A New Representative of the Hypertraguloidea (Tragulina, Ruminantia) from the Khoer-Dzan Locality in Mongolia, with Remarks on the Relationships of the Hypertragulidae

INESA VISLOBOKOVA[1]

ABSTRACT

A new hypertraguloid, *Praetragulus electus,* n. gen. and sp., is described from part of a skull and numerous mandibles, teeth, and limb bones from the lower Oligocene of the Khoer-Dzan locality in eastern Mongolia. Besides species from Khoer-Dzan, *Lophiomeryx gobiae* from Ardyn-Obo is referred to *Praetragulus. Praetragulus* possessed a mixture of primitive and derived features that give evidence of its early offshoot from the Tragulina, connected with the Asian early adaptive radiation of that group. The peculiarities of the skull structure and the short premolar row, together with unfused magnum and trapezoid as well as unfused central metapodials, lead to the assumption of a close relationship between the Central Asian and the North American hypertragulids. The ancestor of the latter group may have invaded North America during the Eurasian-American faunal exchange in the late middle Eocene, approximately 41 Ma.

INTRODUCTION

The numerous fossil remains of a new hypertraguloid, *Praetragulus electus,* n. gen. and sp., were recently discovered in the alluvial sands in the upper part of the Ergilin-Dzo Formation at the Khoer-Dzan locality, 70 km northwest of Dzamyn-Ude station and 200 km east of the well-known Ergilin-Dzo (Ardyn Obo) locality in eastern Mongolia. About five hundred remains from a restricted locality belong to no fewer than 30 individ-

[1] Leading Scientist, Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya, 123, Moscow 117647, Russia.

uals. Besides tragulines, the mammalian species *Hypercoryphodon* sp., *Embolotherium andrewsi*, *Schizotherium* sp., *Ardynia praecox*, *Cadurcodon ardynensis*, *Indricotherium parvum*, *Gigantamynodon* sp., and *Entelodon orientalis* come from the same deposits (Dashzeveg, 1971, 1974; Kurotchkin and Dashzeveg, 1979). The age of the deposits was determined as early Oligocene by the presence of *Ardynia praecox* and *Cadurcodon ardynensis*, also known from the Ergilin-Dzo fauna (Matthew and Granger, 1925a; Devyatkin, 1981; Janovskaja et al., 1977). The Khoer-Dzan fauna containing the remains of hypertraguloids together with *Embolotherium andrewsi* seems to correspond to the fauna from the upper horizon of the Ergilin-Dzo Formation at the Ergilin-Dzo locality. Recently, Berggren and Prothero (1992) proposed that the Ergilin early Oligocene is in actuality late Eocene (the Eocene/Oligocene boundary is estimated by them to be at 34 Ma). However Wang (1992) referred the Ardyn Obo fauna to the middle early Oligocene and correlated it with the Urtyn Obo fauna in Nei Mongol.

The rich material from Khoer-Dzan allowed me to revise the systematic position of "*Lophiomeryx*" *gobiae*, described by Matthew and Granger (1925a) on the basis of upper and lower jaws from Ardyn-Obo, and to include this species in the genus *Praetragulus*, along with the species from Khoer-Dzan. The more primitive *P. gobiae* comes from the lower horizon of the Ergilin-Dzo Formation, in association with *Parabrontops gobiensis*, which is close in morphology to *Brontops brachycephalus* from the Chadronian of North America. The Chadronian, long considered early Oligocene, now appears to be late Eocene in age (Swisher and Prothero, 1990; Berggren and Prothero, 1992).

The hypertraguloids are primarily a North American group known from the late Uintan and Duchesnean (*Simimeryx*) to the late Arikareean (*Hypertragulus* and *Nanotragulus*), approximately 41–24 Ma. In the Eocene of Asia, in addition to the richly represented *Archaeomeryx*, four other genera, *Indomeryx*, *Xinjiangmeryx*, *Notomeryx*, and *Miomeryx*, known by small fragments of jaws, were referred to that group by some investigators (Matthew and Granger, 1925b; Simpson,

1945; Pilgrim, 1928; Viret, 1961; Qiu, 1978; Zheng, 1978). But, as discussed below, there is no consensus concerning the systematic position of these genera. *Praetragulus* seems to be the first indisputable hypertraguloid in Eurasia, which was inhabited mainly by representatives of the traguloids. A considerable proportion of the early Tragulina were discovered in Central Asia—the possible center of their origin. According to recent data, no fewer than nine species, belonging to seven genera, were distributed there during the second half of the Eocene.

The phylogenetic position of hypertraguloids is rather problematic. The main questions concern the ancestry of the group, the early stages of their evolution, and the relationships between the hypertraguloids and early tragulines of Eurasia.

The discovery of a new hypertraguloid in Mongolia permits tracing certain trends not only in the early evolution of the hypertragulids, but also in the Tragulina. Besides questions regarding the dispersal and phylogenetic relationships of the Hypertragulidae, the new evidence raises the question of their origin, considered by many investigators as North American, and indicates the possibility of a Central Asian center of radiation.

The purpose of the present paper is to describe the new material, to posit the relationships of the Hypertragulidae, and to include a short analysis of the systematics, phylogeny, and evolution of the early Tragulina based on my own findings and on data obtained by previous researchers.

my previous manuscript on tragulines and for her very useful comments.

The fossils were collected by teams led by Drs. E. Kurotchkin and V. Reshetov during the field seasons of the Joint Soviet-Mongolian Paleontological Expedition. The photos were made by A. Mazin.

ABBREVIATIONS

Institutional

AMNH   American Museum of Natural History
BMNH   Museum of Natural History, London
CIT   California Institute of Technology (now in Los Angeles County Museum)
PIN   Paleontological Institute, the Russian Academy of Sciences
USNM   United States National Museum of Natural History, Smithsonian Institution
V   Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica

Illustrations

as, alisphenoideum
bo, basioccipitale
bs, basisphenoideum
cas, canalis alisphenoideus
ci, canalis infraorbitalis
fms, fossa m. stapedialis
fmtt, fossa m. tensor tympani
fnpm, fossa n. petrosi majoris
fo, foramen ovale
fs, fossa subarcuata
m, magnum
mc III, metacarpale III
mc IV, metacarpale IV
mt III, metatarsale III
mt IV, metatarsale IV
prs, praesphenoideum
s, scaphoideum
u, unciforme

Measurements and Statistics

DAP, anteroposterior diameter
di, distal
DP, milk upper molars
dp, milk lower molars
DT, transverse diameter
L, length
M, mean
N, sample size

OR, observed range
P, M, permanent upper premolars and molars
p, m, permanent lower premolars and molars
pr, proximal
S, standard deviation
W, width

SYSTEMATICS

ORDER ARTIODACTYLA OWEN, 1848

SUBORDER RUMINANTIA SCOPOLI, 1977

INFRAORDER TRAGULINA FLOWER, 1883

SUPERFAMILY HYPERTRAGULOIDEA SCOTT, 1940

FAMILY HYPERTRAGULIDAE COPE, 1879

INCLUDED GENERA: *Hypertragulus* Cope, 1879; *Hypisodus* Cope, 1873; *Nanotragulus* Lull, 1922; *Simimeryx* Stock, 1934; *Parvitragulus* Emry, 1978, and *Praetragulus* Vislobokova, n. gen.

REMARKS: The family was founded by Cope (1879) based on the genera *Hypertragulus* and *Leptomeryx*. The composition and systematics of the family Hypertragulidae changed over time. Frick (1937) additionally placed *Heteromeryx, Nanotragulus,* and *Hypisodus* in this family and divided it into three tribes: Hypertragulini, Leptomerycini, and Hypisodontini. Simpson (1945) added the leptotragulines and the genera *Archaeomeryx, Simimeryx, Floridatragulus*; he recognized two subfamilies, Hypertragulinae and Archaeomerycinae, and four tribes, Leptotragulini, Hypertragulini, Leptomerycini, and Hypisodontini. *Floridatragulus* was regarded by Simpson (1945) as Hypertragulidae incertae sedis and now is classified as a camel (Olsen, 1962). Viret (1961), adopting Simpson's classification, included three more genera, *Bachitherium, Miomeryx,* and *Indomeryx,* in the tribe Hypertragulini. According to Gazin (1955), the Hypertragulidae were restricted to two subfamilies, Hypertragulinae (with *Simimeryx, Hypertragulus,* and *Nanotragulus*) and Hypisodontinae (*Hypisodus*). Emry (1978) added *Parvitragulus* in the Hypertragulidae but excluded *Simimeryx*.

Gazin's opinion was supported by many researchers. *Archaeomeryx* and leptomerycids were removed from the Hypertragulidae; *Heteromeryx* and leptotragulids were excluded from the Tragulina (Patton and Taylor,

1973; Webb and Taylor, 1980); and *Bachitherium* was referred either to the Pecora (Geraads et al., 1987) or to its own, non-pecoran, family Bachitheriidae (Janis, 1987; Janis and Scott, 1988). The systematic position of *Indomeryx, Miomeryx,* and *Notomeryx* remains uncertain, but their dental morphology indicates a closer relationship to *Archaeomeryx* than to the hypertragulids.

Praetragulus Vislobokova, new genus

TYPE SPECIES: *Praetragulus electus* Vislobokova, n. sp.

INCLUDED SPECIES: Besides type species, *P. gobiae* (Matthew and Granger, 1925a).

DIAGNOSIS: Differs from other hypertragulids in the presence of a mesostyle in unworn teeth.

Differs from *Hypertragulus,* additionally, in a shorter snout, the loss of p1, the absence of the diastema between p2 and p3, lower crowned cheek teeth, less developed selenodonty, an anteriorly open posterior lobe on m3, usually a separate radius and ulna, and a distally detached fibula, unfused with the tibia.

Differs from *Simimeryx* in less developed lower canines, the loss of the protoconule, a compressed parastyle in the permanent upper molars, and in better developed selenodonty.

Differs from *Parvitragulus* in a shorter snout, a more anterior position for the posterior mental foramen, lower crowned cheek teeth and less complex upper and lower premolars.

DISTRIBUTION: Late Eocene–early Oligocene of Mongolia.

Praetragulus electus Vislobokova, new species
Figures 1–10

TYPE: PIN 3110/731, incomplete skull with P2-M3 and lower jaw.

REFERRED MATERIAL: Besides type, five upper jaws, with DP4-M1, 3110/752, with P2-M1, 3110/751, with P3-M3, 3110/756, with M1-M3, 3110/755, and with M2-M3, 3110/1048; 11 lower jaws with p2-m3, 3110/732, 734–736, 747, 755, 758–760, 765, 783; 113 fragments of lower jaw with dp2-m1, 3110/977, with dp3-dp4, 3110/743, 744, 979, 982, 987, 988, 989, with dp3, 3110/981, 983, 1012, 1014, with dp3-m2, 3110/976, with dp4, 3110/990–992, 1014, with dp4-m1, 3110/798, 978, 980, 984–986, with p2-p4, 3110/998, 1016, with p3-p4, 3110/770, 773, 797, 992, 997, 999, 1006, 1007, with p3, 3110/995, 1001, 1001, 1009, 1026, with p4, 3110/993–994, 996, 1000, 1002, 1003, 1004, 1005, 1008, 1010, 1011, with p3-m1, 3110/ 737, 775, 796, with p3-m2, 3110/738, 764, 791, with p3-m3, 3110/761, 763, 784, 788, with p4-m1, 3110/733, 795, 771, with p4-m2, 3110/769, with p4-m3, 3110/768, 772, 777, with m1, 3110/746, 1015, 1017–1025, 1054, with m2, 3110/801, 804, 1056–1066, with m1-m2, 3110/742, 745, 766, 744, 778, 780, 785, 787, 799, 800, with m1-m3, 3110/ 789, 790, with m2-m3, 3110/740, 762, 767, 776, 779, 781, 786, 792, 793, 803, with m3, 3110/739, 741, 783, 794, 802; teeth: nine upper canines, 3110/954, 955, 1041–1047; 15 M3, 3110/753, 1049–1052; 15 lower incisors, 3110/956–958, 1029–1040; 29 m2, 3110/1067–1092; 28 m3, 3110/748, 750, 1093–1118; limb bones: four scapulae, 3110/ 805–808; four radii, 3110/812–815; 21 proximal ends of radii, 3110/816–836; 14 distal ends of radii, 3110/837–850; scaphoid, unciform and magnum, 3110/1207; eight metacarpals, 3110/852–858, 871; 13 proximal ends of metacarpals, 3110/859–871; 18 distal ends of metacarpals, 3110/872–889; four pelves, 3110/809–812; two fragments of tibia, 3110/813, 857; fibula, 3110/1216; calcaneum, 3110/1222; astragalus, PIN 3110/1223; 21 metatarsals, 3110/890–910; 43 fragments of distal parts of metapodials, 3110/911–953; 61 first phalanges, 3110/959–975, 1119–1162; 18 second phalanges, 3110/1163–1190; 15 third phalanges, 3110/1191–1205.

ETYMOLOGY: Genus name from Latin *Prae-*(before) and *Tragulus.* Species name from Latin *electus* (chosen).

DESCRIPTION: Skull: Although the skull is strongly crushed, it possesses features characteristic of hypertragulids (fig. 1). The braincase appears brachycephalic, not very expanded and low. The axis of its base is almost parallel to that of the tooth row. The temporal ridges are well developed and diverge almost at a right angle to each other, close to the line of the postorbital process. The orbits are unclosed and situated rather
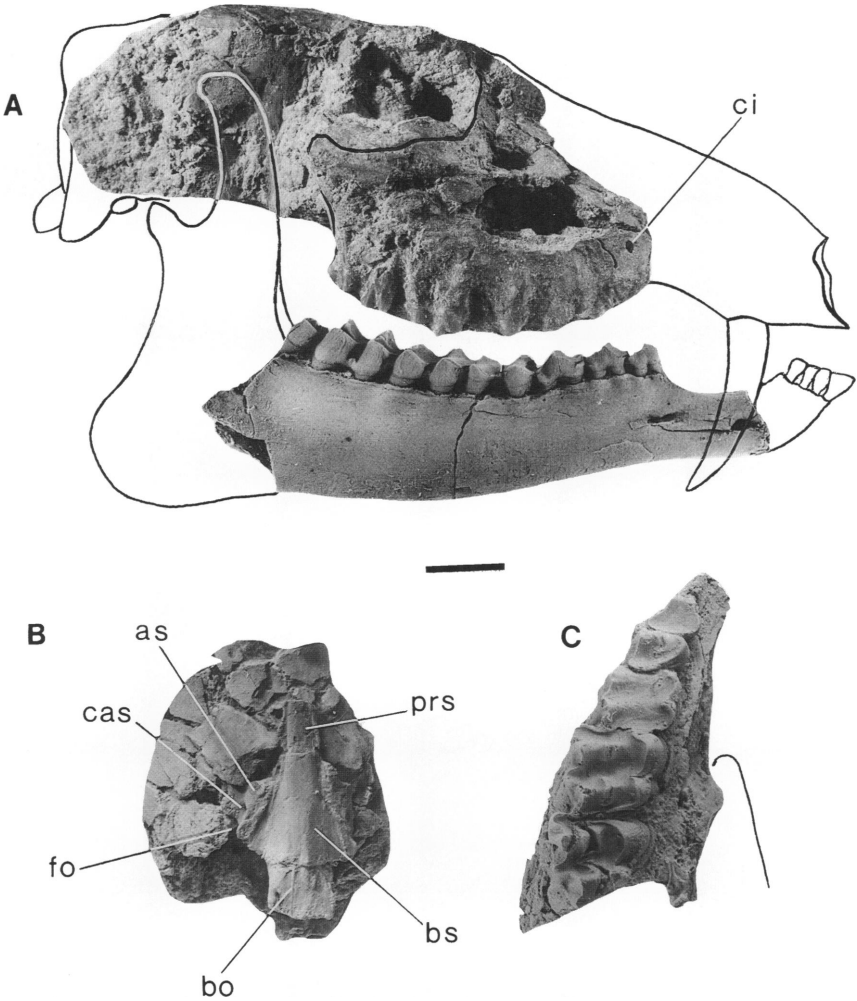
Fig. 1.   Skull fragments of *Praetragulus electus*. Skull fragments, type PIN 3110/731, in (A) lateral and (B, C) ventral views. Scale bar = 1 cm.
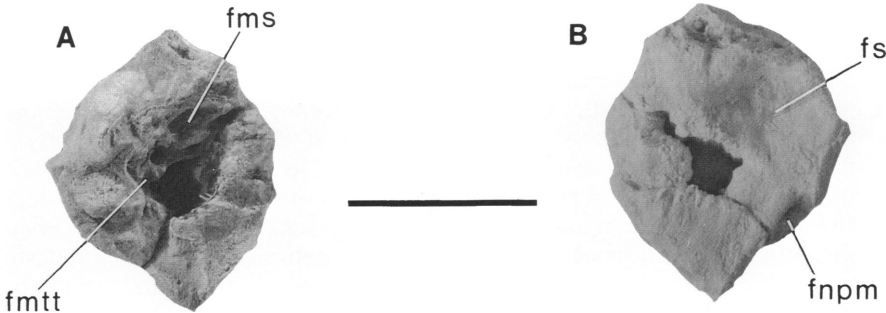

Fig. 2.   Left petromastoid of *Praetragulus electus*, PIN 3110/731, in (A) ventral and (B) dorsal views. Scale bar = 1 cm.
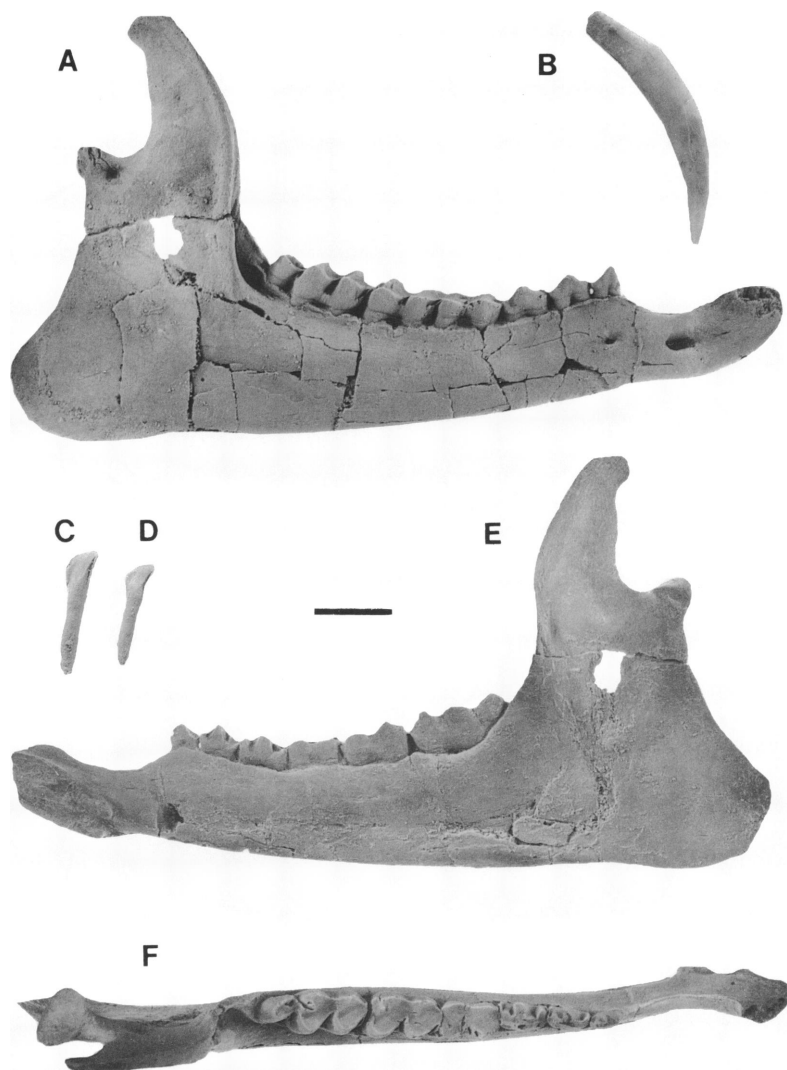
Fig. 3. Lower jaw and teeth of *Praetragulus electus*. Lower jaw, PIN 3110/734, in (**A**) labial, (**E**) lingual and (**F**) occlusal views. Right upper canine, PIN 3110/955, in (**B**) lateral view. Right I1, PIN 3110/957 (**C**) and I2, PIN 3110/958 (**D**) in lingual views. Scale bar = 1 cm.

high. The anterior border of the orbit lies at the level of M1. The anterior opening of the infraorbital canal is very small, situated above P2, and low in position.

The basisphenoid is elongated and strongly expanded posteriorly. Its ventral surface is prominent, and has weak pharyngeal tubercles giving the posterior section of the basispenoid a trapezoidal form.

The alisphenoid broadly contacts the basisphenoid and rises high posteriorly above its ventral surface. A long groove is situated at the base of the alisphenoid along the contact with the basisphenoid. A very small circular foramen of the alisphenoid canal is placed at the anterior extremity of the depression leading to the foramen ovale. The foramen ovale is positioned posteriorly, close to the posterior border of the alisphenoid.

The petromastoid, with a destroyed promontorium, is short and wide (fig. 2). The apex is weakly pointed. A subarcuate fossa for the flocculus of the cerebellum is very deep and wide. A fossa for the tensor tym-
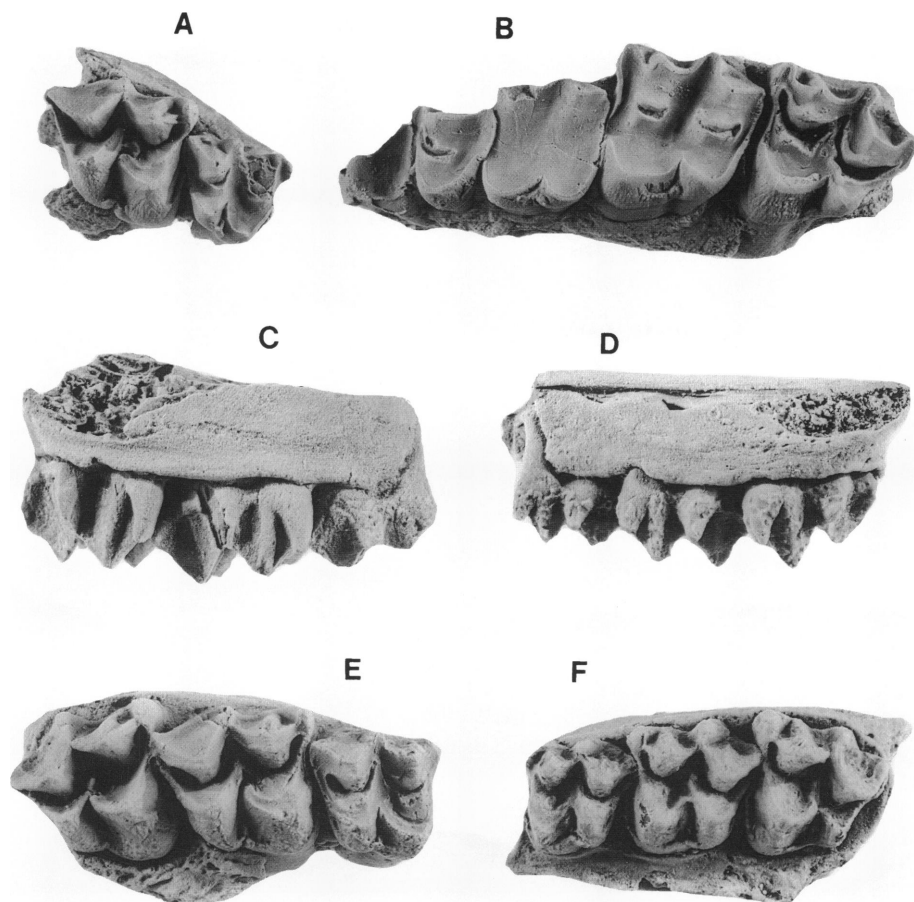
Fig. 4.   Upper jaws. *Praetragulus electus,* DP4-M1, PIN 3110/732 (**A**) and P2-M3, PIN 3110/731 (**B**) in occlusal view, M1-M3, type PIN 3110/731, in (**C**) labial and (**E**) occlusal views. *Praetragulus gobiae,* M1-M3, cast of AMNH 20379, in (**D**) labial and (**F**) occlusal views. Scale bar = 1 cm.

pani muscles is deeply pocketed in the lateral wall. A fossa for the stapedius muscle is narrow and sinuous.

The mastoid exposure is lateral, as in hypertragulids, and broad.

The palatine has a deep medial emargination. Its anterior point (staphylion) reaches the level of M2, as in *Hypertragulus.* In *Archaeomeryx,* leptomerycids, gelocids, and tragulids, it is opposite or posterior to M3.

The mandible is very similar to those of other hypertragulids (fig. 3). The angular process is broad, projecting strongly downward and backward. Its posterior border is less rounded than in *Archaeomeryx* and *Lep-*

tomeryx and resembles that of other hypertragulids. A well-developed masseteric tuberosity for the pars superficialis m. masseter and a 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, narrowing strongly upward, with a convex anterior border. The anterior border is approximately perpendicular to the tooth row axis as in *Simimeryx* and *Hypertragulus.* A deep and long fossa for the m. temporalis lies on the lateral surface of the coronoid process. The articular process lies rather low. The deep pterigoid fovea for the m. pterygoideus lateralis and
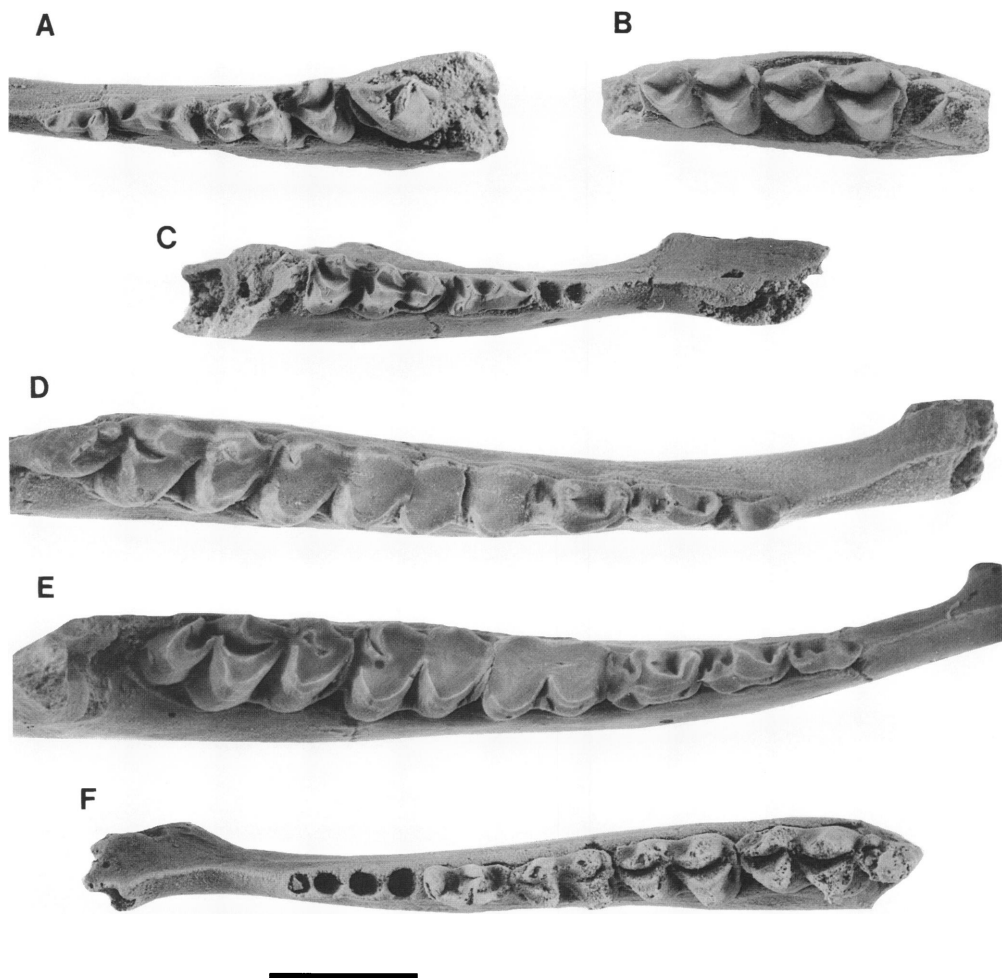
Fig. 5. Lower jaws in occlusal views. *Praetragulus electus,* dp2-m1, PIN 3110/977 (**A**), m1-m3, PIN 3110/789 (**B**), dp3-dp4, PIN 3110/743 (**C**), p2-m3, type PIN 3110/731 (**D**), p2-m3, PIN 3110/732 (**E**). *Praetragulus gobiae,* cast of holotype AMNH 20381 (**F**). Scale bar = 1 cm.

large pterygoid tuberosity for the m. pterygoideus medialis are on the medial surface of the ramus of the mandible.

The body of the mandible descends anteriorly and is markedly higher under m3 than under p2. The anterior mental foramen is large, placed almost at the level of the middle of c-p2 diastema. A small posterior mental foramen is situated beneath p2 as in *Simimeryx* and *Hypertragulus*. In *Parvitragulus* this foramen lies under p3 or p4. The ventral border of the body of the mandible is almost straight, weakly curved downward with two concavities, in front of the angular process and p2.

The rostrum appears to be slightly longer than in *Simimeryx* but shorter than in other hypertragulids.

The diastema, separating the lower canine from p2, is rather short but longer than that in *Simimeryx*. The diastema between the lower canine and third incisor is not developed.

The symphysis is not very long and extends to the level of the anterior mental foramen. It strongly rises labially, and has a rounded anterior border and a concave lingual surface. The latter is inclined backward.

There are four alveoli in the anterior part of the mandible. Based on the size of the alveolae for the lower canine, that tooth was
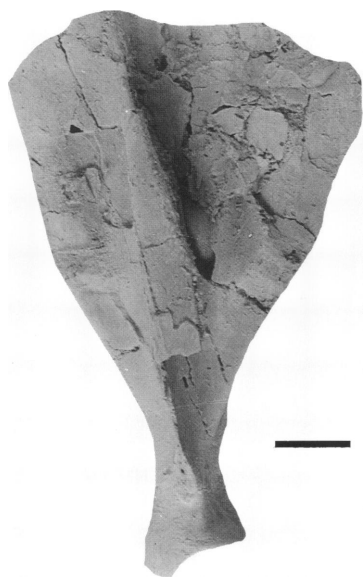
Fig. 6. Scapula of *Praetragulus electus,* PIN 3110/805, in lateral view and its articular surface. Scale bar = 1 cm.

a little larger than the third incisor and seems not to have been as completely included in the incisor row as in *Archaeomeryx.*

The strong development of the m. temporalis and the almost vertical position of its resultant force, as well as the rather oblique direction of the resultant force of the m. masseter, are the primitive conditions for ruminants. However, the position and direction of

Fig. 8. Pelvis of *Praetragulus electus,* PIN 3110/810, in (A) dorsal and (B) ventral views, PIN 3110/809, in (C) lateral view. Scale bar = 1 cm.

Fig. 7. Incomplete left carpal of *Praetragulus electus,* PIN 3110/1207 in (A) dorsal view and lower row in (F) proximal view. Unciform (B, D), magnum (C, H, I), and scaphoid (E, G, J) in (B, C, E) proximal, (G, H) distal (D, I, J), lateral, and medial views. Scale bar = 1 cm.
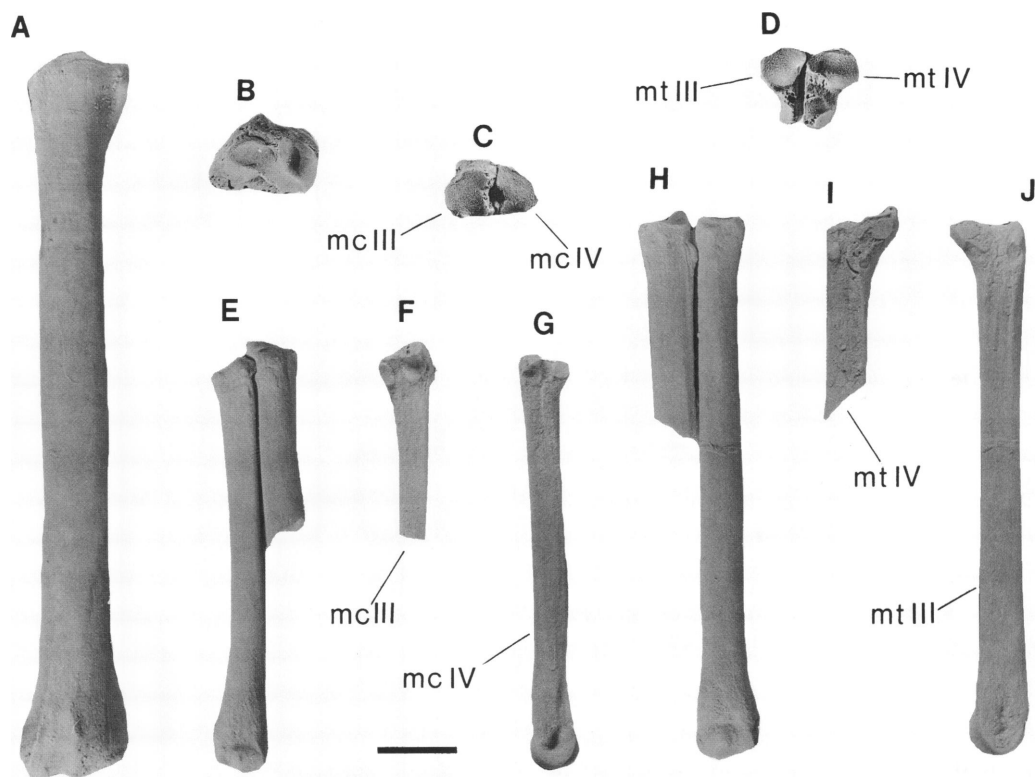
Fig. 9.   Limb bones of *Praetragulus electus*. Left radius, PIN 3110/314, in (**A**) dorsal and (**B**) distal views. Right metacarpals 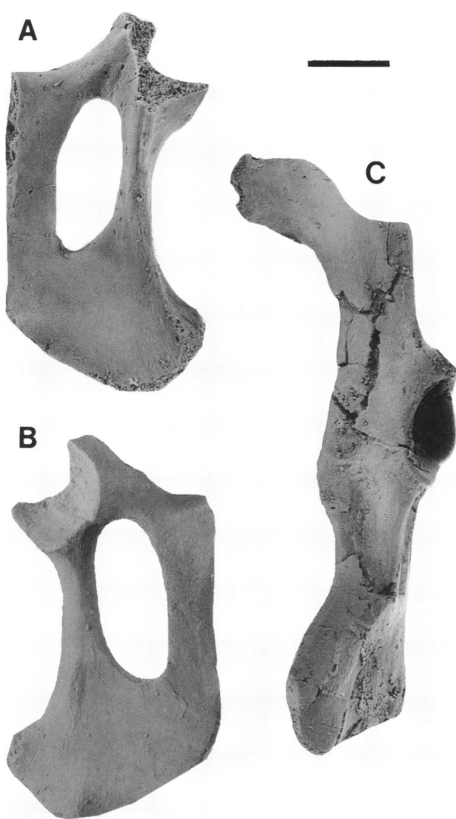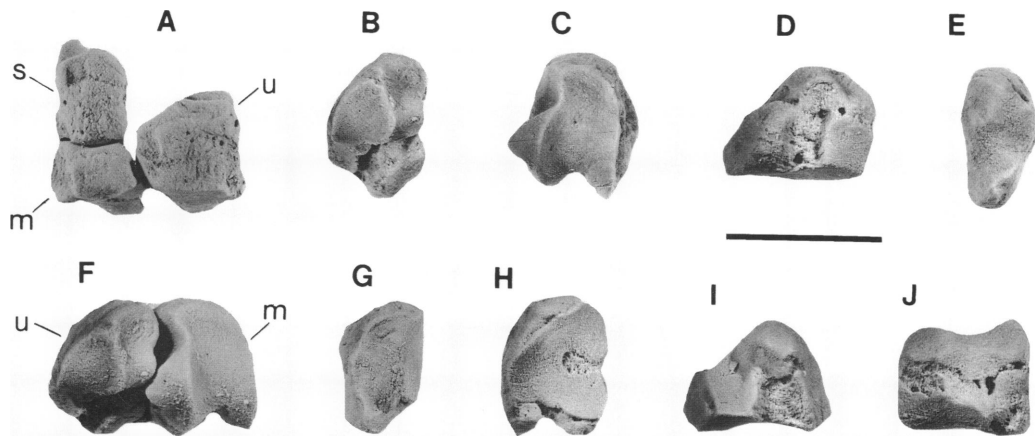III and IV in (**C**) proximal and (**E**) dorsal views. Metacarpal III, PIN 3110/872, in (**F**) lateral view and metacarpals IV, PIN 3110/853, in (**G**) medial view. Metatarsals III and IV in (**D**) proximal and (**H**) dorsal views. Metatarsal IV, PIN 3110/853, in (**I**) medial view and metatarsal III, PIN 3110/872, in (**J**) lateral view. Scale bar = 1 cm.

these muscles permit not only the upward-downward and forward-backward movements of the lower jaw but, together with the muscles pterygoidei, a movement in a lateral-medial direction with a strong stress on

molars as well. The lateral-medial movement, together with a preservation of a primitive enamel structure (not very suitable for rather coarse food), resulted in heavy dental wear relatively early in ontogeny. Almost all

Fig. 10.   Limb bones of *Praetragulus electus*. Left calcaneus, PIN 3110/1222, in (**A**) lateral and (**B**) medial views. Left fibula, PIN 3110/1216 in (**C**) distal view. Anterior and posterior palanges III, PIN 3110/962 (**D**) and PIN 3110/961 (**J**) in lateral views. Anterior phalanx I, PIN 3110/959 (**E**), anterior phalanx II, PIN 3110/963 (**F**), posterior phalanx I, PIN 3110/960 (**G**) in dorsal views. Astragalus, PIN 3110/1223, in (**H**) dorsal and (**I**) caudal views. Scale bar = 1 cm.

of the adults of *P. electus* had heavily worn molars.

The measurements (mm) of mandible are as follows: maximal length, 100.3–107.5; maximal height, 55.2; length of diastema, 11.7–18; depth of body below p2, 11.4–13.8; depth of body below m3, 18.6–21; height of articular process above tooth row, 16.3–20; distance of articular process from tooth row, 25.6–28.7.

Upper dentition: The upper canine is large with convex inner and concave outer surfaces. The anterior edge is rounded and the posterior edge is sharp. The measurements (mm) are as follows: length, 26.5; maximal transverse diameter, 5.5.

Besides skulls, there are five maxillary fragments with teeth, one of them containing the posterior deciduous tooth.

The DP4 is molariform with asymmetrical crown, strongly expanded bucally (fig. 4A). The posterior outer angle of the crown extends backward. The hypocone is very small. The parastyle is wide and rounded as in the molars of *Simimeryx*. The mesostyle is well developed and projected. The entostyle is hardly marked. The cingulum is developed.

Three upper premolars are present in the skull, although P2 is imperfectly preserved. X-rays show P2 to be double-rooted, reduced in size.

P3 is strongly narrowing anteriorly with the low protocone and parastyle. The outer surface of the crown is very oblique to the tooth row axis, the inner one almost parallel to this axis.

P4 is strongly expanded outward with a rounded parastyle. The short oblique valley is open anteriorly in unworn teeth.

In occlusal view, the upper molar crowns are strongly expanded bucally with posterior narrowing (fig. 4E, F). These features increase from M1 to M3.

On M1, the metacone and paracone lie almost in a straight line and become confluent in very early wear. The posterior wing of the protocone is short, directed posteriorly and slightly labially. The anterior wing of the hypocone is long, directed toward the paracone-metacone junction, but not reaching it, even in worn teeth.

On M2 and M3, the transverse diameter of the anterior lobe of the crown is markedly greater than across the posterior lobe, similar to the condition in *Hypertragulus* and *Simimeryx*. A compressed parastyle extends outward and forward as in *Hypertragulus,* whereas in *Simimeryx,* it is broadly rounded.

On M3, the external part of the crown is much larger than the internal one, as in other hypertragulids, but less so than in *Parvitragulus.* The metaconule is very small, not crescentic even in strongly worn teeth, as in *Simimeryx.*

Lower dentition: The lower incisors are small, oblique, and spatulate as in *Hypertragulus.* The first lower incisor is larger than the others. The outer angle of the crown is pulled strongly outward. The inner angle is rounded. The second incisor is a little smaller with a rounded outer angle.

The lower cheek teeth are brachydont, with lower crowns than those of *Hypertragulus.* The crowns are strongly inclined lingually.

The dp2 and dp3 are three-cusped and elongate, weakly narrowing anteriorly. The protoconid is situated close to the anterior border of the crown (at a distance of a third of the total crown length). A weak inner crest is directed obliquely backward from the protoconid cusp. The paraconid and entoconid are lower and have almost equal heights. The paraconid is well developed and placed almost perpendicularly to the longitudinal axis of the tooth. Two weak crests, directed backward from the entoconid, border the triangular valley. The plane of this valley is inclined backward. A rudimentary entostylid is present. A small cingulum is at the outer base of the paraconid.

The dp4 is elongated and strongly narrows anteriorly. The width of the anterior lobe is about three quarters that of the posterior lobe. The anterior lobe is almost twice as short as the posterior one. The para-, meta-, and entoconids are short, situated obliquely to the longitudinal tooth axis. The cusps of the second and third lobes are confluent. The valley of the first lobe is continuous with that of the second. On unworn teeth, the valleys of the lobes are not closed: the valleys of the first and third lobes are open posteriorly and the valley of the second lobe is open anteriorly. The anterolabial cusp is smallest, very weak, and low. The meso- and entostylids

are hardly marked. The cingulum is present on the external and posterior surfaces of the crowns.

The three posterior premolars form a close series as in *Simimeryx*, whereas in *Hypertragulus* p2 is separated from p3 by a short diastema. In external view, the anterior borders of the crowns of p3 and p4 are higher than the posterior as in other hypertragulids.

The p2 resembles that tooth in *Hypertragulus* and *Simimeryx*: it is almost unicusped with a very short anterior part. The tooth possesses a high protoconid and a very low rudimentary hypoconid and entoconid. In external view, the anterior border of p2 is almost vertical. The p2 shows no wear even in old animals, as in *Hypertragulus* (Scott, 1940).

The p3 has a larger protoconid, a small paraconid extending lingually and anteriorly, and a very weak metaconid and entoconid directed lingually and posteriorly.

The p4 has a more developed metaconid extending lingually, a higher paraconid, and a rudimentary entoconid.

On the lower molars, the lingual crescents are weakly developed. On moderately worn teeth, the posterior wing of the entoconid remains distinct (isolated) from that of the hypoconid as in *Simimeryx*, whereas in *Hypertragulus* they are joined. During wear, the confluence of the wings of the meta-, ento-, and protoconids occurs at the same point, and that of the hypoconid joins them below, forming an X-like intersection (fig. 5). The pillars of para- and metaconids are slightly projected only in the upper half of the crowns. A very small mesostylid is present in unworn molars. The parastylid and entostylid are very weak. A very small entostylid is marked on m1. The cingulum is developed at the anterior and posterior bases of the crowns.

On m1 and m2, the valley between the entoconid and hypoconid is continuous with that of the posterior lobe even in well worn teeth.

On m3, the inner wall of the tooth is not complete because the entoconid is not joined to the inner cusp of the posterior lobe even in worn teeth. The posterior lobe is unicusped: the sharp cusp is situated at the posterior edge of m3. Two sharp crests, directed an-

teriorly, lingually, and ventrally enclose a valley that remains open at the base of the entoconid. A small tubercle is sometimes present on the anterior end of the inner crest.

The measurements (in mm) and indices (in parentheses) of the dentition are as follows: length M1-M3, 26.8–28.2 (27.5); length p2-m3, 44.5–51 (48.2); ratio p4/m1, 0.7–1 (0.83); ratio p2-p4/m1-m3, 0.51–0.55 (0.52). The other measurements are given in table 1.

Limb bones: The scapula is wide with a narrow neck (fig. 6). The spine of the scapula is high and strongly turned back in its medial part. The tuber of the scapula is well developed. A short coracoid process bends ventrally. The glenoid cavity is weakly oval with a projection at the coracoid. A strong development of the muscles attaching to the scapula (m. supraspinatus, m. deltoidea, and others) shows that the humeral articulation remained rather mobile.

The radius has a long shaft strongly curved anteriorly. This bone is longer by more than a third than the central metacarpals. The proximal articular surface for the trochlea of the humerus has small lateral and large medial concavities and a wide, but not deep, groove between them. The medial concavity is much wider transversely than the lateral one. The distal articular surface consists of two facets, scaphoid and lunar. The long axes of the facets are oriented strongly obliquely relative to that of the articulation (about 30°). The scaphoid facet has a wider anterior part with a deep concavity and a trochlear posterior part. The boundaries of that facet are clearly outlined and have the appearance of distinct ridges. The lunar facet is long, with a wide concave anterior part and narrow trochlear posterior part. The facet for the cuneiform appears to be on the ulna.

The ulna is usually separated from the radius. Only in the specimen PIN 3110/847 is the lower part of the ulna co-ossified with the shaft of the radius. Partial ossification of the ulna and radius is a more primitive condition than that in *Hypertragulus*, where these bones are completely fused.

The proximal surface of the scaphoid corresponds to the scaphoid facet of the radius and has the wide convex anterior and narrower concave posterior parts. The distal articular surface lies on the magnum (fig. 7).

TABLE 1
Measurements (mm) of the Dentition of *Praetragulus electus*

Tooth		PIN 3110/731	OR	M	S	N
P3	L	6.5				
	W	6.2	6.2–6.5	6.5	0.15	2
P4	L	7.0	6.0–7.0	6.6	0.42	3
	W	7.0	7.0–7.6	7.3	0.23	3
M1	L	8.1	8.1–9.3	8.7	0.46	4
	W	9.1	9.0–9.4	9.2	0.17	3
M2	L	10.4	10.3–11.2	10.6	0.40	3
	W	11.7	11.1–11.7	11.4	0.25	3
M3	L	11.2	10.0–11.4	10.9	0.48	5
	W	11.0	11.0–12.2	11.4	0.42	5
dp3	L	—	5.4–6.4	6.1	0.38	16
	W	—	2.5–3.1	2.7	0.16	15
dp4	L	—	8.5–9.6	8.9	0.37	12
	W	—	3.7–4.4	3.9	0.21	15
p2	L	4.6	4.2–5.0	4.6	0.27	12
	W	2.2	2.0–2.5	2.2	0.16	12
p3	L	6.0	5.5–6.8	6.0	0.35	24
	W	2.8	2.8–3.5	2.9	0.18	26
p4	L	6.8	6.3–7.8	7.0	0.40	41
	W	3.7	3.4–4.8	3.8	0.30	41
m1	L	8.2	7.1–10.0	8.5	0.64	50
	W	5.2	4.8–6.0	5.4	0.24	50
m2	L	8.7	8.7–11.2	9.9	0.60	70
	W	6.2	5.7–7.3	6.4	0.37	69
m3	L	14.5	12.7–16.4	14.3	0.85	49
	W	6.5	5.4–6.5	6.1	0.35	45

The scaphoid facet of the magnum has a very narrow anterior part with a deep median depression and a wide trochlear posterior part. The distal articular surface of the magnum consists of a large facet for metacarpal III, resembling that of *Hypertragulus* (Webb and Taylor, 1980: fig. 9A–C). There are two very small facets for the trapezoid on the plantar surface of the bone. On the lateral surface of the magnum there are a conical projected trochlea and a quadranglular concave facet for the unciform.

The unciform is very high. The proximal articular surface contains the lunar and triquetrum facets. A large facet for metacarpal IV occupies the distal surface having a plantar project with a small facet for metacarpal V.

The central metacarpals are rather long, massive, and unfused. As in *Hypertragulus,* the manus is asymmetrical: metacarpal III is longer than metacarpal IV.

In metacarpal III, the proximal articular surface is an irregular triangle. The facet for the magnum is concave with a lateral border strongly elevated anteriorly. On the proximolateral side are two rounded facets for metacarpal IV. Of these the wider anterior facet is under the projection for the metacarpal IV and unciform and a little away from the anterior border. The smaller posterior facet is in the posterolateral corner. The unciform facet is quadrangular. On the proximoposterior side of metacarpal III, there is a small concave facet and a well-defined depression for metacarpal II, which appears to be long and well-developed. The keels of the distal trochleae, strongly projected posteriorly, are very slightly outlined on the anterodistal surface.

A large flat unciform facet occupies the proximal surface of metacarpal IV. The small medial facets correspond to those of metacarpal III. There is a small facet for meta-

carpal V at the posterolateral corner of the bone.

The pelvis is elongated and similar to that of *Hypertragulus* (AMNH 53802). The body of the ischium is wide and flattened (fig. 8). The symphysis is long. The obturator foramen is large and ellipsoidal. The acetabulum is very deep and faces lateroventrally, in contrast to the condition in other ruminants except *Hypertragulus*. The arch of the ischium is low and wide. The crest of the ischium lies dorsolaterally. The tuber of the pubic bone and the pubic crest are weak. The body of the ilium is long. The upper flaring portion of the ilium is directed dorsolaterally.

The fibula is unfused with the tibia and its distal part forms an os malleolus. A small semilunar flat facet for the tibia lies on the proximal surface of the os malleolus, and an elongated concave facet for the calcaneum occupies its distal surface.

As in *Hypertragulus*, the upper and lower trochleae of the astragalus are almost parallel. A narrow sustentacular facet for the articulation with the calcaneum is divided into a very narrow medial and a wide lateral part by a shallow median sulcus. The posteromedial end of the facet for the navico-cuboid lies very high.

As in *Hypertragulus*, the lateral side of the calcaneum has a long and deep groove. The sustentacular process is rather prominent and its articular surface for the astragalus is divided into two parts. The fibular condyle has a narrow convex facet for the os malleolus. On the medial side of the calcaneum the facet for the astragalus is wide.

The central metatarsals are almost 25% greater in length than the central metacarpals, and similarly do not fuse to form a cannon bone (fig. 9).

On the proximal surface of metatarsal III there are two facets: the anterior for cuneiform II + III and the posterior for cuneiform I. The first is wide, roundly trianglular, and concave with medial and lateral borders elevated to about the same level. The second is small, almost round, flat, slightly inclined on the medial side. A rounded-triangle facet on the posterior side of the plantar process is slightly inclined backward. There are facets and a depression for the metatarsal II at the base of the plantar process. Because of the sizes of these facets it is possible that the lateral metatarsals II and V were almost complete in length like those of *Hypertragulus*. The facets of the lateral side of metatarsal III correspond to those of metatarsal IV.

On the proximal surface of metatarsal IV are two distinct cuboid facets. A larger anterior cuboid facet is wider, concave anteriorly and slightly convex posteriorly. A smaller posterior cuboid facet, placed on the plantar process, is strongly inclined exteriorly and posteriorly and continues on the posterior side. A single oval facet is present on the posterior side of the plantar process. This facet is inclined backward. On the proximomedial surface of metatarsal IV there are two elongated facets for metatarsal III: the anterior with a rounded lower part is situated on a small projection, and the posterior one is found on the plantar process. Two rounded facets and a long groove on the lateral side of metatarsal IV confirm the presence of a well-developed metatarsal V. The almost full length of metatarsal II is present in *Hypertragulus*.

The anterior first phalanges are relatively short.

The third phalanx is short and high with a convex dorsal border (fig. 10D, J). The plantar surface of third phalanx has a strongly convex heel. In the hind leg, the articular surface of the phalanx is almost vertical.

The measurements of limb bones are given in table 2.

DISTRIBUTION: Early Oligocene of Khoer-Dzan, Mongolia.

Praetragulus gobiae
(Matthew and Granger, 1925)
Figures 4D, F, 5F

Lophiomeryx gobiae: Matthew and Granger, 1925a: 10.

HOLOTYPE: AMNH 20381, lower jaw with p4–m3.

PARATYPE: AMNH 20379–80, upper jaws.

REFERRED MATERIAL: PIN 475-1486, fragment of upper jaw with M2–M3.

REVISED DIAGNOSIS: Differs from *P. electus* in its smaller size, a longer premolar row, lower molar crowns and a larger mesostyle. Measurements (mm) and indices are as fol-

TABLE 2.
Measurements (mm) of Limb Bones of *Praetragulus electus*

		OR	M	S	N
Radius	L	89.3–93.0	91.2	1.9	2
	DT pr	12.2–14.6	13.4	0.63	21
	DAP pr	7.7–9.5	8.4	0.42	21
	DT di	13.5–15.5	14.3	0.59	17
	DAP di	9.8–11.7	10.4	0.56	17
Metacarpal III	L	56.2–60.4	57.4	1.5	5
	DT pr	7.0–9.2	8.7	1.7	16
	DAP pr	7.5–8.6	8.0	0.29	6
	DT di	7.2–8.3	7.9	0.38	11
	DAP di	7.0–8.4	7.5	0.33	11
Metacarpal IV	L	55.0–55.3	55.1	0.14	3
	DT pr	6.3–8.0	7.3	0.55	13
	DAP pr	6.2–8.0	7.1	0.44	13
	DT di	7.9–8.2	8.1	0.14	3
	DAP di	7.2–7.5	7.3	0.12	3
Calcaneum	L	28.5	—	—	—
	DT	9.5	—	—	—
	DAP	11.1	—	—	—
Astragalus	L	17.5	—	—	—
	DT	8.4	—	—	—
	DAP	9.8	—	—	—
Metatarsal III	L	69.5–70.6	70.1	0.55	2
	DT pr	6.7–7.8	7.0	0.41	5
	DAP pr	10.2–11.5	10.7	0.48	4
	DT di	8.1–8.6	8.4	0.25	2
	DAP di	7.8–8.6	8.2	0.4	2
Metatarsal IV	L	68.3–71.5	69.7	1.3	3
	DT pr	6.3–7.6	6.7	0.34	15
	DAP pr	10.3–11.2	10.5	0.46	10
	DT di	7.8–8.4	8.1	0.25	3
	DAP pr	7.6–8.0	7.8	0.17	3

lows: length M1-M3, 24; length p2-m3, 42.8; ratio p2-p4/m1-m3, 0.57.

DISCUSSION: Matthew and Granger (1925a, 1925b) had some doubt about the reference of this species to *Lophiomeryx*. It differs from all other species of *Lophiomeryx* in the well-developed hypocone of M3, the loss of p1, and the shortness of the premolar row, and appears to belong to *Praetragulus*.

DISTRIBUTION: Late Eocene of Ergilin-Dzo and early Oligocene of Tatal-Gol, Mongolia.

RELATIONSHIPS OF THE HYPERTRAGULIDAE

PRAETRAGULUS AND AMERICAN HYPERTRA-GULIDS: The most ancient American hypertragulids were represented by late Uintan to early Duchesnean *Simimeryx* and Chadronian *Hypertragulus, Parvitragulus* and *Hypisodus* (Webb, 1998). The characters of skull, mandible, dentition and limb bones suggest a close relationship between *Praetragulus* and these North American hypertragulids.

These genera all retain the same primitive features: (1) brachycephalic cranium, (2) unclosed orbits, (3) weakness of the sagittal crest, (4) shortness of temporal crests and their divergence in a short distance to the posterior edges of orbits, (5) lateral exposure of the mastoid, (6) deep subarcuate fossa, (7) well-developed coronoid process with a semivertical anterior margin, (8) relatively low position of the articular process, (9) smaller development of the tubercles on the posterior lobes of the upper molars in comparison to those of the anterior lobes and,

thus, the narrowing of the upper molars backward and a smaller width of the posterior lobe in comparison to the anterior one, (10) weak development of a hypocone on M3, (11) separation of the trapezoid and magnum, (12) tetradactyl pes.

Praetragulus additionally shares with American hypertragulids the following more derived morphological features: (1) strong medial emargination of the palatine, (2) simplification of the premolars, becoming conical, (3) shortening of the premolar crowns at the expense of the anterior part, (4) external enlargement of the upper molars, (5) decrease and compression of the parastyle, (6) reduction of the mesostyle, (7) decrease of paraconid and entoconid on premolars, and (8) co-ossification of the radius and ulna. They are also similar in the morphological peculiarities of the lower jaw: (1) the decrease of the height of the mandible body anteriorly and (2) extension of the angular process downward and backward. Because of the above-mentioned shared derived features, Praetragulus is placed in the family Hypertragulidae.

Of the known hypertragulids, this genus is closest in general morphology of the lower jaw and lower teeth to the most ancient American hypertragulid Simimeryx described by Stock (1934) from the Sespe section of the Simi Valley, California, and reported also from the LaPoint Local Fauna of the Duchesne River Formation in Utah (Emry et al., 1992).

Praetragulus and Simimeryx (CIT 1764) are similar in a suite of the primitive characters, such as: (1) short snout, (2) lower position of the angular process, (3) very weak inclination of the base of the coronoid process backward, (4) short symphysis, (5) short diastema, (6) weak molarization of the premolars, (7) short crest of the entoconid, (8) not crescentic metaconule on M3, (9) unicusped third lobe on m3, (10) brachydonty. All of these characters indicate a very low stage in the development of rumination.

Additionally, both genera also possess other characters testifying to their similar specialization. These characters can be observed in the morphology of the lower jaw: (1) body of the mandible higher under m3 than under p2 and (2) broad, angular process extending strongly downward.

Praetragulus and Simimeryx also share the following derived features: (1) loss of p1 and (2) shortness of the anterior part of the premolar crowns.

But Praetragulus differs clearly from Simimeryx in such significant features as: (1) retention of a mesostyle, (2) absence of a protoconule, (3) compressed parastyle in the permanent molars, and (4) a smaller lower canine. Of these, only the second and third may be regarded as derived features. Praetragulus appears to be more primitive in the smaller size of the lower canine. Due to these characters, these genera do not appear to be especially closely related.

Praetragulus clearly resembles Hypertragulus in many essential peculiarities of the skull: (1) lateral exposure of the mastoid, (2) very small anterior opening of the infraorbital canal, (3) very deep subarcuate fossa, (4) deep medial emargination of the posterior border of the palatine reaching the level of M2.

In comparison with Hypertragulus, Praetragulus occupies a lower evolutionary level judging from the less elongated snout, the lesser degree of selenodonty of the lower cheek teeth, the wide and rounded parastyle on DP4, the unicusped posterior lobe of m3, the almost complete absence of co-ossification of the ulna and radius, and the distally detached fibula. However, Praetragulus is more derived than Hypertragulus in the loss of p1. The microstructure of the tooth enamel is similar in both genera. The simple short prisms do not form Hunter-Schreger bands (Fig. 11).

Two main types of transformation in the dentition can be distinguished among the early hypertragulids. Simimeryx and Hypertragulus exemplify the differences and appear to belong to different lineages:

(1) The evolution of the Simimeryx lineage was connected with an early reduction of p1, apparently before the main lengthening of the diastema behind the lower canine. The disappearance of p1 might have occurred due to the increase in size of the upper canines. In Simimeryx and, possibly, Parvitragulus, p1 was lost and the large lower canine retained a canine function.

In none of the described specimens of Simimeryx and Parvitragulus, as far as can be determined, is the entire symphysis preserved, and none contains incisors. The presence of only four alveolae in the new genus allows the
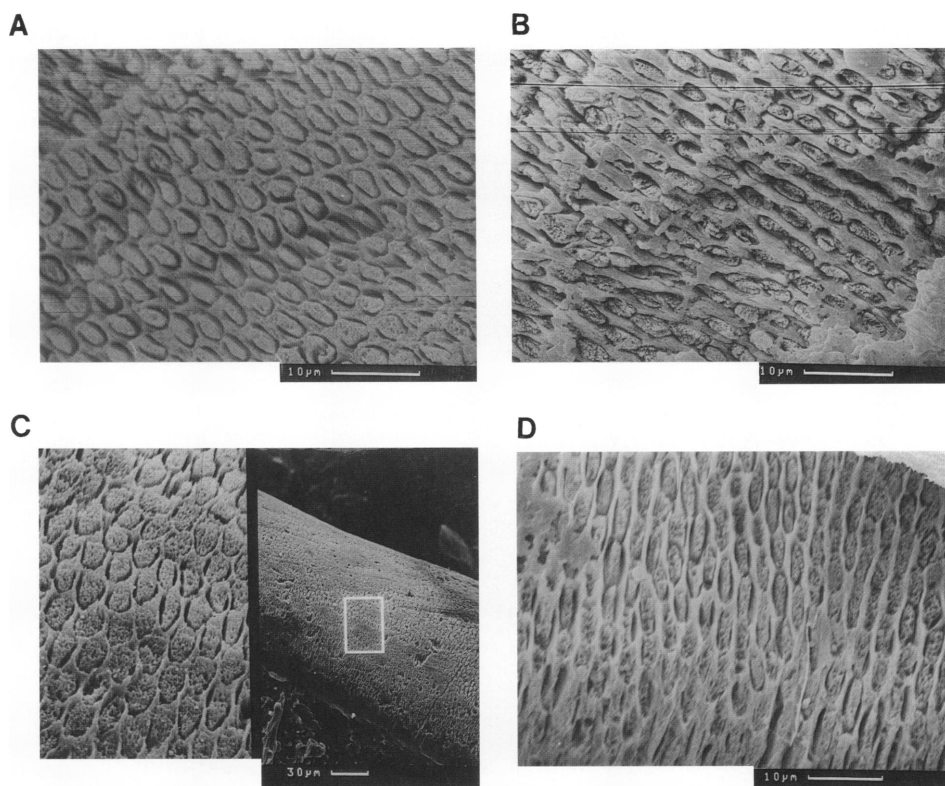
Fig. 11. Microstructure of molars of *Praetragulus electus* (**A, B**) and *Hypertragulus* sp. (**C, D**) in (**A, C**) transverse and (**B, D**) longitudial sections.

suggestion that the larger lateral tooth in *Simimeryx* and *Parvitragulus* (USNM 243970, 243975) might be the lower canine, similar to the condition in all other ruminants, including *Hypertragulus* and *Archaeomeryx,* and not the first premolar as was assumed by Stock (1934) and Emry (1978).

It seems evident that the tendency toward reduction of the premolars in hypertragulids might have led to the disappearance in one of the groups of the first lower premolar as the upper canines increased in size at a very early stage of evolution.

(2) The evolution of the *Hypertragulus* lineage went through the development of a diastema, not only behind the lower canine, but also between p1 and p2, and between p2 and p3, as in many early tragulines, in particular *Archaeomeryx* and *Leptomeryx.*

Those more gradual changes of the *Hypertragulus* dentition were developed in species with small- or medium-sized upper canines

and a small lower canine included in the incisor row. In these species p1 was small and conical. In the lower jaw of a juvenile *Nanotragulus albanensis* Frick, 1937 (AMNH 101262), the lower canine is included in the incisor row, a small sharp p1 is detached, and dp2-dp4 present a closed series.

A small canine appears to be a plesiomorphic character. In the *Simimeryx* lineage the lower canines increased in size, whereas in the *Hypertragulus* lineage they became incisiform and conjoined with the incisor row.

Praetragulus seems to display an intermediate position between *Simimeryx* and *Hypertragulus* characterized by the disappearance of the first lower premolars and the acquisition of incisor function by the lower canines.

The ancestral suite of characters of hypertragulids might include the above mentioned primitive characters as well as the following ones: (1) short snout and symphysis, (2) presence of the posterior opening of the al-

isphenoid canal, (3) posterior position of the foramen ovale, (4) lateral exposure of the mastoid, (5) strong development of the angular process, (6) complete dentition with upper incisors and small canines, (7) partly selenodont but brachydont teeth, (8) wide parastyle, (9) presence of a protoconule and mesostyle, (10) separate trapezoid and magnum, (11) separate radius and ulna, (12) separate tibia and fibula, (13) separate central and complete side metapodials. This suite of characters is apparently similar to that of the most ancient artiodactyls.

PRAETRAGULUS AND EURASIAN TRAGULINES: Apart from the North American hypertragulids, the most ancient Tragulina were known from Asia. Among them, there are several genera referred by some researchers to the family Hypertragulidae. In the Eocene of Asia they were represented by Archaeomeryx, Miomeryx, Notomeryx, Xinjiangmeryx, Lophiomeryx, and Indomeryx (Matthew and Granger, 1925a, 1925b; Pilgrim, 1928; Qiu, 1978; Zheng, 1978). In Europe, only a single genus Bachitherium was sometimes included in the Hypertragulidae (Viret, 1961). But it seems that Praetragulus is the single undoubted representative of the hypertragulids in Eurasia.

Archaeomeryx, first described from Shara-Murun of Nei Mongol, China, is one of the most ancient and well-studied genera of the Tragulina (e.g., Matthew and Granger, 1925b; Colbert, 1941; Patton and Taylor, 1973). According to Berggren and Prothero (1992), the "Sharamurunian land mammal age," traditionally considered as late Eocene and correlated with the Uintan, may be at least partly middle Eocene. Archaeomeryx has been placed either in the family Hypertragulidae (Matthew and Granger, 1925b; Colbert, 1941), often as a separate subfamily Archaeomerycinae (Simpson, 1945) or in the family Leptomerycidae (Webb and Taylor, 1980).

Different suites of primitive characters in Hypertragulus and Archaeomeryx, as well as different apomorphies, clearly show that these genera belonged to different lineages (Patton and Taylor, 1973; Webb and Taylor, 1980; Vislobokova, 1990).

Resembling hypertragulids in many aspects, Praetragulus differs from Archaeomeryx in cranial structure (more lateral position of the mastoid exposure, deep medial emargination of the palatine, etc.), loss of P1, short premolars, and unfused magnum and trapezoid.

The essential differences in the basicranial structure and in the characters of specializations provide evidence that Archaeomeryx and the hypertraguloid lineages diverged apparently no later than the middle Eocene and perhaps even earlier.

Related to Archaeomeryx, Miomeryx from Ergilin-Dzo in Mongolia was referred to hypertragulids (Matthew and Granger, 1925a; Viret, 1961), to gelocids (Simpson, 1945), or to leptomerycids together with Gobiomeryx and Bachitherium (Sudre, 1986). The upper jaw of M. altaicus (AMNH 20383) is very similar to that of Archaeomeryx, but differs in some more derived features (larger size, more elongate premolars, relatively narrower crowns of molars, higher cusps, a weaker metastyle, and a stronger pillar of the paracone). These differences do not exclude the possibility that both genera belong to the same family.

Miomeryx is clearly distinguished from Praetragulus and American hypertragulids by a very long premolar row (with a P2-P4/M1-M3 index of 0.97) and from all hypertragulids except Simimeryx by a rounded parastyle.

Another genus, resembling Archaeomeryx, is Notomeryx from the Bose Basin, China. That genus was initially referred to the Hypertragulidae (Qiu, 1978) but later regarded as a gelocid (Sudre, 1986). The single species, N. besensis Qiu, 1978, is known mainly from the structure of its molars, which are much larger and more crescentic than those in Archaeomeryx.

Notomeryx differs from Praetragulus and American hypertragulids in the robustness of the body of the mandible and the longer premolars. In N. besensis, p3 and m1 are almost equal in length (Qiu, 1978: pl. I, fig. 2).

Xinjiangmeryx, described from the Tufan Basin in Sinkiang, China, was originally referred to the Archaeomerycinae within the Hypertragulidae (Zheng, 1978). Webb and Taylor (1980) believed the genus to belong to the Leptomerycidae. A close relationship between Xinjiangmeryx and Archaeomeryx appears to be quite possible.

Praetragulus also is clearly distinguished from Lophiomeryx and Indomeryx.

Lophiomeryx is a rather well-studied genus (Pomel, 1853; Lydekker, 1885; Matthew and

Granger, 1925a; Colbert, 1935; Flerov, 1938; Gabounia, 1964; Miao, 1982; Brunet and Sudre, 1987; Janis, 1987; Jehenne, 1987; Moyà-Solà, 1988, and others). *Lophiomeryx* was regarded as a gelocid (Simpson, 1945; Viret, 1961; Sudre, 1986, and others), as a hypertragulid (Matthew and Granger, 1925a), as a separate, non-pecoran family (Janis, 1987), and as a "plesion" of the Ruminantia (Geraads et al., 1987).

Similar to *Archaeomeryx* in the basicranial (PIN 3110/964) and postcranial structures but possessing a different set of the plesiomorphic and derived features, *Lophiomeryx* represents undoubtedly a separate, non-hypertraguloid family.

Lophiomeryx is more advanced than *Archaeomeryx* in the following characters: (1) larger saber-like upper canine, (2) longer diastemae between C1-P1 and c1-p1, (3) lengthening of the premolars, (4) more developed selenodonty, (5) diminution of the paraconid, and (6) reduction of mt II and V to stylets. Nevertheless, the posteriorly open orbits in *Lophiomeryx* from Khoer-Dzan, as well as the shorter lingual conids in the most ancient species of *Lophiomeryx-L. angarae* from Ergilin-Dzo in Mongolia (Matthew and Granger, 1925a), *L. shinaoensis,* and *L. gracilis* from Shinao in China (Miao, 1982), testify that *Lophiomeryx* was more primitive than *Archaeomeryx* in some features. Therefore, both genera are clearly divergent and were possibly descendants of the same ancestral group.

Lophiomeryx differs from hypertragulids in the peculiarities of the temporal bone, the absence of the medial emargination of the palatine, the lengthening of premolars, the presence of a separate os malleolus, and in the fusion of the magnum and trapezoid; it differs from *Praetragulus,* additionally, in the presence of p1, a more developed cingulum, the stronger entostyle and ectostylid, and a strong reduction of the lateral metapodials. With their similarly weakly developed hypocone and similarity in the form of the lower incisors, the wear pattern of the lower premolars, the shortness of the inner crests on the lower molars, *Lophiomeryx* and hypertragulids belonged to different phyletic lines of the Tragulina as considered by Simpson (1945).

Indomeryx, known from the Pondaung fauna, Burma, and from the Nadu fauna of the Bose Basin, Guangxi, China, was referred to the Tragulidae (Pilgrim, 1928), to the Hypertragulidae (Colbert, 1938; Qiu, 1978; Xu, 1982), or to the Gelocidae (Simpson, 1945). The lower molars of the type species *I. cotteri* (AMNH 32521) present a very primitive stage of selenodonty, having almost conical lingual conids and a very short anterior wing of the metaconid similar to that of *Simimeryx,* early *Lophiomeryx,* and *Dorcatherium.* According to Pilgrim (1928), the p4 of *Indomeryx* in Indian Museum (k21/538) has a conical protoconid with two posteriorly directed crests and very low para- and hypoconids. Such a structure of p4 clearly distinguishes *Indomeryx* from *Praetragulus* and American hypertragulids.

In *I. youjiangensis* from the Bose Basin (Qiu, 1978: pl. I, fig. 5), p4 (V 4955.1) is longer than m1 as in *Lophiomeryx* and the structure of this tooth is also similar to that of *Lophiomeryx.*

The genus *Bachitherium,* founded by Filhol (1882) from the Stampian of the Phosphorites of Quercy, France, was regarded as a gelocid (Simpson, 1945), as a hypertragulid (Viret, 1961), and was referred to a separate, non-pecoran family (Janis, 1987) or to the Pecora (Geraads et al., 1987). Possessing a rather peculiar morphology, *Bachitherium* appears to belong to a separate family, as Janis (1987) supposed.

Resembling hypertragulids in the form of the lower jaw and in a detached caniniform p1, *Bachitherium* differs from them in a very long, prominent sagittal crest, a high facial part of the skull and its convex facial profile, small orbits, a very robust postorbital bar, and in a number of derived postcranial features similar those of the Pecora (Bouvrain and Geraads, 1985; Geraads et al., 1987), although the astragalus is not of the typical pecoran form (Janis, 1987). Additionally, in contrast to hypertragulids, *Bachitherium* possesses a quite different pattern of the lower premolar molarization. In this genus p4 lacks a metaconid and possesses two posterior crests.

Similar suites of plesiomorphic characters in *Bachitherium* and tragulids, as well as similar apomorphies, testify that both groups belonged to the same branch of the Tragulina.

Another group of this branch is represent-

ed by *Gobiomeryx,* also clearly distinguished from *Praetragulus.* *Gobiomeryx,* recorded from Erghil Obo, Mongolia, and placed in the Gelocidae, differs from *Praetragulus* in a longer premolar row, the presence of p1, the enlargement of the metaconid on p4 and its oblique direction. *Gobiomeryx* is characterized by the very narrow crowns of the lower molars (the length of m1 and m2 is almost twice as longer as the width), a two-cusped third lobe of m3, and well-developed ectostylids (Trofimov, 1957). Besides Mongolia, that genus is recorded from Kazakhstan (Kiin-Kerish), where it is represented by two fragments of upper and lower jaws with first and second molars (Musakulova, 1963). New findings from Mongolia (Vislobokova et al., 1996) show that *Gobiomeryx* is very similar to *Archaeomeryx* and *Lophiomeryx* in the morphology of the lower cheek teeth and in the presence of p1, but differs in the more progressive molarization of the premolars and more developed selenodonty. The metaconid in p4 is enlarged and slightly oblique and extends outward, but the hypoconid is reduced. In p2 and p3, the latter is present. The molars are more crescentic than in *Archaeomeryx* and *Lophiomeryx* and possess the *Dorcatherium* fold.

COMMENTS ON SYSTEMATICS AND PHYLOGENY: Following Scott (1940), the Hypertragulidae together with the Protoceratidae for a long time were placed in the superfamily Hypertraguloidea. But in contrast to Scott (1940), who had referred the Hypertraguloidea to the Tylopoda, that superfamily was usually regarded as a member of the infraorder Tragulina (Simpson, 1945; Viret, 1961).

The Protoceratidae are certainly referred to the Tylopoda (Lavocat, 1951; Viret, 1961; Patton and Taylor, 1973). Thus, the Hypertraguloidea are restricted now to the single family Hypertragulidae.

According to cladistic analysis, almost all recent researchers have concluded that *Hypertragulus* was the most primitive representative of the Ruminantia (Webb and Taylor, 1980; Bouvrain and Geraads, 1985; Geraads et al., 1987; Janis and Scott, 1988; Scott and Janis, 1987, 1992, and others). But whereas some workers, following Webb and Taylor (1980), placed the Hypertragulidae within the Tragulina (Scott and Janis, 1987, 1992),

others regarded *Hypertragulus* only as the most primitive ruminant after *Amphimeryx* (Geraads et al., 1987) or, controversially, more primitive than *Amphimeryx* (Gentry and Hooker, 1988). Geraads et al. (1987) suggested a separate "plesion" Hypertragulidae apart from the Tragulina within the infraorder Ruminantia.

However, the combinations of cranial, dental, and limb characters in hypertragulids and traguloids show that those groups probably represented two independent branches of the Tragulina: the superfamilies Hypertraguloidea and Traguloidea. The Traguloidea links the family Tragulidae and closely related groups (archaeomerycids, leptomerycids, lophiomerycids, bachitheriids, and gelocids). The superfamily Hypertraguloidea, founded by Scott (1940) and adopted by Simpson (1945), is revived here due to the morphological peculiarities, retention of many plesiomorphies, early appearance and diversity, and the important synapomorphies shared with traguloids, which confirms the possible divergence of hypertraguloids and traguloids from a common basal group of the Tragulina.

According to recent data on the early Tragulina of Asia, at least four main phyletic lines existed during the Eocene: (1) archaeomerycids (possibly also including *Miomeryx, Notomeryx,* and *Xinjiangmeryx*), (2) lophiomerycids (possibly including *Indomeryx*), (3) gelocids (*Gobiomeryx*), and (4) hypertraguloids (*Praetragulus*). The first three, having many basicranial and skeletal characters in common with the Tragulidae, belonged to the Traguloidea. The fourth, sharing many characters with the North American hypertragulids, provides evidence of early adaptive radiation of the Tragulina in Asia.

COMMENTS ON ORIGIN AND DISPERSAL: The hypertragulids were regarded as an early offshoot of the primitive ruminant stock (Matthew, 1905; Webb and Taylor, 1980), as an offshoot of the tylopod stock (Scott, 1929), or as a descendant of ancient suiformes (Schlosser, 1886, and others).

The following groups of suiformes were suggested as the remote ancestor of the Tragulina: hyopotamids (Kowalevsky, 1974), dichobunids (Schlosser, 1886), and oreodonts (Cope, 1887). The view of Schlosser (1886) was the most widely accepted for a long

time. The dichobunids were placed at the base of all artiodactyls by Matthew (1934). Pilgrim (1941) believed that tragulids take their origin from helohyids. The origin of hypertragulids was more often connected with homacodonts like *Mesomeryx* (Stock, 1934; Gazin, 1955; Golz, 1976). Gentry and Hooker (1988) referred the Dichobunidae (s.s.) together with Ruminantia to the new suborder Merycotheria. On their cladogram the clade Hypertragulidae is placed above that of Hyperdichobunidae. Besides these groups, the amphimerycids also were considered as possible ancestors for the hypertragulids (Colbert, 1941; Simpson, 1945).

But by their morphology almost none of the above-mentioned groups is suitable for the role of the ancestor of the Tragulina. I agree with Simpson (1945) that traguloids and hypertraguloids arose from the same ancestral group, though possibly not in the Eocene, as Simpson assumed, but earlier, and not from the Amphimerycidae but from an unknown basal group of the Tragulina.

The similarity of the ancestral suite of characters of early tragulines with that of dichobunids, and different trends of evolution of both these groups, leads to the conclusion that the appearance of the tragulines was close to the adaptive radiation of the oldest artiodactyls and, therefore, that there was a very early origin of the infraorder Tragulina and the suborder Ruminantia on the whole. Kowalevsky (1874) might be correct in supposing that the divergence of ancient ungulates into "pari- and imparidigitata" (Artiodactyla and Perissodactyla) had already occurred in the Cretaceous. Scott (1929) had a similar opinion, believing that the artiodactyls and perissodactyls could arise from the condylarths or condylarthrous descendants either at the end of the Cretaceous or at the beginning of the Tertiary period. There is much evidence of the deep similarity of the artiodactyls and arctocyonoid and hyopsodontid condylarths (Schaeffer, 1947; Van Valen, 1971, and others). But the possibility of the origin of artiodactyls from these condylarths appears to be rather unlikely (Rose, 1982; Prothero et al., 1988).

Although the identity of the ancestor of the Tragulina is unknown now, nevertheless that ancestor could have existed already in the Paleocene when the ecological conditions promoting radiation of herbivorous mammals were established (Wing and Tiffney, 1987).

Both Asian and American locations for the origin of the Tragulina have their believers. The Asian origin was presumed by Pilgrim (1941), Simpson (1945), Webb (1977), and others. Stock (1934), Gazin (1955), Golz (1976), and others believed that the most primitive Ruminantia might have originated in the late Eocene of North America.

However, the discovery of rather primitive early hypertraguloids in Asia and data on the distribution of early traguloids support the Asian origin of the Tragulina.

Hypertraguloids, which were originally a part of the earliest radiation of the Tragulina in Asia, could have invaded North America from the Old World by the late Uintan (late middle Eocene, about 41 Ma). *Praetragulus,* evolving in parallel with American hypertragulids, apparently represented an advanced Asian survivor of the ancient hypertraguloid ancestor.

REFERENCES

Berggren, W. A., and D. R. Prothero
    1992. Eocene-Oligocene climatic and biotic evolution: an overview. *In* D. R. Prothero and W. A. Berggren (eds.), Eocene and Oligocene climatic and biotic evolution: 1–28. Princeton, NJ: Princeton Univ. Press.

Black, C. C.
    1978. Paleontology and geology of the Badwatre Creek Area, Central Wyoming. Pt. 14. The artiodactyls. Ann. Carnegie Mus. 47(10): 223–259.

Bouvrain, G., and D. Geraads
    1985. Un squelette complet de *Bachitherium* (Artiodactyla, Mammalia), de l'Oligocène de Céreste (Alpes de Haute-Provence). Remarques sur la systématique des ruminants primitifs. C. R. Acad. Sci. Paris, ser. 2, 300(2): 75–78.

Bouvrain, G., D. Geraads, and J. Sudre
    1986. Révision taxonomique de quelques ruminants oligocènes des phosphorites du Quercy. C. R. Acad. Sci. Paris, ser. 2, 302(2): 101–104.

Brunet, M., and J. Sudre
  1987. Evolution et systematique du genre *Lophiomeryx* Pomel 1853 (Mammalia, Artiodactyla). Münch. Geowiss. Abh. (A) 10: 225–242.

Colbert, E. H.
  1935. Siwalik mammals in the American Museum of Natural History. Trans. Am. Philos. Soc. 26: 1–401.
  1938. Fossil mammals from Burma in the American Museum of Natural History. Bull. Am. Mus. Nat. Hist. 74(6): 255–436.
  1941. The osteology and relationships of *Archaeomeryx*, an ancestral ruminant. Am. Mus. Novitates 1135: 24 pp.

Cope, E. D.
  1879. Observation on the faunae of the Miocene tertiares of Oregon. Bull. U.S. Geol. Geogr. Surv. Terr. 5(1): 55–69.
  1887. The classification and phylogeny of Artiodactyla. Proc. Am. Philos. Soc. 24: 377–400.

Dashzeveg, D.
  1971. Stratigraphy and fauna of the Upper Paleogene of Mongolian People's Republic. Ph.D. diss., Geological Institute Academy of Sciences of the USSR, Moscow.
  1974. The chalikotheriine *Schizotherium avitum* Matthew and Granger from the Oligocene of Ergilin-Dzo, eastern Gobi, and a review of vertebrates from this locality. *In* N. N. Kramarenko (ed.), Fauna and biostratigraphy of the Mesozoic and Cenozoic of Mongolia: 74–79. Moscow: Science.

Devyatkin, E. V.
  1981. Cenozoic of Inner Asia (stratigraphy, geochronology, correlation). Moscow: Science, 196 pp.

Emry, R. J.
  1978. A new hypertragulid (Mammalia, Ruminantia) from the Early Chadronian of Wyoming and Texas. J. Paleontol. 52(5): 1004–1014.

Emry, R. J., P. R. Bjork, and L. S. Russell
  1992. The Chadronian, Orellan, and Whitnean North American land mammal ages. *In* D. R. Prothero and W. A. Berggren (eds.), Eocene-Oligocene climatic and biotic evolution: 118–152. Princeton, NJ: Princeton Univ. Press.

Filhol, H.
  1877. Recherches sur les Phosphorites du Quercy. Étude des fossiles qu'on y recontre, et specialement des mammifères. Ann. Sci. Geol. Paris 8(1): 1–340.

Flerov, K. K.
  1938. On the remains of the Ungulata from Betpakdala. C. R. Acad. Sci. USSR 21 (1–2): 95–96.

Frick, Ch.
  1937. Horned ruminants of North America. Bull. Am. Mus. Nat. Hist. 69: 669 pp.

Gabounia, L.
  1964. Benara fauna of Oligocene vertebrates. Tbilissi: Metsniereba, 267 pp.

Gazin, C. L.
  1955. A review of the Upper Eocene Artiodactyla of North America. Smithson. Misc. Collect. 128(8): 96 pp.

Gentry, A. W., and J. J. Hooker
  1988. The phylogeny of the Artiodactyla. *In* M. J. Benton (ed.), The phylogeny and classification of the Tetrapods, vol. 2: Mammals: 235–272. Oxford: Clarendon Press.

Geraads, D., G. Bouvrain, and J. Sudre
  1987. Relations phylétiques de *Bachitherium* Filhol, ruminant de l'Oligocène d'Europe occidentale. Palaeovertebrata 17(2): 43–73.

Golz, D. J.
  1976. Eocene Artiodactyla of southern California. Nat. Hist. Mus. Los Angeles Cty. Sci. Bull. 26: 1–85.

Janis, C.
  1984. Tragulids as living fossils. *In* N. Eldredge and S. Stanley (eds.), Living fossils: 87–94. New York: Springer-Verlag.
  1987. Grades and clades in hornless ruminant evolution: the reality of the Gelocidae and the systematic position of *Lophiomeryx* and *Bachitherium*. J. Vertebr. Paleontol. 7(2): 200–216.

Janis, C., and K. Scott
  1987. The origin of the higher ruminant families with special emphasis on the members of the Cervoidea. Am. Mus. Novitates 2893: 85 pp.
  1988. The phylogeny of the Ruminantia (Artiodactyla, Mammalia). *In* M. J. Benton (ed.), The phylogeny and classification of the tetrapods, vol. 2, Mammals: 273–282. Oxford: Clarendon Press.

Janovskaja, N. M., E. N. Kurotchkin, and E. V. Devjatkin
  1977. Ergeleen-Dzo locality—the stratotype of Lower Oligocene in South-East Mongolia. *In* B. A. Trofimov (ed.), Mezozoic and Cenozoic faunas, floras and biostratigraphy of Mongolia: 14–33. Moscow: Science.

Jehenne, Y.
1987. Intérêt biostratigraphique des ruminants primitifs du Paléogène et du Néogène inférieur d'Europe occidentale. Münch. Geowiss. Abh. (A) 10: 131–140.

Kowalevsky, W.
1874. Monographie der Gattung *Anthracotherium* Cuv. und Versuch einer natürlichen Klassification der fossilen Huftiere. Palaeontographica 2: 211–290.

Kurotchkin, E. N., and D. Dashzeveg
1979. New occurrence of *Coryphodon* from Oligocene of Mongolia. In L. P. Tatarinov (ed.), Mesosoic and Cenozoic faunas of Mongolia: 7–9. Moscow: Science.

Lavocat, R.
1951. Révision de la faune des mammifères Oligocènes d'Auvergne et du Velay. Paris: Ed. Sciences et Avenir, 154 pp.

Lydekker, R.
1885. Catalogue of the fossil mammalia in the British Museum (Nat. Hist.). Part II. London: Londres, 323 pp.

Lull, R. S.
1922. Primitive Pecora in the Yale Museum. Am. J. Sci., Ser. 5, 4(20): 111–119.

Matthew, W. D.
1905. Notice of two new genera of mammals from the Oligocene of South Dakota. Bull. Am. Mus. Nat. Hist. 21: 21–26.
1929. Reclassification of the artiodactyl families. Bull. Geol. Soc. Am. 40: 403–408.
1934. A phylogenetic chart of the Artiodactyla. J. Mammal. 15: 207–209.

Matthew, W. D., and W. Granger
1925a. New ungulates from the Ardyn Obo formation of Mongolia, with faunal list and remarks on correlation. Am. Mus. Novitates 195: 12 pp.
1925b. New mammals from the Shara Murun Eocene of Mongolia. Ibid. 196: 11 pp.

Mayr, E.
1969. Principles of systematic zoology. New York: McGraw-Hill.

Miao, D.
1982. Early Tertiary fossil mammals from the Shinao Basin, Panxian County, Guizhou Province. Acta Palaeontol. Sin. 21(5): 20–21.

Moyà-Solà, S.
1988. Morphology of lower molars of the ruminants (Artiodactyla, Mammalia): phylogenetic implication. Paleontol. Evol. 22: 61–70.

Musakulova, L. T.
1963. *Gobiomeryx* from the Paleogene of Kazakhstan. In I. G. Galuzo (ed.), Materials on the history of the fauna and flora of Kazakhstan, vol. 4: 201–203. Alma-Ata: Akad. Sci. Kazakhstan SSR.

Olsen, S. J.
1962. The Thomas Farm fossil Quarry. Quat. J. Florida Acad. Sci. 25(2): 142–146.

Patton, T. H., and B. E. Taylor
1973. The Protoceratinae (Mammalia, Tylopoda, Protoceratidae) and the systematics of the Protoceratidae. Bull. Am. Mus. Nat. Hist. 150: 347–414.

Pilgrim, G. E.
1928. The Artiodactyla of the Eocene of Burma. Palaeontol. Indica n.s. 13: 1–39.
1941. The dispersal of the Artiodactyla. Biol. Rev. 16: 134–163.

Pommel, A.
1853. Catalogue méthodique et descriptif des vertébrés fossiles decouverts dans le bassin hydrogeographique superieur de la Loire. Paris: Bailliere, 140 pp.

Prothero, D. R., E. M. Manning, and M. Fischer
1988. The phylogeny of the ungulates. In M. J. Benton (ed.), The phylogeny and classification of the tetrapods, vol. 2: 201–234. Oxford: Clarendon Press.

Qiu, Zh.
1978. Late Eocene hypertragulids of Baise Basin, Kwangsi. Vertebr. PalAsiat. 16(1): 7–12.

Rose, K. D.
1982. Skeleton of *Diacodexis*, oldest known artiodactyl. Science 216(4546): 621–623.

Schaeffer, B.
1947. Notes on the origin and function of the artiodactyl tarsus. Am. Mus. Novitates 1356: 24 pp.

Schlosser, M.
1886. Beiträge zur Kenntnis der Stammesgeschichte der Hufthiere und Versuch einer Systematik der Paar- und Unpaarhufer. Morphol. Jahrb. 12: 1–133.

Scott, K. M., and C. M. Janis
1987. The phylogenetic position of the Cervidae, and the case for a superfamily Cervoidea. In C. Wemmer (ed.), The biology and management of the Cervidae: 3–20. Washington, DC: Smithson. Inst.
1992. Relationships of the Ruminantia (Artiodactyla) and analysis of the characters used in ruminant taxonomy. In F.-S. Szalay, M. J. Novacek, and M. C. McKenna (eds.), Mammal phylogeny, Placentals: 282–302. New York: Springer-Verlag.

Scott, W. B.
1929. A history of land mammals in Western Hemisphere. New York: Macmillan, 693 pp.
1940. The mammalian fauna of the White River Oligocene. Artiodactyla. Trans. Am. Philos. Soc. n. s. 28(4): 363–746.

Simpson, G. G.
1945. The principles of classification and a classification of mammals. Bull. Am. Mus. Nat. Hist. 85: 1–350.

Stock, C.
1934. A hypertragulid from the Sespe uppermost Eocene, California. Proc. Nat. Acad. Sci. 20(12): 625–629.

Sudre, J.
1986. Le genre *Bachitherium* Filhol 1882 (Mammalia, Artiodactyla): diversité, spécifique, phylogénie, extension chronologique. C. R. Acad. Sci. Paris 303(8): 749–754.

Swisher, C. C., and D. R. Prothero
1990. Single-crystal 40 Ar/39Ar dating of the Eocene-Oligocene transition in North America. Science 249: 760–762.

Taylor, B. E., and S. D. Webb
1976. Miocene Leptomerycidae (Artiodactyla, Ruminantia) and their relationships. Am. Mus. Novitates 2596: 22 pp.

Trofimov, B. A.
1957. Nouvelles données sur les Ruminantia les plus ancient d'Asie. Curs. Conf. Inst. "Lucas Mallada" 4: 137–141.

Van Valen, L.
1971. Toward the origin of artiodactyls. Evolution 25(3): 523–529.

Viret, J.
1961. Artiodactyla. *In* J. Piveteau (ed.), Traité de Paléontologie, t. 6, vol. 1, 887–1021. Paris: Masson et Cie.

Vislobokova, I.
1990. The basic feature of historical development and classification of the Ruminantia. Paleontol. J. 4: 3–14.

Vislobokova, I., E. Dmitrieva, and B. Trofimov
1996. Ruminants on the Paleogene–Neogene boundary in Mongolia. Paleontol. J. 30(1): 99–108.

Wang, B.
1992. The Chinese Oligocene: a preliminary review of mammalian localities and local faunas. *In* D. R. Prothero and W. A. Berggren (eds.), Eocene and Oligocene climatic and biotic evolution: 530–547. Princeton, NJ: Princeton Univ. Press.

Webb, S. D.
1977. A history of savanna vertebrates in the New World, Part I: North America. Annu. Rev. Ecol. Syst. 8: 355–380.
1998. Hornless ruminants. *In* C. M. Janis, K. M. Scott, and L. L. Jaulos (eds.), Evolution of Tertiary mammals of North America. New York: Cambridge Univ. Press. (in press).

Webb, S. D., and B. E. Taylor
1980. The phylogeny of hornless ruminants and a description of the cranium of *Archaeomeryx*. Bull. Am. Mus. Nat. Hist. 167(3): 117–158.

White, T. E.
1940. New Miocene vertebrates from Florida. Proc. New England Zool. Club 18: 31–38.

Wing, S., and B. Tiffney
1987. The reciprocal interaction of angiosperm evolution and tetrapod herbivory. Rev. Paleobot. Palynol. 50: 179–210.

Xu, Q.
1982. Paleogene climate change and mammalian fauna in Bose Basin of Guangxi. Vertebr. PalAsiat. 20(4): 327–336.

Zheng, J.
1978. Description of some late Eocene mammals from Lian-Kan formation of Turfan Basin, Sinkiang. Mem. Inst. Vertebr. Palaeontol. Palaeoanthrop. Acad. Sin. 13: 116–125.