an increase in the crown height (greatest in *Hypisodus*).

### Adaptations of Sensory and Respiratory Organs

The perfection of the respirator apparatus was emphasized in the following peculiarities:

(1) An increase in the anterior opening of the nasal cavity and choanae correlated with the development of cursorial adaptations.

(2) The elongation of the nasal cavity due to the elongation of the muzzle.

The elongation occurred in two ways: (a) posterior displacement of the choanae correlated with posterior extension of the palatines (in traguloids) or (b) anterior displacement of the choanae (in hypertraguloids), possibly as a compensation for the elongation of the muzzle.

The anterior displacement of the choanae may also be linked to early adaptation of breathing in a relatively arid environment and fast locomotion.

Common features in the perfection of the acoustic organs were expressed in the enlargement of the bulla, elongation of the external acoustic meatus, and the above noted changes in the petrosal.

### Cursorial Adaptations

The main trends associated with the perfection of the postcranial structure and more advantageous specialization are evident in the evolution of the Tragulina, particularly in the changes of the locomotor apparatus. Many similar modifications provided (1) the restriction (transformation) of feet motion to the parasagittal plane, (2) the consolidation of the limb bones required



for the strengthening of feet and their energy perfection, and (3) a greater speed to avoid predators.

A greater mechanical efficiency of the locomotor apparatus was attained by redistribution of the load in the articulations and limbs and by the simplification and elimination of some elements.

In addition, the elongation of the zygopodium and autopodium occurred independently and reached different levels in various lineages of Tragulina.

The most common trends in the development of the limbs were discussed in the previous chapter, and most can be summarized as follows:

(1) The replacement of hemispherical heads of the humerus and femur by semicylindrical heads.

(2) The elongation of the radius, enlargement of its epiphyses, and displacement of the triquetrum facet from the ulna to the distal epiphysis of the radius.

(3) The elongation of the tibia and an increase in the crural index.

(4) A weak lateral shift of the main body weight and enlargement of the lateral parts of the distal epiphyses of the humerus and femur and those of the proximal and distal epiphyses of the radius and tibia.

(5) A reduction of the ulna and fibula, and fusion of the radius and ulna and the tibia and fibula (the latter is most developed in *Hypertragulus*).

(6) A shortening and consolidation of the basipodium bones.

(7) Fusion of the magnum and trapezoid (except in hypertraguloids).

(8) Perfection of the malleolar articulation.

(9) An increase in the mobility of the tarsal joints in the parasagittal plane and restriction of lateral motions.

Transformation of the astragalus toward a pattern similar to that of pecorans, involving aligned and almost parallel proximal and distal trochleae and enlarged, relatively flattened, and extended sustentacular facet.

(10) The elongation of and tendency toward the fusion of metapodials III and IV and reduction of the side metapodials. Incomplete fusion between metacarpals III and IV is very rare among tragulines and occurred in highly specialized forms, such as *Prodremotherium*.

(11) An increase in digits III and IV and reduction of the side digits.

#### PHYLOGENETIC PATTERNS

Traguline evolution exhibited broad adaptive radiation against a background of increased habitat diversity.

The basal adaptive radiation of the Tragulina happened very early, judging by the low levels of diver-

gence of the main trends of the development of cranial, dental, and postcranial structures.

The divergence in cranial features began from a primitive brachycephalic type with a very weakly elongated snout.

The dentition diverged at the level of primitive procumbent incisors and canines, almost nonmolarized premolars, and incompletely quadricuspid molars with a very weak metaconule of M3 resembling in shape and structure the tribosphenic type of primitive eutherians and ancient *Protungulatum*-like arctocyonids. The divergence in the development of the limbs occurred at a level close to the generalized pentadactyl foot with only initial shifts to paraxony and cursorial adaptations. As shown above, the earliest stage of limb development in tragulines, seen in *Archaeomeryx* and *Miomeryx*, preceded the appearance of the double-pulley astragalus typical of most ruminants.

#### Traguloids and Hypertraguloids

The fundamental structure and many synapomorphies shared by traguloids and hypertraguloids support the close relationships between them. However, traguloids and hypertraguloids undoubtedly represented two separate lineages that may have arisen as a result of adaptive radiation of the basal traguline group.

A very profound dichotomy of tragulines into the traguloid and hypertraguloid lineages is corroborated by essential differences in the basicranial structure and in the peculiarities of specialization. This divergence was expressed in two main types of the morphology of the palate, two main directions of premolar molarization, two types of the basipodium, and in two different ways of strengthening the tibiofibular articulation. Moreover, traguloids and hypertraguloids are distinguished by numerous other sets of plesiomorphies, apparent in *Archaeomeryx* and *Hypertragulus* (Table 3).

*Archaeomeryx* is more primitive than *Hypertragulus* in the following characters:

- (1) a more brachycephalic skull;
- (2) a much longer and stronger projecting dorsally and posteriorly occipital crest;
- (3) a more anterior divergence of the temporal crests;
- (4) the absence of the alisphenoid canal;
- (5) primitive characters of the orbital mosaic;
- (6) the absence of the anterior protrusion of the nasals;
- (7) a short and ovoid anterior opening of the nasal cavity in dorsal view;
- (8) the presence of upper incisors;

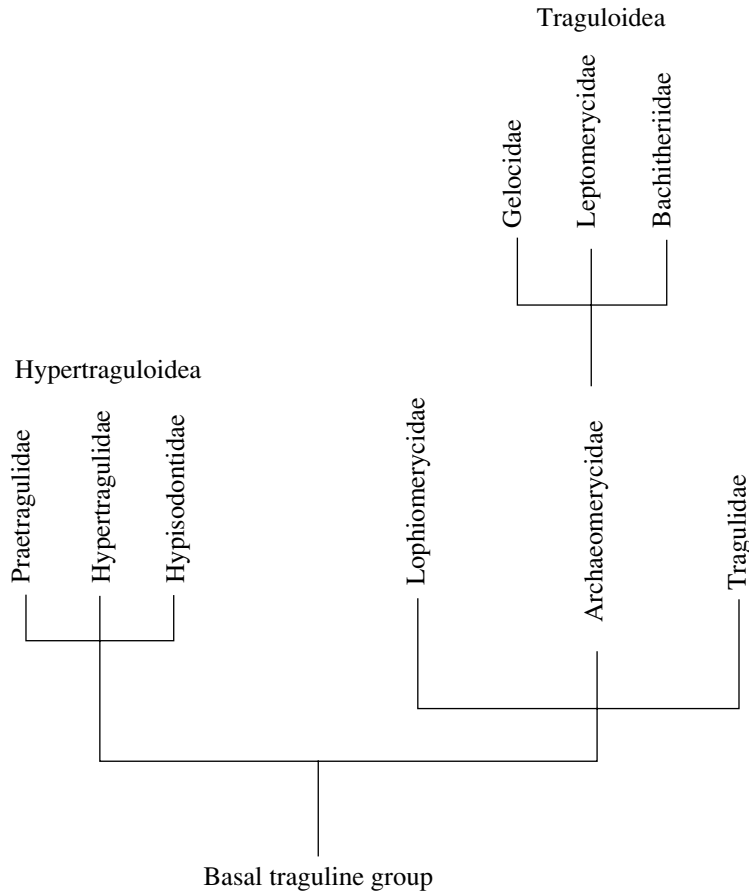


Fig. 19. Proposed relationships within the Tragulina.

- (9) a simple, not particularly thick molar enamel;  
 (10) a fused radius and ulna, etc.

The set of plesiomorphic characters of *Hypertragulus* includes

- (1) posteriorly open orbits;
- (2) a separate jugular foramen;
- (3) the presence of P1;
- (4) unicuspid anterior premolars; and
- (5) an unfused magnum and trapezoid.

In addition to these different sets of plesiomorphic characters, traguloids and hypertraguloids differ from each other in certain derived features of the skull, dentition, and postcranial skeleton, thus reflecting two main trends of traguline evolution. The most important defining characters of the groups are given in the chapter entitled *Classification*.

The first trend was connected with the earlier and rather gradual adaptation to plant food (expressed in the elongation of the palate, the formation of the diastemata between the canine and premolar row, reduction of P1, etc.) and more effective postcranial transformation. The

latter was reflected in the strong dorsoventral curvature of the basipodium, the fusion of the magnum and trapezoid, an early reduction of the distal part of the tibia to the malleolar bone, etc. This trend was followed not only by *Archaeomeryx* but also by many other traguloid groups, as well as extant tragulids and pecorans. *Archaeomeryx*, belonging to this main stream of ruminant evolution, was a widely adapted animal that lacked a narrow range of feeding specialization and was adapted to inhabit diverse landscapes (Vislobokova and Trofimov, 2000b).

The second trend was distinguished by a peculiar combination of primitive and very derived characters, probably reflecting a sharper and faster morphological transformation toward rumination and limb perfection. This trend was accompanied by a greater adaptation to relatively arid habitats.

Such adaptation was already displayed in Middle Eocene hypertraguloids in the disappearance of the upper incisors and in the development of certain important peculiarities of the cheek teeth and limbs. In contrast to ancient traguloids, early hypertraguloids possessed a stronger selenodonty, higher and more sym-

metrical molar crowns, a more symmetrical astragalus, and a longer autopodium. Derived characters were combined with the primitive structure of the anterior premolars and with the development of a harder distal tibiofibular joint. Hypertraguloids that followed this trend became extinct at the beginning of the Early Miocene, apparently because of an increase in the humidity of the climate. They showed certain parallelisms with early tylopods in the development of the dentition.

### Traguloids

At least six main lineages are traced within the traguloid stock, i.e., archaeomerycids, lophiomerycids, tragulids, leptomerycids, gelocids, and bachitheriids (Fig. 19).

The first three groups are part of the earliest adaptive radiation of traguloids that occurred not later than the Middle Eocene. The most primitive of them, archaeomerycids, undoubtedly belonged to the main stream of ruminant evolution.

Lophiomerycids. Lophiomerycids are very close to archaeomerycids in the set of plesiomorphic characters and are distinguished from the latter by certain features of the basicranium and dentition. Additionally, lophiomerycids (as well as gelocids) are more advanced in the herbivorous and cursorial adaptations.

Lophiomerycids are very similar to archaeomerycids in brachycephaly, lateral exposure of the mastoid, the lacrimal structure, the orbital mosaic, the absence of the alisphenoid and pterygoid canals, the shape and position of the promontorium fenestra vestibuli and the stapedial fossa, a primitive position of the posterior opening of the infraorbital canal in the maxilla, etc.

*Lophiomeryx* is more primitive than *Archaeomeryx* in certain cranial and dental characters (including the presence of both anterior and middle palatine foramina, a small postglenoid foramen, a very short facial part of the lacrimal, and short lingual conids of the lower molars) and undoubtedly represents one of the earliest traguloid lineages.

The most important synapomorphies of lophiomerycids include the following:

- (1) the position of the petrosal closer to the parasagittal plane and strongly pressed to the basioccipital and alisphenoid;
- (2) a close contact between the postglenoid process and the auditory bulla;
- (3) an almost straight posterior median edge of the palate;
- (4) a reduced paraconid of the lower premolars;
- (5) a reduced mesostyle of the upper molars; and
- (6) central metacarpals and metatarsals almost equal in length.

Lophiomerycids are also more advanced than archaeomerycids in the trend of the premolar molarization and in the development of the malleolar bone.

Lophiomerycids and tragulids altogether are more advanced than archaeomerycids in the following characters:

- (1) the ruminant type of the anterior opening of the nasal cavity;
- (2) a stronger enlarged upper canine;
- (3) a more elongated snout and longer diastemata between C1–P2 and c1–p1;
- (4) a stronger elongation of the premolars; and
- (5) higher crowns of the cheek teeth.

Besides, lophiomerycids and tragulids were evolutionarily more advanced than archaeomerycids in the following cursorial adaptations:

- (1) transformation of the astragalus to the double-pulley form (but with nonparallel trochleae) usual for most ruminants;
- (2) elongation of limbs;
- (3) a decrease in the difference in length between the fore and hind limbs;
- (4) diminution of the inclination to the ground of the autopodium;
- (5) a decrease in the difference in length between the metacarpals and metatarsals;
- (6) an increase in the angles of the limb joints;
- (7) a strong enlargement of the central metapodials; and
- (8) reduction of metatarsals II and V to stylets.

Tragulids. Tragulids are distinguished from archaeomerycids in such symplesiomorphies as (1) the presence of both the anterior and middle palatine foramina and (2) the absence of the postglenoid process.

The defining characters of tragulids, besides the features of the basicranium (posterior extension of the palatine bone, expanded auditory bulla, etc.), are the development of the *Dorcatherium* fold and concave malleolar articulation, enumerated by Webb and Taylor (1980), also include the following synapomorphies:

- (1) a non-robust postorbital bar (consisting mostly of the jugal);
- (2) a pattern of the orbital mosaic close to the pecoran type;
- (3) the displacement of the infraorbital canal to the incisure of the inferior edge of the lacrimal (as in pecorans); and
- (4) the development of the pterygoid canal.

Tragulids are evidently more advanced than archaeomerycids and lophiomerycids in the enlargement of the braincase; transformations of the masticatory apparatus, orbital region, and petrosal; an enlarged lacrimal both in facial and orbital parts; the absence of p1; the

co-ossification of the distal part of the fibula with the tibia; and the fusion of metatarsals III and IV. The tragulid petrosal differs from that of archaeomerycids and lophiomerycids in a larger fenestra vestibuli, a broader tensor tympani fossa, and a more anterior position of the tensor tympani fossa.

**Leptomerycids, Gelocids, and Bachitheriids.** More advanced groups, leptomerycids, gelocids, and bachitheriids, arose during the next Eocene adaptive radiation of traguloids. These groups, as higher ruminants, are the descendants of archaeomerycids. All were better adapted to plant feeding and more cursorial than their ancestors.

In addition to the characters of specialization, leptomerycids, gelocids, and bachitheriids possessed the basic traguloid structure inherited from archaeomerycids. However, they usually possessed more advanced modifications of that structure represented by different sets of characters in distinct groups.

It is important to note that the specialization stayed within certain limits of traguloid structure. None of the advanced traguloid groups reached the level of selenodont mastication and rumination developed in pecorans. This is very apparent in the primitive structure of their masticatory apparatus, the level of premolar molarization, the molar structure, and the enamel ultrastructure. Likewise, advanced traguloids apparently did not have a true functional ruminant stomach judging by the absence of a psalterium and a primitive, non-pecoran abomasum in the stomach of Recent tragulids. All advanced traguloids were also less adapted to fast running than pecorans. In traguloids, the level of specialization of the postcranial skeleton and simplification of limbs remained lower than in pecorans.

Leptomerycids, gelocids, and bachitheriids preserved such characters as a posterior position of the foramen ovale; a non-inflated auditory bulla; the development of the postglenoid process; and the separate central metacarpals (with the tendency to be partly fused in some gelocids). In addition, gelocids and bachitheriids retained the following characters: a strong, long sagittal and well-developed short temporal crests; a moderate postglenoid foramen; relatively small orbits; a low position of the infraorbital canal; and the structure of the palate.

Leptomerycids inherited many peculiarities of cranial, dental, and postcranial structures (including the form of the postorbital bar) from archaeomerycids and differ from them mostly in the higher level of their development (including a more expanded braincase, derived changes in the basicranium, orbital mosaic pattern, and derived enamel ultrastructure).

The main synapomorphies of leptomerycids are as follows:

(1) almost confluent optic foramina (resembling those of tragulids);

- (2) a long, slitlike foramen ovale;
- (3) large parietal foramina;
- (4) the presence of the pterygoid canal (as in tragulids); and
- (5) enlarged and procumbent lower incisors.

Together with many apomorphic characters of the skull, teeth, and limb bones, shared by leptomerycids with tragulids and pecorans, these features clearly distinguish leptomerycids from archaeomerycids and confirm the family level of this group.

Besides the common plesiomorphies with leptomerycids and bachitheriids, gelocids resemble archaeomerycids in the following plesiomorphic characters:

- (1) a very narrow brachycephalic skull;
- (2) a primitive pattern of the orbital mosaic;
- (3) the absence of the alisphenoid and pterygoid canals;
- (4) the posterior position of the tensor tympani and stapedial muscle fossae;
- (5) a low position of the lacrimal foramen (close to the jugal-lacrimal contact);
- (6) a primitive position of the posterior opening of the infraorbital canal (in maxilla);
- (7) a short anterior dorsal process of the jugal; and
- (8) a long symphysis of the mandible.

However, gelocids are more advanced than archaeomerycids in the following characters:

- (1) the loss of the stapedial artery;
- (2) an enlarged stapedial muscle fossa;
- (3) a very shallow subarcuate fossa;
- (4) thinner bone over the promontorium [(1–4) are after Webb and Taylor (1980)];
- (5) an enclosed postglenoid foramen;
- (6) a large fenestra vestibuli;
- (7) occipital mastoid exposure;
- (8) better developed selenodonty;
- (9) the presence of Hunter-Schreger bands in some genera; and
- (10) considerable elongation of the forelimbs (almost equal in length in *Prodremotherium*, etc.).

The most important synapomorphies for gelocids are as follows:

- (1) a strongly elongated snout;
- (2) a large ovate foramen ovale;
- (3) the postorbital bar consisting mostly of frontal;
- (4) a large fenestra vestibuli;

- (5) the auditory bulla in a short distance from the basioccipital and postglenoid process;
- (6) spatulate and enlarged first lower incisors;
- (7) a premolariform p1; and
- (8) lost metastylid in the lower molars.

From archaeomerycids, bachitheriids retained the small orbits, low position of the infraorbital canal, and the primitive structure of the palatine.

The main synapomorphies of bachitheriids are as follows:

- (1) a robust postorbital bar consisting mostly of the jugal;
- (2) a small auditory bulla pressed to the postglenoid process and to the basioccipital;
- (3) a caniniform p1; and
- (4) a distinct pattern of the lower premolar molarization.

These characters reflect peculiar trends of the evolution of bachitheriids within traguloids.

Leptomerycids, gelocids, and bachitheriids share a number of derived cranial, dental, and podial features resembling those of the Pecora and the Tragulidae. These features include, in particular, a developed protocone on P2 and P3, a complex talonid on dp3, a developed entoconid on the lower premolars, a double-pulley astragalus, the fusion of metatarsals III and IV, and the strongly reduced side metapodials (Webb and Taylor, 1980; etc.). Due to these apomorphic characters, leptomerycids and gelocids were regarded by some researchers as ancestral groups to the higher ruminants (Schlosser, 1886), and bachitheriids and some gelocids were even included in pecorans (Webb and Taylor, 1980; Geraads *et al.*, 1987; Moyá-Solá, 1988; Scott and Janis, 1992).

Common pecoran apomorphic characters of leptomerycids, gelocids, and bachitheriids also include the following:

- (1) a well-developed ethmoidal fissure;
- (2) typical ruminant anterior opening of the nasal cavity;
- (3) confluence of the jugal foramen with the posterior lacerate foramen;
- (4) the occipital mastoid exposure and position of the mastoid foramen in the mastoid–occipital suture;
- (5) a slightly enlarged auditory bulla with a longer external acoustic meatus than in *Archaeomeryx*;
- (6) the stylohyoid vagina encroaching upon the auditory bulla;
- (7) a short supraorbital sulcus that ends at the posterior border of the ethmoidal fissure;
- (8) the position of the nasofrontal suture opposite or anterior to the antorbital rim;

- (9) the nasals posteriorly widened;
- (10) an expanded facial part of the lacrimals;
- (11) reduced upper incisors;
- (12) enlarged upper canines;
- (13) higher than in archaeomerycids stage of premolar molarization; and
- (14) a well-developed malleolar bone, and typical early ruminant cursorial adaptations similar to these in lophiomerycids and tragulids.

In addition, gelocids and leptomerycids share the presence of the promontory sulcus, a lingual elaboration of the lower premolars, and a concavoconvex articulation between the calcaneum and the malleolar bone; gelocids and bachitheriids together possess an enclosed postglenoid foramen; leptomerycids and bachitheriids are linked by enlarged lacrimals both in facial and orbital parts.

Almost all these characters (except the enlargement of the ethmoidal fissure, the position of the mastoid and mastoid foramen, and the position of the anterior ends of the supraorbital sulcus) are shared by leptomerycids, gelocids, bachitheriids, and tragulids.

Leptomerycids, whose morphology is known better than that of gelocids and bachitheriids, display even more resemblance to Recent tragulids:

- (1) the presence of the pterygoid canal;
- (2) the orbital mosaic pattern;
- (3) the level of complication of the promontorium;
- (4) the position of the stapedia fossa (displaced anteriorly at the level of the fenestra vestibuli); and
- (5) mostly squamosal lateral wall of the epitympanic recess.

The comparative morphological data confirm the position of gelocids and bachitheriids within traguloids but not among pecorans. The results obtained support the classical views of Matthew (1929), Colbert (1941), and Simpson (1945), and are in direct contradiction to most cladistic analyses based mainly on apomorphic characters of teeth and limbs. These characters refer to the usual herbivorous and cursorial adaptations (often in their rather advanced states) and might have developed in parallel in various ruminant groups.

Despite numerous similarities, between pecorans and leptomerycids, gelocids, and bachitheriids the latter three could not be their ancestors, but may be regarded as their sister groups. All differ from pecorans in quite peculiar directions of their specialization seen, in particular, in their synapomorphies.

By some derived features, these groups of traguloids often were more advanced than ancient pecorans. Leptomerycids surpassed the ancient cervoid pecorans in the high development of the ethmoidal fissure and in a closed position of the optic foramina. Gelocids evolved

further than the early pecorans in the elongation of the snout and in the enlargement of the fenestra vestibuli, accompanied by a considerable elongation of the forelimbs. Bachitheriids developed a strongly enlarged caniniform p1 and, in addition, had a peculiar postorbital bar.

The less specialized archaeomerycids, possessing the important "prepecoran" set of characters, appear to be more plausible ancestors for pecorans. In their structure, archaeomerycids were closer to the basal branches of higher ruminants than other traguloids, which showed peculiar specialization.

### Hypertraguloids

The relationships within hypertraguloids were recently analyzed by Webb (1998) and Vislobokova (1998).

According to Webb (1998), *Parvitrágulus* and *Simimeryx*, which are linked by the caniniform p1 and the loss of the mesostyle, compose a sister group to other hypertraguloids (*Hypertragulus*, *Nanotragulus*, and *Hypisodus*). In Webb's cladogram, *Hypertragulus* and *Hypisodus* have more similarities and share narrow premolars, an increased hypsodonty, the loss of the paraconule, and a diastema behind p2; *Hypertragulus* and *Nanotragulus* share a diastema behind P2; and *Hypisodus* is characterized by extreme root hypsodonty, the loss of upper teeth anterior to P3, and a flexed cranium (Webb, 1998).

New data on Asian hypertraguloids confirm an early divergence of hypertraguloids into three main branches: hypertragulids, hypisodontids, and praetragulids.

These groups share such important primitive conditions as:

- (1) a brachycephalic cranium;
- (2) a separate jugular foramen;
- (3) the absence of the pterygoid canal;
- (4) the lateral exposure of the mastoid; and
- (5) an unfused magnum and trapezoid.

Their main synapomorphies include the following:

- (1) a high frontal process of the lacrimal;
- (2) a strong median concavity of the posterior border of the palate;
- (3) an enlarged auditory bulla with medium long external acoustic meatus;
- (4) simplification of the premolars to a conical shape;
- (5) shortening of the premolar crowns at the expense of the anterior part;
- (6) external enlargement of the upper molars;
- (7) a decrease in size and compression of the parastyle;
- (8) the reduction of the mesostyle;
- (9) a decrease in the paraconid and entoconid on the premolars;
- (10) co-ossification of the radius and ulna;
- (11) co-ossification of the tibia and fibula; and
- (12) a double-pulley astragalus.

Being better adapted to coarser food and to faster running than most other contemporaneous traguline groups, hypertraguloids could exist in relatively arid environments and open landscapes. This is seen in the structure of their sense and respiratory organs, teeth, and limbs. Anterior displacement of the choanae and a well-developed auditory bullae could be within such adaptations. The choanae and auditory bullae are the most enlarged in hypisodontids.

As a whole, hypertraguloids were not highly specialized to herbivory but demonstrate one of the first attempts to develop certain herbivorous adaptations. The skull transformations to herbivory were not so advanced as those in some gelocid traguloids. The resistance of molars to wear developed through an increase in crown height and enamel density (mainly the frequency of prisms); both characteristics were maximum in hypisodontids. The enamel structure did not reach the stage of development typical of some traguloids (Vislobokova and Dmitrieva, 2000).

Hypertraguloids are more advanced than many traguloids in the double pulley astragalus, the elongation of limb bones, and partial co-ossification of the radius and ulna, the tibia and fibula, and in the perfection of the tarsal joints. These derived conditions were combined with the primitive structure of the basipodium, the unfused magnum and trapezoid, and other plesiomorphic characters.

Hypertragulids, hypisodontids, and praetragulids differ clearly in different sets of plesiomorphic features, adaptation trends, and other apomorphies.

Among early hypertraguloids, there were three main types of dentition transformations corresponding to these three lineages and representing three adaptive strategies:

(1) In hypertragulids with small or medium-sized upper canines, the small lower canines are included in the incisor row, as in many early traguloids, and the diastemata are developed, not only behind the lower canine and between p1 and p2, but also between p2 and p3.

(2) Praetragulids, with enlarged upper canines and small lower canines incompletely included in the incisor row, lose P1 and p1 very early and develop C-P2 and c-p2 diastemata that are characteristic of most tragulines. In this group, the early reduction of p1 seems to correlate with the early increase in upper canine size.

(3) Hypisodontids with small or vestigial upper canines and incisiform lower canines were advanced in the greater reduction and simplicity of the anterior upper premolars (lost P1, vestigial P2, and small trenchant P3) and molar hypsodonty.

Being relatively weakly specialized hypertraguloids, praetragulids share more similarities with primitive traguloids than other groups. Among these features are the following:

- (1) a short snout and symphysis;
- (2) a relatively small and posteriorly open orbits; and

(3) a weak promontorium, corresponding to the main whorl of the cochlea.

The latter two features remain in hypertragulids as well.

*Praetragulus* and *Simimeryx* also resemble primitive traguloids in:

- (1) the low position of the articular process;
- (2) a very weak backward inclination of the anterior edge of the coronoid process;
- (3) a strongly posteroventrally projecting angular process;
- (4) a weak molarization of the premolars;
- (5) a short crest of the entoconid;
- (6) a non-crescentic metaconule on M3;
- (7) a unicuspid talonid of m3; and
- (8) the brachyodonty.

*Praetragulus*, the most primitive member of the family, retains small lower canines, a wide and rounded parastyle, a developed mesostyle, a distally detached fibula, etc. However, it is close to other praetragulids and hypertraguloids in the tendency to reduce the parastyle and mesostyle and to fuse the radius and ulna. *Praetragulus gobiae* resembles grazerlike forms in its almost straight incisor row.

Praetragulids share such derived features with hypertragulids as the following:

- (1) the presence of the alisphenoid canal;
- (2) the displacement of the foramen ovale to the midlength of the alisphenoid;
- (3) enlarged fenestra vestibuli; and
- (4) the presence of the promontory sulcus.

Hypertragulids and hypisodontids perhaps represent mixed feeders inhabiting open landscapes, judging from their elongated muzzles with a narrow rostrum, and the marked difference in the width between its anterior part and the region behind P2, pointed premolars, and strongly crescentic and high crowned molars. These features are strongly expressed in *Hypisodus*. Despite these similarities, these families represent different evolutionary trends seen in skull and dentition transformation.

Hypertragulids are most primitive within hypertraguloids in the small peariform anterior opening of the nasal cavity, procumbent upper canines, the presence of P1, unicuspid anterior lower premolars, pentadactyl manus, and in the retention of a reduced digit I. In the presence of a pointed P1, they resemble primitive tylopods. The main synapomorphies of hypertragulids are as follows:

- (1) inflection of the basicranial axis;
- (2) the position of the posterior opening of the infraorbital canal at the junction between the lacrimal and maxilla;
- (3) the presence of only the middle palatine foramen;
- (4) enlarged caniniform P1 and p1;

- (5) compressed parastyle;
- (6) the absence of the mesostyle;
- (7) fused radius and ulna; and
- (8) fused tibia and fibula.

*Hypisodus*, the only member of the highly specialized hypisodontids, was the smallest and most rabbit-like artiodactyl (Meehan and Martin, 1997). Among the main plesiomorphies of *Hypisodus*, there are procumbent lower incisors.

This genus was probably convergent on the rabbit ecomorph.

*Hypisodus* shares a number of advanced characters with leporids, such as: a narrow rostrum, large orbits, high crowned molars, an enlarged auditory bulla with an upward oriented external acoustic meatus of large diameter, slender elongated limbs, and a short tail. These animals may have used burrows, as do some rabbits, certain pigs (warthog), and some oreodont tylopods (Meehan and Martin, 1997). Articulated specimens were found in well-preserved borrows in the Orellan community in Wyoming (Meehan and Martin, 1997). The strongly enlarged auditory bullae could be adapted to arid conditions, as well as to a nocturnal mode of life. The enlarged choanae may be an adaptation to a dry climate and may also be associated with more active running.

Being obviously functionally didactyl, *Hypisodus* has more advanced cursorial adaptation than other hypertraguloids. The manus of *Hypisodus* has a reduced digit V and, probably, a reduced digit II (Meehan and Martin, 1997). This genus also has more developed limb articulations, which are more efficient for the parasagittal plane movement of the limbs.

The other synapomorphies of *Hypisodus* include the following:

- (1) a strongly inflected basicranial axis;
- (2) a preorbital fossa;
- (3) small and vestigial upper canines;
- (4) incisiform lower canines;
- (5) a caniniform p1;
- (6) a more central position of the main body weight in limbs and a displacement of the triquetrum facet to the radius;
- (7) the fusion of the ulna and radius;
- (8) the elongation of the tibia and fibula; and
- (9) the elongation and compression of the central metapodials.

The crural index of *Hypisodus* is high (about 1.3), and central metacarpals and metatarsals are almost equal in length.

## Chapter 4

## DISPERSAL OF TRAGULINES

Traguloids have occurred in both Eurasia and North America since the Middle Eocene (Fig. 20). Three groups, archaeomerycids, lophiomerycids, and bachitheriids, seem to exist in only Eurasia. Gelocids and tragulids occurred in Eurasia and Africa. In America, traguloids were represented by leptomerycids and gelocids.

Hypertraguloids, mainly North American groups, were spread from the late Middle Eocene (Late Uintan) through the beginning of the Oligocene in both the Old and New Worlds and up to the Early Miocene in North America. The presence of *Hypertraguloidea* gen. et sp. is reported from the Middle Eocene Khaichin Ula II Fauna from Mongolia (Badamgarav and Reshetov, 1985). In the Late Eocene to the Early Oligocene of Mongolia, hypertraguloids were represented by *Praetragulus* (Vislobokova, 1998).

Although there is no direct evidence on the place of origin of tragulines, Asia seems to be very plausible as the site of their early development. During the Late Cretaceous, Asia was a very large continent with very diverse biotopes. Possible ancestors of artiodactyls had already existed there. The primitive structure and a large diversity of Eocene tragulines in Asia also confirms the Asian origin of this group (Vislobokova, 1997).

Six traguline genera occurred in the Middle Eocene of Asia. The most ancient of them were represented by the archaeomerycids *Archaeomeryx* and *Xinjiangmeryx*. *Archaeomeryx* is known in the Irindinmanhan and Sharamurunian mammal ages of China, which are correlated to most of the Rhenanian (Late Lutetian to Early Bartonian, MP12–MP16) of western Europe and to the Uintan of North America (Matthew and Granger, 1925b; Tong *et al.*, 1995). This genus was widespread in Central Asia, including Mongolia and Kazakhstan (Gabounia, 1977; Vislobokova, 1990b). *Xinjiangmeryx* is known from only the Sinkiang fauna of the Tufan Basin, China (Zheng, 1978). The four other genera appeared at the end of the Middle Eocene. Among them, the archaeomerycids *Miomeryx* and *Notomeryx* and the lophiomerycid *Lophiomeryx* were found in

China (Matthew and Granger, 1925a; Miao, 1982; Qiu, 1978) and the lophiomerycid *Indomeryx* was reported from Burma and China (Pilgrim, 1928; Qiu, 1978).

At the Middle–Late Eocene boundary (about 38 Ma), the diversity of tragulines in Asia sharply increased: the gelocid *Gobiomeryx*, the tragulid *Krabimeryx*, and the hypertraguloid *Praetragulus* spread in Asia (Matthew and Granger, 1925a; Trofimov, 1957; Ducrocq, 1992; Vislobokova, 1998; Wang, 1992).

At least three adaptive radiation events preceded the diversity of tragulines in Asia. The two first of them happened earlier than 49 Ma. The first radiation led to the appearance of the traguloid and hypertraguloid branches. During the second radiation, traguloids were divided into archaeomerycids, lophiomerycids, and tragulids. The third radiation was in the late Middle Eocene and gave origin to gelocids and, probably, leptomerycids. At the same time or later, at the Eocene/Oligocene boundary, bachitheriids branched out from archaeomerycids.

Hypertraguloids and ancestors of leptomerycids dispersed into North America apparently at the end of the Middle Eocene (not later than 41 Ma). The most ancient hypertraguloid *Simimeryx* is known from the Late Uintan of California and the central Great Plains (Stock, 1934; Webb, 1998). The first appearance of the leptomerycids *Leptomeryx* and *Hendryomeryx* happened at the Early–Late Uintan boundary (Leidy, 1853; Black, 1978; etc.). The adaptive radiation of hypertraguloids, with the appearance of *Parvitragulus*, *Hypertragulus*, and *Hypisodus*, occurred at the end of the Middle Eocene at the Late Uintan–Duchesnean boundary (about 39.5 Ma) (Webb, 1998). During the Oligocene, tragulines developed independently in Asia and America.

In the Late Eocene, gelocids penetrated into Europe (Pavlow, 1900), which was almost completely isolated from Asia. The first adaptive radiation of gelocids in Europe evidently occurred in the middle of the Late Eocene (later 35.5 Ma): *Gelocus* and *Phaneromeryx* are found in France in the faunas correlated to the MP19 zone



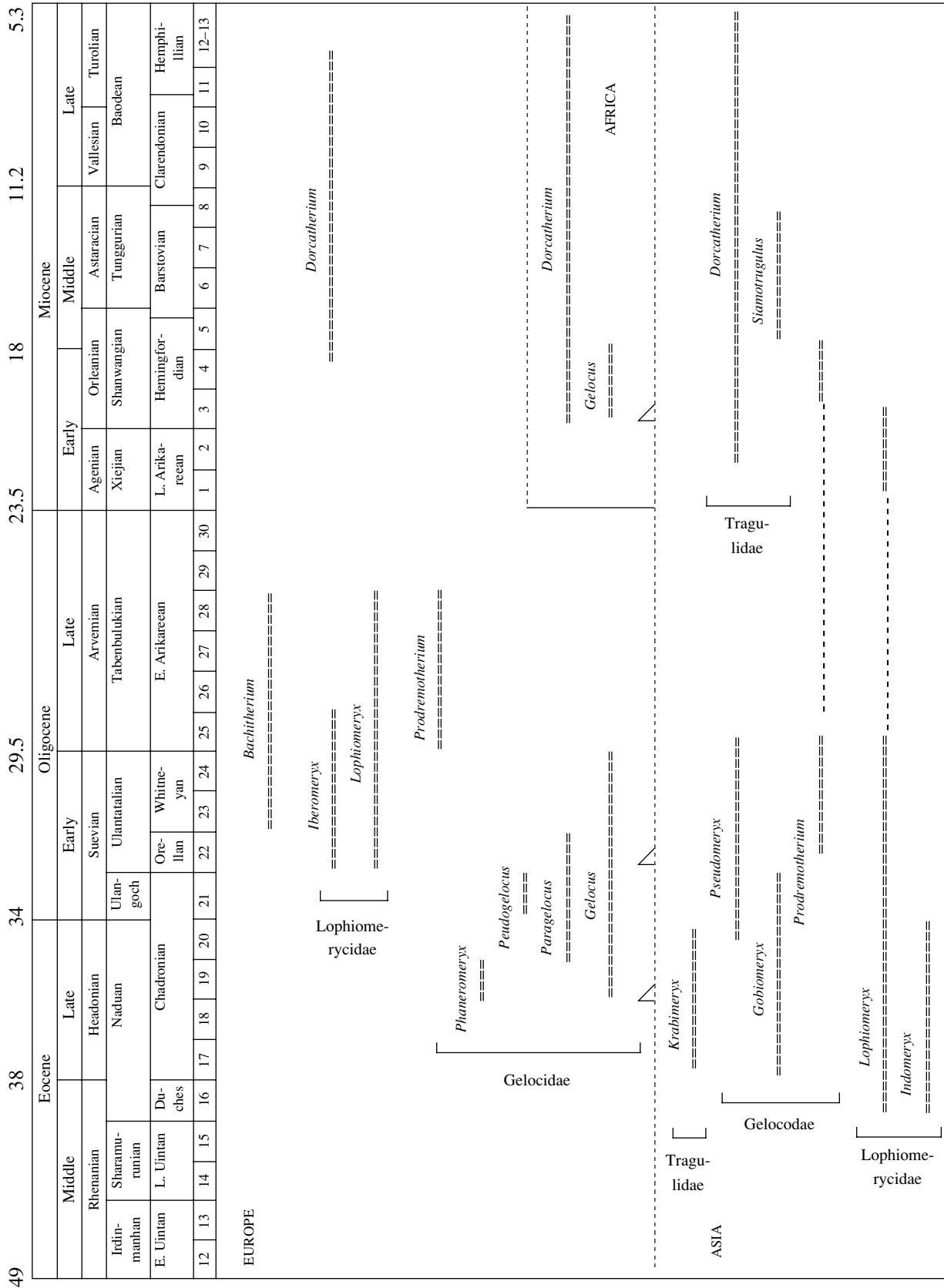


Fig. 20. Eocene-Miocene occurrence of the Tragulina and the main dispersal dates (indicated by triangles).

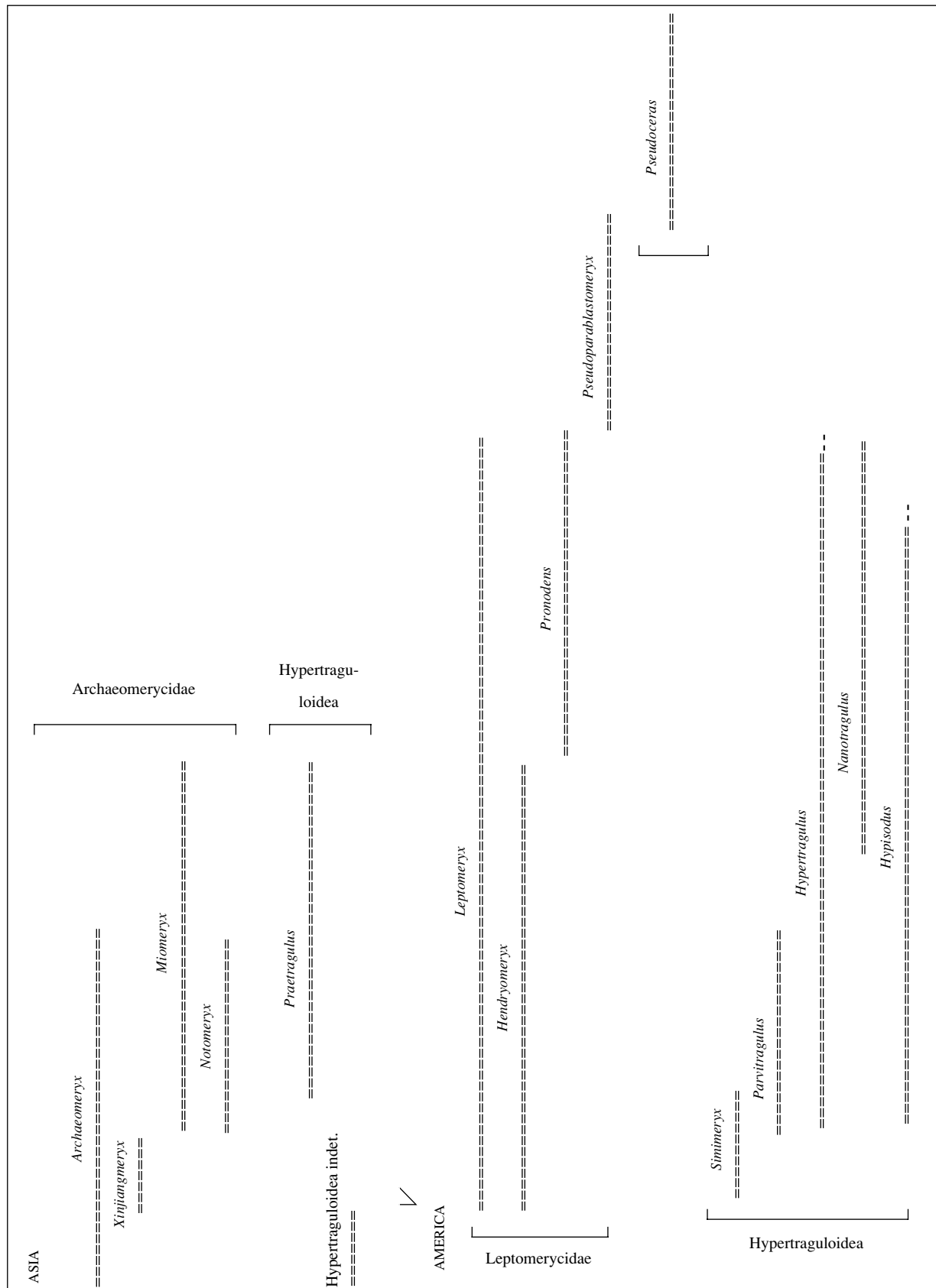


Fig. 20. (Contd.)

and *Paragelocus* is known from the MP20 zone in Germany (Blondel, 1996; Sudre and Blondel, 1996; etc.).

The gelocids *Gelocus*, *Pseudogelocus*, and *Prodremotherium* became widespread in Europe after the Grande Coupure together with other Asian immigrants (Gervais, 1848; Filhol, 1876; Lydekker, 1885; Brunet and Jehenne, 1976; Heissig, 1978; Ginsburg and Huguency, 1987; Jehenne, 1987; *et al.*).

Later, at the beginning of the Early Oligocene (about 32 Ma, MP22), lophiomerycids dispersed into Europe. *Lophiomeryx* and *Iberomeryx* became common there (Gabounia, 1964; Sudre, 1995; etc.). In Asia, lophiomerycids reached the Indian subcontinent. *Lophiomeryx kargilensis* and *Iberomeryx savagei* are reported from the Upper Oligocene of Kargil basin in the Ladakh Himalaya (Nanda and Sahni, 1990).

Bachitheriids occurred in Europe during most of the Oligocene in the interval 31–26 Ma (MP23–MP28).

In the Late Oligocene (about 26 Ma), lophiomerycids and bachitheriids disappeared in Eurasia. In the Early Miocene, the ranges of the gelocids *Prodremotherium* and *Gelocus* decreased and were displaced in southern Asia. These genera were represented in the Bugti fauna of Pakistan (Pilgrim, 1912).

At approximately 21 Ma (MN3), *Gelocus* and the tragulid *Dorcatherium* first dispersed in Africa (Whitworth, 1958; Hamilton, 1973; Gentry, 1978, 1994). In

Europe and China, the first appearance of *Dorcatherium* was at the end of the Early Miocene (MN4) (Qiu and Gu, 1991; Gentry *et al.*, 1999).

In America, hypertraguloids became extinct during the early Miocene and leptomerycids did not survive after the Middle Miocene. The last occurrences of these groups, according to Webb (1998), are 17.5 and 11 Ma, respectively.

During the Miocene, gelocids also penetrated America but were represented by a single genus, *Pseudoceras*. Its occurrence was restricted by the Late Miocene (Webb, 1998).

At the end of the Early Miocene, most tragulines became extinct. In the Middle and Late Miocene, Eurasia was populated mainly by the tragulid *Dorcatherium* (Fahlbusch, 1985; Czyzewska and Stefaniak, 1994; Gentry *et al.*, 1999; etc.), which perhaps came from Africa. The first and last appearance of this genus in the Siwalik Sequences are dated as greater than 18 and 6.4 Ma, respectively (Barry and Flynn, 1990). In addition to this genus, the tragulid *Siamotragulus* is found in the Middle Miocene of Thailand (Thomas *et al.*, 1990) and *Yunnanotherium* is reported from the Late Miocene of China. Up to recent time, only two tragulid genera persist, *Tragulus* in Asia and *Hyemoschus*.

## Chapter 5

## CLASSIFICATION OF TRAGULINES

The Tragulina is regarded as an infraorder of the suborder Ruminantia within the order Artiodactyla.

Tragulines share with other ruminants the same adaptive trends in the changes of the digestive system and sense, respiratory, and locomotor organs.

This group possesses the following apomorphic features: reduction and loss of the upper incisors, inclusion of the lower canines in the incisor row, development of selenodonty, fusion of the cuboid and navicular, and development and perfection of the double-pulley astragalus.

The infraorder comprises nine families, which are divided into two superfamilies (Table 2). Due to priority, the taxonomic names Traguloidea and Hypertraguloidea are retained for them.

### Superfamily Traguloidea Gill, 1872

Families included: Tragulidae Milne-Edwards, 1864; Gelocidae Schlosser, 1886; Leptomerycidae Zittel, 1893; Archaeomerycidae Simpson, 1945; Lophiomerycidae Janis, 1987; and Bachitheriidae Janis, 1987.

Defining characters. Orbits closed posteriorly or open. Jugular foramen confluent with posterior lacerate foramen. Alisphenoid canal absent. Pterygoid canal absent or present. Mastoid exposure on lateral or occipital surfaces. Supraorbital sulci weakly convergent anteriorly or parallel. Facial part of lacrimal without high frontal process. Posterior border of palatine with weak medial concavity opposite or behind M3. Upper canines medium-sized or large. Lower canines incisiform. Premolars elongated or not shortened. Radius and ulna separate. Malleolar bone usually developed. Magnum and trapezoid fused. Metapodials III and IV separate or fused.

#### Family Tragulidae Milne-Edwards, 1864

Genera included: *Tragulus* Brisson, 1762; *Dorcatherium* Kaup, 1833; *Hyemoschus* Gray, 1845; *Yunnanotherium* Han, 1986; *Siamotragulus* Thomas, Ginsburg, Hintong, et Suteethorn, 1990; and *Krabimeryx* Ducrocq, 1992.

Defining characters. Braincase more enlarged and expanded than in other traguloids. Sagittal and temporal crests very weak. Sagittal crest short. Temporal crests curved posteriorly. Orbits large and closed posteriorly. Postorbital bar formed mostly of jugal. Postglenoid process absent. Auditory bulla large, inflated, with medium-long external acoustic meatus. Stylohyoid vagina deep, narrow, encroaching upon bulla, and enclosed posteriorly. Mastoid exposure mainly on lateral surface. Mastoid foramen large and lateral. Foramen ovale small and placed posteriorly. Pterygoid canal sometimes present. Promontorium well developed and elongated, with two posterior whorls, almost equal in

height. Fenestra vestibuli large. Tensor tympani fossa broadened, encroaching upon promontorium, and pocketed in medial wall. Stapedial muscle fossa placed opposite fenestra vestibuli. Subarcuate fossa deep and pocketed anteromedially. Lateral wall of epitympanic recess formed by squamosal. Lacrimal with enlarged facial and orbital parts and single lacrimal foramen within orbit. Posterior opening of infraorbital canal placed between lacrimal and maxilla. Nasofrontal suture anterior to orbits. Ethmoidal fissure absent or very small and mainly triangular. Nasals relatively short, gradually narrowed anteriorly, and strongly projecting above anterior opening of nasal cavity. Upper incisors absent. Lower i1 enlarged. Upper canine in males enlarged, not procumbent, and almost vertical in lateral view. P1 and p1 absent. *Dorcatherium* fold often present. Radius and ulna separate. Fibula usually fused distally with tibia. Metacarpals III and IV separated. Astragalus with almost parallel trochleae. Calcaneum with concave fibular facet. Metatarsals III and IV fused.

Comments. Following Gentry (1978), *Dorcabune*, known only from dental materials (Pilgrim, 1910), is excluded from the family composition. It is most probably an anthracotheriid, as Gentry (1978) suggested.

#### Family Gelocidae Schlosser, 1886

Genera included: *Gelocus* Aymard, 1855; *Phaneroemeryx* Schlosser, 1886; *Prodremotherium* Filhol, 1877; *Paragelocus* Schlosser, 1902; *Pseudogelocus* Schlosser, 1902; *Pseudoceras* Frick, 1937; *Gobiomeryx* Trofimov, 1957; and *Pseudomeryx* Trofimov, 1957.

Defining characters. Skull brachycephalic, with braincase less enlarged and expanded and snout more elongated than in tragulids. Sagittal crest long. Temporal crests better developed than in tragulids and curved anteriorly. Postorbital bar complete, formed mostly by frontal. Postglenoid process developed. Foramen ovale large and ovate. Alisphenoid and pterygoid canals absent. Auditory bulla small, with medium-long external acoustic meatus. Stylohyoid vagina encroaching upon bulla. Mastoid exposure mainly on occipital surface. Mastoid foramen small and posterodorsal. Promontorium elongated, with two posterior whorls almost equal in height. Fenestra vestibuli small or large. Tensor tympani and stapedial muscle fossae broad and placed posteriorly. Subarcuate fossa shallow. Facial part of lacrimal small and triangular, with single lacrimal foramen within the orbit. Posterior opening of the infraorbital canal placed in maxilla. Ethmoidal fissure large and quadrangular. Nasofrontal suture anterior to orbit. Nasals longer than in tragulids, projected strongly above anterior opening of nasal cavity. Median concavity of posterior border of palatine opposite M3. Upper incisors absent. First lower incisors spatulate

and enlarged. Upper canines enlarged. Cheek teeth more strongly molarized with more developed crescents than in tragulids. P1 absent. In contrast to tragulids, the lower canine is still larger than i1 and premolar row relatively long. Lower p1 premolariform is reduced or lost. *Dorcatherium* fold absent. Odontoid process of axis shallow and spoutlike. Fore and hind limbs approximately equal in length. Radius and ulna, tibia and fibula separate. Fibula reduced to proximal rudiment and malleolar bone. Malleolar bone with almost parallel proximal and distal sides. Ecto- and mesocuneiform fused. Entocuneiform separate. Metapodials elongated. Metacarpals III and IV separate or incompletely fused. Metatarsals III and IV form cannon bone, with unclosed gully. Side metapodials strongly reduced. Astragalus of pecoran type, with almost parallel trochleae.

**Comments.** Schlosser (1886) included only two genera, *Gelocus* and *Prodremotherium*, in the Gelocidae.

Simpson (1945) increased the family to ten genera, *Gelocus*, *Prodremotherium*, *Indomeryx*, *Miomeryx*, *Phaneromeryx*, *Lophiomeryx*, *Cryptomeryx*, *Paragelocus*, *Pseudogelocus*, and *Bachitherium* (Pomel, 1853; Aymard, 1855; Filhol, 1877, 1882; Schlosser, 1886, 1902; Pilgrim, 1928). Trofimov (1957) described two additional genera, *Gobiomeryx* and *Pseudomeryx*.

Viret (1961) restricted the family to four genera, *Gelocus*, *Lophiomeryx*, *Eumeryx*, and *Prodremotherium*. Sudre (1984) added the genus *Rutitherium* to it, but this genus was shown to be a junior synonym of *Gelocus* by Bouvrain *et al.* (1986).

Janis (1987) provided dental evidence for the exclusion of *Lophiomeryx* and *Bachitherium* from the Gelocidae, which is supported here by cranial data. *Eumeryx* undoubtedly belongs to the Cervidae (Matthew and Granger, 1924; Vislobokova, 1983, 1990a, 1990b). *Indomeryx* and *Miomeryx* are closer to other traguloid groups than to the Gelocidae.

Besides the seven Eurasian genera (*Gelocus*, *Phaneromeryx*, *Paragelocus*, *Pseudogelocus*, *Prodremotherium*, *Pseudomeryx*, and *Gobiomeryx*) we, following Webb (1998), place one American genus, *Pseudoceras*, in the Gelocidae. Progressive classifications of gelocid genera are given by Jehenne (1987), Blondel (1996), Sudre and Blondel (1996).

#### Family Leptomerycidae Zittel, 1893

(= Leptomerycinae Zittel, 1893; = Leptomerycini Frick, 1937)

**Genera included:** *Leptomeryx* Leidy, 1853; *Pseudoparablastomeryx* Frick, 1937; *Pronodens* Koerner, 1940; and *Hendryomeryx* Black, 1978.

**Defining characters.** Skull with more enlarged braincase than in archaeomerycids. Sagittal crest shorter than in archaeomerycids, lophiomerycids, and gelocids. Temporal crests fused much more posteriorly to coronal suture. Postorbital bar complete and forms half of frontal and half of jugal. Parietal foramen large, sometimes double. Auditory bulla small, with medium-long

external acoustic meatus. Stylohyoid vagina encroaching upon bulla with sharp lateral border. Mastoid exposure mainly on occipital surface. Mastoid foramen large and placed laterally. Foramen ovale slitlike, located posteriorly. Pterygoid canal present. Petrosal enlarged with ventral side sitting closer to horizontal plane than to parasagittal one; anteroventral border of petrosal laterally almost reaching the postglenoid foramen. Promontorium well developed, as in tragulids. Fenestra vestibuli small. Stapedial muscle fossa opposite fenestra vestibuli. Epitympanic recess formed by petrosal, as in tragulids. Lacrimal with enlarged facial and orbital parts and with single lacrimal foramen within orbit, as in tragulids. Jugal with well-developed anterior process. Posterior opening of infraorbital canal between lacrimal and maxilla, as in tragulids. Ethmoidal fissure well developed. Nasals shorter than in archaeomerycids, not narrowed posteriorly. Median concavity of palate opposite posterior border of M3. Anterior opening of nasal cavity with projected anteriorly nasals. Upper incisors absent. Lower i1 enlarged, strongly procumbent. Upper canines reduced. P1 absent. The p1 present or lost. Odontoid process of axis spout-like. Forelimbs much shorter than hindlimbs. Radius and ulna, tibia and fibula separate. Fibula reduced to separate proximal rudiment and malleolar bone. Manus tetradactyl. Metacarpals separate and arranged in paraxonic symmetry. Metatarsals III and IV form cannon bone with unclosed gully. Proximal splits of metatarsals II and V fused with cannon bone. Ecto- and mesocuneiforms fused. Entocuneiform separate. Astragalus of pecoran type with parallel trochleae.

**Comments.** For a long time, leptomerycids were united with hypertragulids in the Hypertragulidae (Frick, 1937; Scott, 1940; Simpson, 1945; Viret, 1961).

Gazin (1955) showed the essential differences in the dentition of leptomerycids and hypertragulids.

The works of Taylor and Webb (1976), Webb and Taylor (1980), and Webb (1998) provided additional cranial and postcranial evidence to support retention of the Leptomerycidae as a distinct family.

Several genera were mistakenly included in the Leptomerycidae: *Miomeryx*, *Bachitherium* (Lavocat, 1951; Viret, 1961), *Gobiomeryx* (Sudre, 1984), and *Archaeomeryx* (Webb and Taylor, 1980).

Concerning the composition of the family, we follow Taylor and Webb (1976) and Webb (1998), but exclude *Archaeomeryx*, which we place in a separate family (Vislobokova and Trofimov, 2000a).

#### Family Archaeomerycidae Simpson, 1945

(= Archaeomerycinae Simpson, 1945)

**Genera included:** *Archaeomeryx* Matthew et Granger, 1925; *Miomeryx* Matthew et Granger, 1925; *Notomeryx* Qiu, 1978; and *Xinjiangmeryx* Zheng, 1978.

**Defining characters.** Skull brachycephalic with very short snout. Sagittal, temporal, and occipital crests

strong. Sagittal crest long. Temporal crests curved anteriorly and joined close to coronal suture. Orbits small, placed centrally, and closed posteriorly. Postorbital bar formed half of frontal and half of jugal. Parietal foramina small. Foramen ovale small, placed posteriorly. Mastoid exposure mainly lateral. Auditory bulla very small without contact with postglenoid process. External meatus weakly developed. Stylohyoid vagina extremely shallow, very widely open posteriorly. Petrosal small, short, and broad, set closer to horizontal plane than to parasagittal one, and pressed closely against basioccipital; anteroventral border of petrosal placed far from postglenoid process. Promontorium weak, short, corresponding to main whorl of cochlea. Fenestra vestibuli small. Tensor tympani fossa small and located posteriorly. Behind fenestrae vestibuli and cochleae, stapedial muscle fossa narrow. Epitympanic recess on petrosal. Lacrimal with small facial and orbital parts. Lacrimal foramen within orbit. Ethmoidal fissure small and triangular or absent. Nasals elongated, not projecting anteriorly above anterior opening of nasal cavity. Palate flattened. Median concavity of palate a little behind M3. Posterior opening of infraorbital canal placed in maxilla. Anterior opening of nasal cavity ovoid in dorsal view. Angular process of mandible narrow and strongly projecting posteriorly. Upper incisors very small. Canines small and procumbent, lower canine spatulate. P1 absent. Forelimbs shorter than hindlimbs. Radius and ulna, tibia and fibula, and central metapodials separate. Fibula strongly reduced but os malleolus incompletely developed. Astragalus elongated and tripulley, with nonparallel trochleae. Metapodials separate. Manus pentadactyl. Pes tetradactyl.

**Comments.** A separate subfamily Archaeomerycinae within the Hypertragulidae was proposed by Simpson (1945) with a single genus *Archaeomeryx* (Matthew and Granger, 1925b; Colbert, 1941). Simpson (1945) included it in the family Hypertragulidae following Matthew and Granger (1925b) and Colbert (1941).

Webb and Taylor (1980) later placed *Archaeomeryx* in the family Leptomerycidae. This opinion is supported by Sudre (1984) and Janis and Scott (1987) but is rejected by some other workers (Geraads *et al.*, 1987; Gentry and Hooker, 1988).

Key differences separating *Archaeomeryx* from the Leptomerycidae allowed us to distinguish a separate family Archaeomerycidae. (Vislobokova and Trofimov, 2000a). Three other Asian genera, *Miomeryx*, *Xinjiangmeryx*, and *Notomeryx*, with similar mandibular and dental characters, are also included in this family.

#### Family Lophiomerycidae Janis, 1987

**Genera included:** *Lophiomeryx* Pomel, 1853; *Indomeryx* Pilgrim, 1928; and *Iberomeryx* Gabunia, 1964.

**Defining characters.** Skull brachycephalic, with snout weakly elongated. Orbits small, in anterior position, and apparently open posteriorly. Foramen ovale small and more anteriorly positioned than in archae-

omerycids. Alisphenoid and pterygoid canals absent. Postglenoid process present. Postglenoid foramen small, circular, and not enclosed by bulla. Auditory bulla small, in contact with postglenoid process. External acoustic meatus very short but longer than in archaeomerycids. Stylohyoid vagina shallow and widely open posteriorly. Petrosal placed closer to parasagittal plane than to horizontal one and pressed against basioccipital and alisphenoid. Promontorium, fenestra vestibuli, and stapedial muscle fossa similar to those in archaeomerycids. Lateral wall of epitympanic recess formed by squamosal. Mastoid exposure lateral. Lacrimal with very short facial part and single lacrimal foramen on antorbital rim. Jugal high with short anterior process. Palate concave, median border of palate almost straight and located opposite M3. Posterior opening of infraorbital canal located in maxilla. Mandible slightly descending anteriorly with long symphysis, posteriorly projected angular process, and semivertical anterior border of coronoid process. Upper canines large. Lower canines incisiform. P1 absent; p1 small and detached. Other premolars elongated and weakly molarized. Lower p4 longer than m1. Lingual crescents of lower molars weakly developed. *Dorcatherium* fold absent. Radius and ulna, tibia and fibula, and central metapodials separate. Distal end of fibula reduced to malleolar bone. Astragalus double-pulley, with nonparallel trochleae. Metapodials separate.

**Comments.** This family was erected by Janis (1987) to include the genera *Lophiomeryx*, *Cryptomeryx*, and *Iberomeryx*. The structure of the skull, described in the chapter *Comparative Morphology*, confirms the validity of the Lophiomerycidae.

*Cryptomeryx*, with the type species *L. gaudry* Filhol, 1877, must be excluded from the family as it is a synonym of *Lophiomeryx* (Bouvrain *et al.*, 1986).

*Iberomeryx* and *Indomeryx* are placed in the family based on the similarity of their cheek teeth to those of *Lophiomeryx*.

Up to date classifications of *Lophiomeryx* and *Iberomeryx* were given in works of Brunet and Sudre (1987) and Blondel (1996).

#### Family Bachitheriidae Janis, 1987

**Genera included:** *Bachitherium* Filhol, 1882.

**Defining characters.** Sagittal and temporal crests strong. Sagittal crest long. Mastoid exposure occipital. Orbits small and located in more posterior position than in other traguloids, except *Prodremotherium*. Postorbital bar very robust and formed mostly from jugal, as in tragulids. Auditory bullae small. Lacrimal small and triangular, with one lacrimal foramen within orbit. Orbital part of lacrimal inflated and enlarged. Jugal anteriorly short. Ethmoidal fissure moderately developed. Upper incisors absent. Upper canines large. Lower canines incisiform. Lower i1 small. The p1 enlarged and caniniform. Radius and ulna, tibia and fib-

ula separate. Metacarpals III and IV separate. Metatarsals III and IV incompletely fused.

**Comments.** The family was proposed by Janis (1987) and was supported by Sudre (1995) and Blondel (1996), who elucidated relationships within the *Bachitherium* group. While it is close to other traguloid groups, *Bachitheriidae* is undoubtedly a separate family.

### Superfamily Hypertraguloidea Scott, 1940

**Families included:** Hypertragulidae Cope, 1879; Hypisodontidae Cope, 1887; Praetragulidae, fam. nov.

**Defining characters.** Orbits open or closed posteriorly. Jugular foramen not confluent with posterior lacrimate foramen. Alisphenoid canal present. Pterygoid canal absent. Mastoid exposure mainly lateral. Supraorbital sulcus strongly convergent anteriorly and curved laterally. Facial part of lacrimal with high frontal process. Orbital part of lacrimal enlarged. Posterior opening of orbital canal placed between lacrimal and maxilla, as in tragulids and leptomerycids. Median concavity of palate opposite M2 and very strong. Upper canines medium-sized or enlarged. Lower canines may or may not be incisiform. P1 and p1 present or lost; when present, they detached and caniniform. Radius and ulna separate or fused. Magnum and trapezoid separate. Fibula separate or fused distally with tibia. Metapodials separate.

#### Family Hypertragulidae Cope, 1879

(pars Hypertragulini Frick, 1937; pars Hypertragulinae Gazin, 1955)

**Genera included:** *Hypertragulus* Cope, 1873 and *Nanotragulus* Lull, 1922.

**Defining characters.** Skull brachycephalic, with moderately elongated snout. Rostrum narrow. Orbits large, centrally placed with incomplete postorbital bar. Foramen ovale small, ovate, and placed approximately in midlength of alisphenoid. Auditory bulla small and moderately inflated, with medium-long external acoustic meatus. Stylohyoid vagina encroached upon bulla and enclosed posteriorly. Petrosal small, short, and broad, set closer to horizontal plane than to parasagittal one; anteroventral border of petrosal located far from postglenoid process. Promontorium weak, short, and corresponding to main whorl of cochlea. Tensor tympani fossa pocketed both in lateral and medial walls. Stapedial muscle fossa narrow, sinuous, and located posteriorly. Lacrimal foramen located within orbit. Ethmoidal fissure well developed. Nasals elongated and weakly projecting anteriorly above anterior opening of nasal cavity. Palate concave. Anterior opening of nasal cavity peariform in *Hypertragulus*. Upper incisors absent. Upper canines medium-sized and procumbent. Lower canines incisiform. Anterior premolars shortened. P1 and p1 detached and caniniform. Odontoid process on axis short and peglike. Forelimbs short.

Radius and ulna tend to be co-ossified. Fibula fused distally with tibia. Astragalus with nonparallel trochleae. Central metapodials separate. Manus pentadactyl. Pes tetradactyl.

**Comments.** The composition and taxonomy of the family Hypertragulidae has changed over time (Cope, 1873, 1879, 1887; Lull, 1922; Frick, 1937; Simpson, 1945; Gazin, 1955; Viret, 1961; Black, 1978; Emry, 1978; Webb, 1998).

Taking into account recent data (Webb, 1998; Vislobokova, 1998), the family Hypertragulidae sensu stricto is restricted here to two genera, *Hypertragulus* and *Nanotragulus*. It corresponds approximately to the Hypertragulini after Frick (1937) and Hypertragulinae sensu Gazin (1955).

The revised classifications of *Hypertragulus* and *Nanotragulus*, as well as those of other American hypertraguloids, are given by Webb (1998).

#### Family Hypisodontidae Cope, 1887, rank nov.

(= Hypisodontinae Cope, 1887; = Hypisodontini Frick, 1937)

**Genera included:** *Hypisodus* Cope, 1873.

**Defining characters.** Small in size. Skull brachycephalic with long and slender rostrum. Orbits large. Postorbital region anteriorly compressed. Postorbital bar complete, formed mostly by frontal. Auditory bullae large, strongly inflated, and meeting midventrally. External acoustic meatus medium long. Stylohyoid vagina encroaching upon bulla and enclosed posteriorly. Anterior opening of nasal cavity small. Upper canines large. Anterior premolars reduced; the first two of these lost. Radius and ulna fused. Fibula reduced and distally fused with tibia. Central metapodials III and IV closely appressed.

#### Family Praetragulidae Vislobokova, fam. nov.

**Genera included:** *Praetragulus* Vislobokova, 1998; *Simimeryx* Stock, 1934; and *Parvitragulus* Emry, 1978.

**Defining characters.** Skull brachycephalic with shorter snout than in hypertragulids and hypisodontids. Orbits not very large. Postorbital bar apparently open. Foramen ovale small, ovate, and placed as in hypertragulids. Petrosal short and broad. Promontorium weak, short, and corresponding to main whorl of cochlea. Tensor tympani fossa pocketed both in lateral and medial wall. Stapedial muscle fossa narrow, sinuous, and located posteriorly. Upper canines large. Lower canines not completely included in incisor row, small or enlarged. P1 and p1 lost. Diastemata behind p2 absent. Radius and ulna usually separate. Fibula distally detached, not fused to tibia. Central metapodials separate.

Thus, the revised classification of the infraorder Tragulina is as follows (Table 9).

**Table 9.** Revised classification of the infraorder Tragulina

Superfamily **Traguloidea** Gill, 1872; M. Eocene–Recent; Asia; L. Eocene–Miocene; Europe; E. Miocene; Africa; L. Miocene; N. America

Family **Tragulidae** Milne-Edwards, 1864; L. Eocene–Recent; Asia.

*Tragulus* Brisson, 1762; Pliocene–Recent; Asia.

*T. javanicus* Pallas, 1777 and five recent species; Asia.

+*T. sivalensis* Lydekker, 1882; Pliocene (M. Sivaliks); Asia.

+*Dorcatherium* Kaup, 1833; Miocene–Pliocene; Asia; E.-M. Miocene; Africa; Miocene; Europe;

+*D. naui* Kaup, 1833; E. Miocene (MN 4); Europe.

+*D. guntianum* Meyer, 1846; E.-M. Miocene (MN 4–6); Europe.

+*D. crassum* (Lartet, 1851); M.-L. Miocene (MN 9–10); Europe.

+*D. jordani* (Deperet, 1887); L. Miocene (MN 9–11); Europe; M. Asia.

+*D. penecke* (Hofmann, 1892); E.-M. Miocene (MN 5–6); Europe.

+*D. puyhauberti* Arambourg et Piveteau, 1929; L. Miocene (MN 9–13); Europe.

+*D. chappuisi* Arambourg, 1933; E.-M. Miocene; Africa.

+*D. vindobnense* Meyer, 1846 (=D. rodgeri Hofman, 1909); E.-M. Miocene (MN 4–6); Europe.

+*D. majus* Lydekker, 1876; M. Miocene–Pliocene (E.-M. Siwaliks); S. Asia.

+*D. minus* Lydekker, 1876; M. Miocene–Pliocene (E.-M. Siwaliks); S. Asia.

+*D. songhorensis* Whitworth, 1958; E. Miocene; Africa.

+*D. pigotti* Whitworth, 1958; E. Miocene; Africa.

+*D. parvum* Whitworth, 1958; E. Miocene; Africa.

+*D. bulgaricus* Bakalov et Nikilov, 1962; ?Pliocene; Europe.

+*D. libiensis* Hamilton, 1973; M. Miocene; Africa.

+*D. orientale* Qui et Gu, 1991; E. Pliocene; China.

*Hyemoschus* Gray, 1845; Pleistocene–Recent; Africa.

*H. aquaticus* Gray, 1845; Recent; Africa.

+*Yunnanotherium* Han, 1986; L. Miocene; China.

+*Yu. simplex* Han, 1986; L. Miocene; China.

+*Siamotragulus* Thomas, Ginsburg, Hintong et Suteethorn, 1990; M. Miocene; S. Asia.

+*S. sanyathanai* Thomas, Ginsburg, Hintong et Suteethorn, 1990; M. Miocene; S. Asia.

+*Krabimeryx* Ducrocq, 1992; L. Eocene; S. Asia.

+*K. primitivus* Ducrocq, 1992; L. Eocene; S. Asia.

+Family **Gelocidae** Schlosser, 1886; L. Eocene–E. Miocene; Asia; L. Eocene–Oligocene; Europe; E. Miocene; Africa; L. Miocene; N. America.

+*Gelocus* Aymard, 1855 (=Rutitherium Filhol, 1876); L. Eocene–E. Oligocene; Europe; E. Miocene; Africa; E. Miocene; S. Asia.

+*G. minor* Pavlov, 1900; L. Eocene (MP 18/19); Europe.

+*G. communis* (Aymard, 1846); E. Oligocene (MP 21); Europe.

+*G. gajense* Pilgrim 1912; E. Miocene; S. Asia.



**Table 9.** (Contd.)

- 
- +*G. indicus* Cooper, 1915; E. Miocene; S. Asia.
  - +*G. whitworthi* Hamilton, 1973, E. Miocene; Africa.
  - +*G. villebramarensis* Brunett et Jehenne, 1976; E. Oligocene (MP 22); Europe.
  - +*G. quercyi* Jehenne, 1987; E. Oligocene; Europe.
  - +*Phaneromeryx* Schlosser 1886; L. Eocene; Europe.
  - +*Ph. geliensis* (Gervais, 1848); L. Eocene; Europe.
  - +*Prodremotherium* Filhol, 1877; E. Oligocene–E. Miocene; Asia; L. Oligocene; Europe.
  - +*P. elongatum* Filhol, 1877; Oligocene (MP 22–28); Europe.
  - +*P. beatrix* Pilgrim, 1912; E. Miocene; S. Asia.
  - +*P. flerowi* Trofimov, 1957; E. Oligocene; Kazakhstan.
  - +*P. trepidum* Gabunia, 1964; L. Oligocene; Georgia (Benara).
  - +*Pseudogelocus* Schlosser, 1902; ?L. Eocene–E. Oligocene; Europe; E. Oligocene; Asia.
  - +*P. suevicus* Schlosser, 1902; E. Oligocene (MP 22); Europe.
  - +*Paragelocus* Schlosser, 1902; E. Oligocene; Europe; E. Oligocene; Asia.
  - +*P. scotti* Schlosser, 1902; E. Oligocene (MP 22); Europe.
  - +*P. laubei* (Schlosser, 1901); E. Oligocene (MP 21–22); Europe.
  - +*Pseudoceras* Frick, 1937; L. Miocene; N. America.
  - +*P. skinneri* Frick, 1937; L. Miocene; N. America.
  - +*P. wilsoni* Frick, 1937; L. Miocene; N. America.
  - +*P. potteri* Frick, 1937; L. Miocene; N. America.
  - +*Gobiomeryx* Trofimov, 1957; L. Eocene–E. Oligocene; Asia.
  - +*G. dubius* Trofimov, 1957; L. Eocene–E. Oligocene; Asia.
  - +*Pseudomeryx* Trofimov, 1957; E. Oligocene; Asia.
  - +*P. gobiensis* Trofimov, 1957; E. Oligocene; Asia.
  - +Family **Leptomerycidae** Zittel, 1893; M. Eocene–M. Miocene; N. America.
  - +*Leptomeryx* Leidy, 1853; M. Eocene–E. Miocene; N. America.
  - +*L. evansi* Leidy, 1853; L. Eocene–E. Oligocene (Chadronian–Whitneyan); N. America.
  - +*L. blacki*; M.-L. Eocene (Duchesnean–E. Chadronian); N. America.
  - +*L. mammifer* Cope, 1886 (= *L. esulcatus* Cope, 1889 and *L. semicinctus* Cope, 1889);  
L. Eocene–E. Oligocene (Chadronian); N. America.
  - +*L. speciosus* Lambe, 1908; L. Eocene–E. Oligocene (Chadronian); N. America.
  - +*L. obliquidens* Lull, 1922 (= *L. agatensis*); Oligocene (Whitneyan–E. Arikarean); N. America.
  - +*L. yoderi* Schlaikjer, 1935; M.-L. Eocene (Duchesnean–E. Chadronian); N. America.
  - +*Pseudoparablastomeryx* Frick, 1937; E.-M. Miocene; N. America.
  - +*P. scotti* Frick, 1937; M.-L. Miocene (E. Hemingfordian–Barstovian); N. America.
  - +*P. francescita* (Frick, 1937). M. Miocene (Barstovian); N. America.
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**Table 9.** (Contd.)

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- +*Pronodens* Koerner, 1940; L. Oligocene–E. Miocene; N. America.
    - +*P. silberlingi* Koerner, 1940; L. Oligocene–E. Miocene (Arikareean); N. America.
  - +*Hendryomeryx* Black, 1978; M. Eocene–E. Oligocene; N. America.
    - +*H. wilsoni* Black, 1978; M. Eocene (Uintan–Duchesnian); N. America.
    - +*H. defordi* (Wilson, 1974); L. Eocene (E. Chadronian); N. America.
    - +*H. esulcatus* (Cope, 1889); L. Eocene–E. Oligocene (Chadronian–Whitneyan); N. America.
  
  - +Family **Archaeomerycidae** Simpson, 1945 (= Archaeomerycinae Simpson, 1945); M. Eocene–E. Oligocene; Asia.
    - +*Archaeomeryx* Matthew et Granger, 1925; M.-L. Eocene; Asia.
      - +*A. optatus* Matthew et Granger, 1925; M. Eocene; Asia.
    - +*Xinjiangmeryx* Zheng, 1978; M. Eocene; China.
      - +*X. parvus* Zheng, 1978; M. Eocene; China.
    - +*Miomeryx* Matthew et Granger, 1925; L. Eocene–E. Oligocene; Asia.
      - +*M. altaicus* Matthew et Granger, 1925; E. Oligocene; Mongolia.
    - +*Notomeryx* Qiu, 1978; M. Eocene; China.
      - +*N. besensis* Qiu, 1978; M. Eocene; China.
  
  - +Family **Lophiomerycidae** Janis, 1987; M. Eocene–?E. Miocene; Asia; Oligocene; Europe.
    - +*Lophiomeryx* Pomel, 1853 (= *Cryptomeryx* Schosser, 1886)
      - +*L. chalaniati* Pomel, 1853; L. Oligocene (MP25–MP28); Europe.
      - +*L. minor* Lydekker, 1885; Oligocene; Europe.
      - +*L. gaudryi* Filhol, 1877; E. Oligocene; Europe.
      - +*L. angarae* Matthew et Granger, 1925; L. Eocene–E. Oligocene; Asia.
      - +*L. turgaicus* Flerov, 1938; E. Oligocene; Asia.
      - +*L. benarensis* Gabunia, 1964; E. Oligocene; Georgia.
      - +*L. shinaoensis* Miao, 1982; E. Oligocene; China.
      - +*L. gracilis* Miao, 1982; E. Oligocene; China.
      - +*L. mouchelini* Brunet et Sudre, 1987; Early Oligocene (MP 22–23); Europe.
    - +*Indomeryx* Pilgrim, 1928; Late Eocene; Asia.
      - +*I. cotteri* Pilgrim, 1928; Late Eocene; Asia.
      - +*I. youjiangensis* Qui, 1978; Late Eocene; Asia.
    - +*Iberomeryx* Gabunia, 1964; Oligocene (MP 22–25); Europe.
      - +*I. parvus* Gabunia, 1964; L. Oligocene; Georgia (Benara).
      - +*I. minus* (Filhol, 1882); E. Oligocene (MP 22–23); Europe.
  
  - +Family **Bachitheriidae** Janis, 1987; Oligocene (MP 23–28); Europe.
    - +*Bachitherium* Filhol, 1882; Oligocene (MP 23–28); Europe.
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**Table 9.** (Contd.)

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- +*B. curtum* (Filhol, 1877); E. Oligocene (MP 23–26); Europe.
  - +*B. insigne* (Filhol, 1882); L. Oligocene (MP 25–26); Europe.
  - +*B. vireti* Sudre, 1986; E. Oligocene (MP 23); Europe.
  - +*B. lavocati* Sudre, 1986; L. Oligocene (MP 28); Europe.
  - +*B. guirounetensis* Sudre, 1995; L. Oligocene (MP 25); Europe.

Superfamily **Hypertraguloidea** Scott, 1940; M. Eocene–E. Oligocene; Asia; M. Eocene–E. Miocene; N. America.

+Family **Hypertragulidae** Cope, 1879; M. Eocene–E. Miocene; N. America.

+*Hypertragulus* Cope, 1873; M. Eocene–E. Miocene; N. America.

+*H. calcaratus* Cope, 1873; Oligocene (L. Chadronian–E.E. Arikareean); N. America.

+*H. hesperius* Hay, 1902; Oligocene (Whitneyan–E. Arikareean); N. America.

+*H. minutus* Lull, 1922; L. Oligocene–E. Miocene (L.E.-L.L. Arikareean); N. America.

+*H. heikeni* Ferrusquia–Villafranca, 1969; M.-L. Eocene (M. Duchesnean–E. Chadronian); N. America.

+*Nanotragulus* Lull, 1922; Oligocene–E. Miocene; N. America.

+*N. loomisi* Lull, 1922; (= *N. intermedius*); L. Oligocene–E. Miocene (E.E. Arikareean–E.L. Arikareean); N. America.

+*N. fontanus*; L. Oligocene (E.E. Arikareean); N. America.

+*N. ordinatus* (Matthew, 1907); Miocene (E.L. Arikareean–E. Hemingfordian); N. America.

+*N. planiceps* Sinclair, 1905; Oligocene (Whitneyan–E. Arikareean); N. America.

+Family **Hypisodontidae** Cope, 1887, rank nov. (=Hypisodontinae Cope, 1887, =Hypisodontini Frick, 1937); M. Eocene–Oligocene; N. America.

+*Hypisodus* Cope, 1873; M. Eocene–Oligocene; N. America.

+*H. minimus* Cope, 1873; L. Eocene–E. Oligocene (Chadronian–Whitneyan); N. America.

+Family **Praetragulidae** Vislobokova, fam. nov.; L. Eocene–E. Oligocene; Mongolia.

+*Praetragulus* Vislobokova, 1998; L. Eocene–E. Oligocene; Mongolia.

+*P. electus* Vislobokova, 1998; E. Oligocene; Mongolia.

+*P. gobiae* (Matthew et Granger, 1925); L. Eocene–E. Oligocene; Mongolia.

+*Simimeryx* Stock, 1934; M. Eocene; N. America.

+*S. hudsoni* Stock, 1934; M. Eocene (L. Uintan–E. Duchesnean); N. America.

+*S. minutus* (Peterson, 1934); M. Eocene (L. Uintan–?L. Duchesnean); N. America.

+*Parvitragulus* Emry, 1978; M.-L. Eocene; N. America.

+*P. priscus* Emry, 1978; M.-L. Eocene (Duchesnean–Chadronian); N. America.

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## CONCLUSION

Morphological study has provided new evidence for the understanding of the main trends in the evolution of tragulines and for the reconstruction of their phylogeny.

Many essential plesiomorphies and key apomorphies distinguish tragulines from other known artiodactyls and confirm their position within the basal groups of the Artiodactyla. Ancient tragulines retained numerous morphological peculiarities of primitive eutherians but possessed distinctive cranial, dental, and postcranial features that demonstrated the first shifts towards rumination and the paraxonic foot. In spite of close similarities to dichobunoid diacodexids, tragulines undoubtedly represent a separate evolutionary direction.

The ancestor of the Tragulina had to be more primitive than the known Late Cretaceous arctocyonids and the most ancient Early Eocene dichobunoids. The roots of the Tragulina should be looked for much earlier than the Eocene, when artiodactyls appeared in the paleontological records.

New data on tragulines indicate the necessity of a revision of opinions on the origin of the Artiodactyla. I believe that future investigations could resolve this problem, described by Rose (1996, p. 1705) as "one of the great enigmas of mammalian history."

The undoubted ancestors of the higher ruminants, tragulines are united with them in a single suborder, as was proposed by Matthew (1929). Morphological and paleozoological evidence support the monophyly of the infraorder Tragulina.

The old classical division of the Tragulina into the superfamilies Traguloidea and Hypertraguloidea is renewed based on a very deep dichotomy of these groups. Besides the Tragulidae and Leptomerycidae, four families (Archaeomerycidae, Lophiomerycidae, Gelocidae, and Bachitheriidae) are included in the composition of the Traguloidea. Gelocids and bachitheriids, highly specialized traguloids that retain the basic traguline structure, could not be the basal pecorans or their ancestors. The Hypertraguloidea comprise three families, Hypertragulidae, Hypisodontidae, and Praetragulidae. A new rank is given here to the Hypisodontidae. A new family, Praetragulidae, is introduced.

The dichotomy of the common traguline stock into the traguloid and hypertraguloid branches occurred in Asia rather than in North America. The main adaptive radiation of traguloids took place in Asia in the Middle Eocene (before the Irindmanhan which is correlated to the Early Uintan) and led to the appearance of archaeomerycids, lophiomerycids, and, possibly, tragulids. Archaeomerycids were the ancestors of gelocids, leptomerycids, bachitheriids, and pecorans.

The ancient tragulines originally dispersed from Asia. Hypertraguloids and leptomerycids invaded North America at the end of the Middle Eocene. The first gelocid tragulines penetrated into Europe in the middle of the Late Eocene. Gelocids and tragulids

probably only reached Africa at the beginning of the Early Miocene.

## ACKNOWLEDGMENTS

I am grateful to R.H. Tedford, S.D. Webb, M. Norell, and M.F. Ivakhnenko for their reading of the manuscript and for very useful comments; to J.J. Hooker, J. Sudre, A. Lister, and L. Martin for discussions and help with collections; to L. de Bonis, J.J. Hooker, and J. Alexander for casts; to A.Yu. Rozanov for kind support; and to G.S. Rautian who helped to prepare the manuscript for publication. I also gratefully acknowledge all the people who took part in the collecting of fossil material and A. Mazin for producing photos.

The study was supported by the Russian Foundation for Basic Research, project nos. 96-15-98069, 98-04-49089, and 00-15-97754; and by grants from the J. Carter Foundation of the American Museum of Natural History, and the Royal Society of London.

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