

THE PHYLOGENY OF
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A DESCRIPTION OF THE
CRANIUM OF ARCHAEMERYX

S. DAVID WEBB AND BERYL E. TAYLOR

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S. DAVID WEBB

*Curator of Fossil Vertebrates, Florida State Museum
University of Florida*

BERYL E. TAYLOR

*Frick Associate Curator, Department of Vertebrate Paleontology
American Museum of Natural History*

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ABSTRACT

We analyze the interrelationships of the several groups of hornless ruminants and show which of them lie nearest the higher ruminants. The phylogenetic progression within Ruminantia proceeds from Hypertragulidae through Tragulidae to Leptomerycidae to Gelocidae to Moschidae and thence to the horned ruminants. *Archaeomeryx* of the late Eocene is recognized as a primitive member of the Leptomerycidae; the living Tragulidae actually represent a more primitive ruminant stock. We introduce the name *Moschina* for the Gelocidae and Moschidae and the term *Eupecora* for the higher ruminant groups bearing horns, antlers, and ossicones. We also propose *Neoselenodontia*, above the subordinal level, to

include both the Ruminantia and their sister group, the Tylopoda.

The stratigraphic records of the five lower ruminant families appear relatively complete with the exception of the Tragulidae, which are poorly known prior to the Miocene. The exclusively North American distribution of the family Hypertragulidae and many of the Tylopoda suggests that the Ruminantia may have originated in North America. The Tragulidae, exclusively Old World and predominantly subtropical, presumably originated by colonization and isolation in the Old World. Thereafter ruminant evolution centered in the Old World, but representatives of every major group reached North America.

INTRODUCTION

As the most successful living group of large mammals and as a major source of food and clothing for man, the ruminants command considerable attention. Within the Ruminantia, however, the hornless groups receive little study in comparison with that expended on the Pecora (higher ruminants). This discrepancy is evident both in Recent and in fossil studies.

The lower ruminants span a great and formative evolutionary void between the late Eocene radiation of selenodont artiodactyls (of which only the Camelidae survive) and the middle Miocene flowering of the higher (horned, antlered, or ossiconed) ruminants. Like so many groups that spawned successful evolutionary radiations, the hornless ruminants are relatively small, often rare, and generally unobtrusive in character. As fossils they are generally difficult to study, partly because they are rare, partly because they lack the cranial appendages that provide such a ready key to the relationships of the higher ruminants. Lower jaws, the most frequently preserved elements of lower ruminants, are difficult to place in a phylogenetic framework. Only complete skeletons provide a satisfactory basis for broad analysis. The few living lower ruminants (in the Tragulidae and Moschidae) are such specialized

relicts that they require thorough comparison with fossil groups before they cast light into the void. Thus, many practical factors have hindered the study of hornless ruminants.

The purpose of this study is to revise the interrelationships of the hornless ruminants and to clarify the origins of the horned ruminants. This study is warranted by the greatly improved collections of mid-Tertiary ruminants that have become available during the past few decades. We have also found that further preparation of old collections can produce new diagnostic characters, as in our restudy of *Archaeomeryx*.

For this study we reviewed the osteology of taxa representing all major groups of fossil and living lower ruminants. We separately analyzed each of three sets of osteological data: (1) cranial data, particularly details of the basicranium and petrosal; (2) dental data, especially premolar patterns; and (3) postcranial data, especially podial features. As we shall show, each of the three data sets gave essentially concordant results. Further testing of our phylogenetic hypotheses will come from future analysis of still other characters and from discovery of other lower ruminant fossils.

ACKNOWLEDGMENTS

We relied primarily on the fossil and Recent collections of four museums for this comparative survey: American Museum of Natural History (New York), British Museum of Natural History (London), Museum National d'Histoire Naturelle (Paris), and the Basle Naturhistorisches Museum. A Guggenheim Fellowship in 1973 permitted Webb to study early ruminants in various western European museums. We thank our many colleagues who have helped us by offering their hospitality and encouragement and by sharing their knowledge and insights. Deep appreciation is expressed to Dr. Richard H. Tedford, Mr. Earl Manning and the late Dr. Roger Hamilton for critically reading the manuscript and giving helpful sugges-

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ABBREVIATIONS

AMNH, Department of Vertebrate Paleontology, American Museum of Natural History
 AMNH (M), American Museum of Natural History, Modern Mammals
 F:AM, Frick American Mammals, Department of Vertebrate Paleontology, American Museum of Natural History
 USNM, United States National Museum, Smithsonian Institution

PREVIOUS PHYLOGENETIC VIEWS

The first question about ruminant relationships concerns their origins. Surely they emerged in the late Eocene radiation of selenodont artiodactyls, and are now the only really successful product of that radiation. In the Miocene or later it is a simple matter to distinguish ruminants from other lingering selenodont groups, but in the late Eocene the ruminants are easily lost in the evolutionary ferment of a dozen selenodont families in north temperate regions.

One looks almost automatically for evidence of ruminant origins among the wealth of selenodont artiodactyls from the late Eocene of western North America. There during the last 25 years immense progress has been made in sampling the richly diversified selenodont faunas through successive formations of Uintan and Duchesnean ages. Gazin (1955) provided an excellent review of late Eocene selenodont phylogeny in the Rocky Mountain region. And his work has been amplified by the work of Ferrusquia-V. (1969) in Chihuahua, Wilson (1974) in west Texas, Black (1978) in Wyoming, and Golz (1976) in California.

Unfortunately, students of North Ameri-

can early selenodonts generally have made only limited comparisons with Eurasian groups. For example, Gazin (1955, p. 15) remarked "I fail to find . . . any justification for considering our selenodont stocks as derived from those of Europe. The trend toward selenodonty has surely progressed independently . . . in the two areas." This view has been supported by Golz (1976) and especially by Black (1978) who produced a cladogram of *North American* late Eocene selenodont families. Such separatist views extend back into the nineteenth century when Rutimeyer (1883) and Scott (e.g., 1899) promulgated them.

This prevailing separatist view of early selenodont phylogeny was questioned by Matthew and Granger's (1925) description of *Archaeomeryx* from late Eocene deposits of Mongolia and their recognition that it was related to at least some early selenodonts in North America. Wilson (1974) renewed this concern by noting the dental resemblances between *Archaeomeryx* and late Eocene *Leptomeryx* (now *Hendryomeryx* of Black, 1978) in North America. Likewise Lavocat (1951) and Viret (1961) recognized *Bachithe-*

rium and *Miomeryx* as European and Asiatic Leptomerycidae, thus indicating that this family maintained a Holarctic distribution during the Oligocene as well. Such evidence suggests that the study of early ruminants must not be confined to North America but must also include Eurasia. (See Addendum.)

Among many views as to which ruminants are the most primitive, four rival claims have some currency. These four rivals are *Archaeomeryx* from the late Eocene of Mongolia; Hypertragulidae from the late Eocene and younger of North America; Amphimerycidae from the late Eocene and lower Oligocene of Europe; and Tragulidae, still living in parts of the Old World tropics.

The main claim of *Archaeomeryx* as a primitive ruminant was its great antiquity. Although few late Eocene ruminants were adequately known when Matthew and Granger (1925) described *Archaeomeryx*, it is now obvious, especially in North America, that there are several late Eocene genera, of which at least *Simimeryx* is older than *Archaeomeryx* (Golz, 1976). In any case, the antiquity of a taxon is an inadequate basis for asserting its primitiveness.

We have suggested elsewhere (Taylor and Webb, 1976), that *Archaeomeryx* is an early leptomerycid. We further support this view here and show that, in many respects, the Leptomerycidae are more derived than the Hypertragulidae. Thus, we may narrow the search for the most primitive ruminant family to the Tragulidae, Hypertragulidae, and Amphimerycidae.

Many neomammalogists and a few paleontologists have regarded the Tragulidae as the most primitive ruminants. Indeed, some authorities have been so impressed by the primitive nature of the Tragulidae that they have questioned their inclusion in the Ruminantia altogether. For example, Walker (1975, p. 1379) stated that tragulids "seem to be more closely related to camelids (Camelidae) and pigs (Suidae) than to deer (Cervidae)." Dubost (1965), calling upon his extensive field experience with chevrotains, showed that in a number of their ethological traits, including their manner of lying down, copulating, and fighting, they are more "por-

cins" than ruminants. Most startling are Duwe's (1969) immunological comparisons in which *Tragulus javanicus* shares more skeletal muscle antigens with the suiforms, *Dicotyles tajacu* and *Phacochoerus aethiopicus*, than with the ruminants, *Bos taurus*, *Okapia johnstoni*, and *Odocoileus virginianus*. Chromosome studies in two species of *Tragulus* yield a diploid number of 32 and a normal sex-determining mechanism (Yong, 1973 and Todd, 1975), which can be compared about as well with a number of suiforms as with *Giraffa*, although Todd emphasized the latter. Also, *Tragulus* X-chromosomes are clearly distinguishable from those of cervoids and bovovoids by the absence of the characteristic translocation-fusion of an autosomal fragment (Todd, 1975). While these diverse lines of evidence emphasize how remotely the tragulids appear to be related to the higher ruminants (Pecora), they do so only by primitive features. Such features do not place them outside of the ruminants, since they do not relate them to some alternative group.

Substantial evidence as to how the Tragulidae are allied to Ruminantia has been provided by a long line of distinguishing anatomists. Serious work began with A. Milne-Edwards's great dissertation published in 1864. More detailed contributions to knowledge of tragulid visceral anatomy were made by Flower (1867), Garrod (1877), Boas (1890), and Strahl (1905) after which Pocock (1919) produced his usual careful survey of the external characters. Finally, Carlsson (1926) provided a critical review of all anatomical features with comparative phylogenetic significance. In the course of these classic studies the tragulids were set apart first from the musk deer (*Moschus*) and the Cervidae by Milne-Edwards, and then from all higher ruminants by Flower. In Flower's classification of 1883 the Tragulina became one of the four artiodactyl suborders, set far from Suina and falling between the Tylopoda (camels) and the Pecora (higher ruminants). Indeed, each of these classical anatomists placed the Tragulidae as the sister group of the Pecora rather than the Tylopoda. For example, Boas (1890) found that the tragulid

stomach has the reticulum and other ruminant structural modifications, even though the middle gut (psalterium or omasum) is nearly absent as in small antelopes such as *Cephalophus*. Although the camelid stomach is also essentially three chambered, it is not at all tragulid-like for it lacks a true reticulum and has a long and distinctively thin walled middle gut. Likewise, the fusion of the cubonavicular in the pes and the trapezoidomagnum in the wrist are derived features shared by the Tragulidae and Pecora, but not by Tylopoda. For such reasons the Tragulidae were correctly allied with the Pecora rather than with the Tylopoda.

The question of whether the Tragulidae or Hypertragulidae are the more primitive ruminants has not been resolved. Simpson (1945) adopted the "working theory . . . that hypertragulids and tragulids arose in the Eocene from the same immediately ancestral group"; Whitmore (1953, p. 155) expressed his frustration with the unresolved problem as follows:

"No conclusive evidence has been adduced concerning the relationship between the Hypertragulidae and the Tragulidae. Many similarities exist between the extinct family and the living one, but probably most of these are due to small skull size." Thus the Hypertragulidae and the Tragulidae have persisted as rivals for the title of most primitive ruminants.

A third family of late Eocene artiodactyls, the Amphimerycidae, have been mentioned as a primitive possible member of the Ruminantia. The only basis for this hypothesis is the fused cubonavicular described by Pomel (1851) from the Phosphorites of Quercy and attributed by him and by Stehlin (1906-1910) to *Amphimeryx*. This single character has not led most students of artiodactyl phylogeny, such as Stehlin (1906-1910), Lavocat (1951), or Viret (1961) to include Amphimerycidae within the Ruminantia. Rather, they have allied the Amphimerycidae with Xiphodontidae on the basis of a large suite of primitive and derived characters in common. These features include narrow elongate premolars in closed series or with a small diastema behind P_2 , a premolariform lower canine adja-

cent to a similar P_1 ; five-crested, triangular upper molars with extremely strong lingual cingula, and elongate metapodials with precociously reduced side toes. We do not believe that one (possibly incorrect) resemblance between Amphimerycidae and true ruminants is an adequate basis for recognizing a special relationship. We suspect that the cubonavicular fusion arose independently in these two groups. We therefore follow Viret (1961) in excluding the Amphimerycidae from early ruminants pending further evidence.

We turn next to the question of which hornless ruminants are thought to lie nearest the horned ruminants. This question too is unresolved in the present literature. At least three mutually exclusive views currently claim support (fig. 1). One view favors the Tragulidae, another favors *Archaeomeryx*, and another favors *Gelocus* as the nearest relatives of higher ruminants. None of these views has been documented to the point where it has supplanted all of the others.

The principal impetus for regarding the Tragulidae as most closely related to horned ruminants comes from the study of Recent forms. There is no disputing that, *of the living forms*, the Tragulidae, more than the Tylopoda, are the nearest allies of the Pecora (Flower, 1883). In an inadvertent and ironic way the fossil record has lent support to this view, by virtue of the late appearance of definite Tragulidae in known rock strata. *Dorcatherium*, *Dorcabune*, and *Tragulus* itself appear after the beginning of the Miocene in Europe, Africa, and Asia. Earlier possible Tragulidae generally have been discounted.¹ Most recently, Friant (1967) has maintained that the Tragulidae (*sensu stricto*) include the immediate ancestors of higher ruminants.

Paleontologists generally have advocated

¹ Tragulidae may have existed during the early Oligocene in Mongolia whence Trofimov (1957, 1958) has described *Gobiomeryx*, to which Musakulova (1963) has referred additional material. Furthermore, the status of Schlosser's (1886) *Cryptomeryx*, known only from a few molar teeth from the late Eocene of Bavaria, has never been satisfactorily resolved, although he, Carlsson (1926), and others suggested that it may be a tragulid.

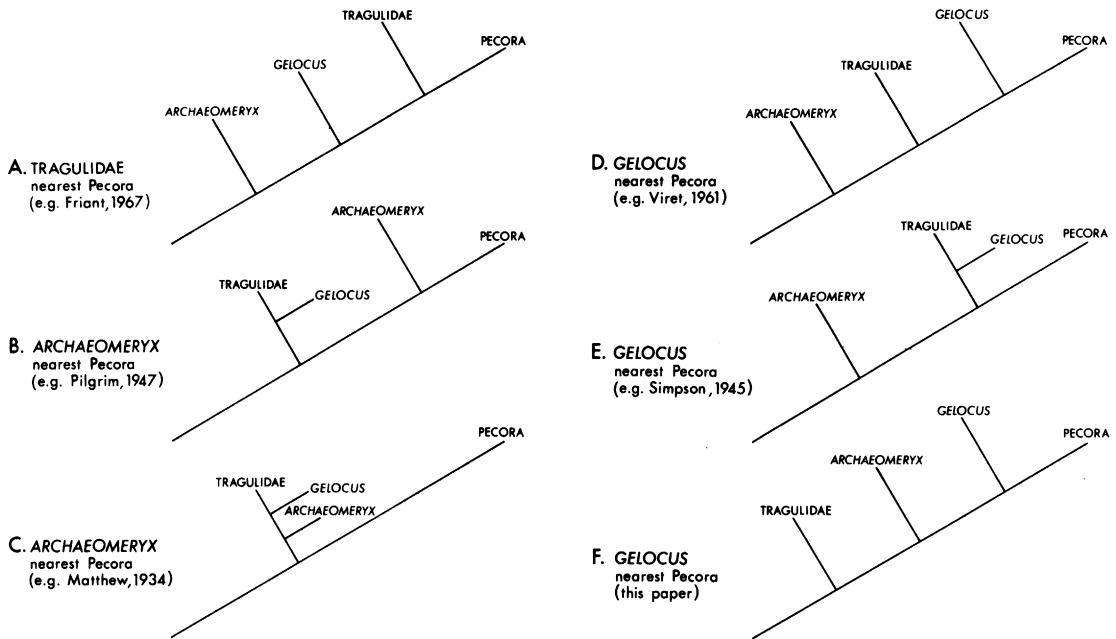


FIG. 1. Cladograms depicting some previous views of relationships among hornless ruminants. (See text.)

either *Gelocus* or *Archaeomeryx* as the nearest relative (or even ancestor) of the higher ruminants. Continental Europeans (e.g., Viret, 1961) usually have supported *Gelocus* from Europe for this role, while Americans (e.g., Colbert, 1941) generally have favored *Archaeomeryx* from Asia.

Kowalevsky (1876) proposed the little Oligocene ruminant, *Gelocus*, as the probable ancestor of the higher ruminants. Subsequent European students, including Filhol (1882), Schlosser (1886), Pavlow (1900), Stehlin (1906–1910), Lavocat (1951), and Viret (1961) have elaborated his work, extending the range of *Gelocus* back into the late Eocene, adding a number of related genera, and establishing the family Gelocidae.

Some 50 years ago, the Central Asiatic Expeditions of the American Museum of Natural History produced the remarkable *Archaeomeryx* from the late Eocene of Mongolia. First Matthew and Granger (1925) and then Colbert (1941) emphasized that *Archaeomeryx* lacked most of the specializations that barred other early selenodonts

from being recognized as the ancestors of higher ruminants.

The dilemma of whether *Gelocus* or *Archaeomeryx* is the more likely progenitor of higher ruminants has persisted for over 50 years. Some paleontologists have tried to espouse both views. For example, in his text Colbert (1941) advocated Matthew and Granger's view of *Archaeomeryx* as ruminant progenitor, but in his dendrogram he placed the Gelocidae in the direct ancestry of the higher ruminants, and relegated *Archaeomeryx* with the Hypertragulidae as sterile cousins. Romer (1966, p. 274) did the reverse by speaking of the gelocid ancestry of ruminants in the text but placing the Gelocidae aside in his phylogenetic diagram. Pilgrim (1947, p. 273) while favoring *Archaeomeryx*, expressed decided ambivalence in the following passage: "*Gelocus* and *Prodremotherium* . . . belong to the family of chevrotains (Tragulidae) but they belong to a side branch which did not lead directly to the living species. *Archaeomeryx* may be more truly regarded as an ancestral chevrotain, but, to-

gether with other genera which are less closely on the direct pecoran ancestry, it has been classified as a distinct family, the Hypertragulidae.”

This dilemma has been minimized by closely allying the Gelocidae and Hypertragulidae (including *Archaeomeryx*). Matthew (1934) and Colbert (1941) merged both extinct families with the surviving Tragulidae. This reversed Colbert's own advice (Colbert, 1938, p. 396) that recognizing such “an inclusive family, Tragulidae is an obviously bad procedure . . .” Matthew's (1929) earlier classification brigaded the Hypertragulidae with the Tragulidae, and did not mention the Gelocidae at all.

A similar dilemma concerns the Tragulidae and the Gelocidae. Brigading them both in one family does not dispel the basic disagreement as to which of these two groups is more closely related to the higher ruminants. Thus, Simpson (1945) supposed that the Tragulidae (in which he included Gelocidae) were the more progressive, but Viret (1961) denied this arrangement and implied that the Tragulidae must have diverged early from the common ancestry of the Gelocidae and higher ruminants. This difference between Viret and Simpson was not based on the contents or definitions of the families in question, for both workers included essentially the same genera. One suspects that Simpson was influenced by stratigraphic evidence, for he stated (1945, pp. 265–266) that since the tragulids “cannot be traced back very far (late Miocene)” and since the older gelocids “are similar to *Tragulus* in basic structure . . .” the Gelocidae may be placed “with their least modified descendants.” Simpson astutely noted that “the resemblance [between the Gelocidae and Tragulidae] is mostly in primitive characters and so does not imply direct phylogenetic connection

. . . .” Likewise, the character cited by Viret (1961) and Romer (1966) to unite the Gelocidae with the Tragulidae, namely the presence of a premolariform first lower premolar, is merely a primitive one (see discussion under Dental Comparisons). Thus, we are left with unresolved family-level relationships at the top and at the bottom of the whole array of hornless ruminants.

As noted above, many past studies have grouped all of the lower ruminants into one or two families. Even so distinguished a student of artiodactyls as Matthew (1929, 1934) placed all lower ruminants in the family Tragulidae. This does not adequately represent the broad array of phyletic branches and morphological distinctions that have arisen in the course of early ruminant evolution. We therefore support the recent tendency to more carefully divide the hornless ruminants. We urge the distinction between the extinct families Hypertragulidae and Leptomerycidae, suggested by Gazin (1955) and previously supported by us (Taylor and Webb, 1976). Similarly, for reasons we develop below, we advocate recognition of the family Gelocidae, a group well established in the European literature since Schlosser (1886) introduced it. We also encourage broader use of the Moschidae of Gray (1872) to include long-fanged antlerless fossil taxa such as *Blastomeryx* and *Dremotherium* with the living musk deer, *Moschus* (see Sigogneau, 1968). On the other hand, addition of the name Dremotheriidae of Ginsburg and Heintz (1966) in this same part of the phylogeny seems redundant.

Of the various groups thus studied, we here recognize five families of hornless ruminants. Two of them, Tragulidae and Moschidae, have living representatives; the other three, Hypertragulidae, Leptomerycidae, and Gelocidae, are wholly extinct.

DESCRIPTION OF *ARCHAEOMERYX* CRANIUM

As we have noted, *Archaeomeryx* has figured crucially in discussions of ruminant origins and relationships. Yet, curiously, its cranium has received very limited study. Be-

fore comparing other ruminant crania, therefore, we provide a description of the cranium of *Archaeomeryx*.

This description of the cranium is based

primarily upon a crushed skull of a young adult, AMNH 20311, which is the type of *Archaeomeryx optatus* from the Shara Marun Formation near Ula Usu, Inner Mongolia autonomous region of China. The braincase was crushed in an exact dorsoventral orientation so that the dorsal and ventral features are not skewed sideways; all measurements are approximate. The entire right petrosal bone and much of the left one are preserved uncrushed and with only minor fractures. The accompanying figures were made from camera lucida drawings.

CRANIAL ROOF: The frontals and parietals are the best preserved bones in the skull, having suffered only one crack and negligible distortion. They present an essentially flat dorsal surface, about as in *Leptomeryx* or *Hyemoschus*, although these are larger-skulled taxa. The profile figured by Colbert (1941) cannot be accurate, as the frontal "forehead" is much too prominent. A slight slope does emerge near the posterior edges of the orbits as in other Leptomerycidae, Hypertragulidae, and Tragulidae. The orbital rims lie within the frontal plane, whereas in *Hypertragulus* they rise above that plane. In this young adult specimen the distance between the midline and the orbital rim is 12.5 mm. A large supraorbital foramen lies 8.5 mm. anterior to the parietal suture and 3.5 mm. medial to the orbital rim. From that foramen a deep vascular groove extends anteriorly and slightly medially. In the depth and size of this groove *Archaeomeryx* resembles *Leptomeryx* more than *Hypertragulus*.

The frontoparietal suture is well marked in the young *Archaeomeryx* skull, and the suture trends laterally and anteriorly from the midline toward the postorbital bar. Its course is sinuous, presenting a posterior convexity in its medial portion and posterior concavity in its lateral portion. Essentially the same pattern occurs in *Leptomeryx*. In *Hypertragulus* the medial convexity is more pronounced and the lateral concavity is hardly noticeable, perhaps in correlation with the weaker postorbital constriction of the genus.

A weak parietal crest, marking the origin of the anterodorsal part of the temporal mus-

cle, can be seen in *Archaeomeryx*. It arises from the weak sagittal crest on the midline 9 mm. posterior to the frontal suture and 33 mm. anterior to the strong lambdoidal crest. It proceeds toward the postorbital bar but disappears after 10 mm. The parietal crests diverge more abruptly in *Archaeomeryx* than in *Leptomeryx*, thus resembling *Hypertragulus*.

A conspicuous postparietal foramen lies 4.5 mm. lateral to the sagittal crest in the posterior third of the parietal. From it a shallow groove runs posteromedially. This foramen corresponds very closely with the postparietal foramen in *Leptomeryx* (Whitmore, 1953).

BASICRANIUM: Several important features can be discerned in the crushed basicranial region of *Archaeomeryx*. Near the anterior end, the ventral foramen of the supraorbital canal is evident. Centrally, the anterior end of the basisphenoid is 2.6 mm. wide. The roots of the pterygoids are firmly fused to it. The anterior edge of the alisphenoid bone can be observed on the right side of the skull. A large foramen orbitorotundum, poorly preserved, is present as in all Ruminantia and Tylopoda. A prominent crest proceeds posterolaterally a distance of nearly 10 mm. separating the course of the eustachian canal from the origin of the tensor veli palatini muscle.

The long deep eustachian canal, represented on both sides of the skull, closely resembles the same structure in *Leptomeryx*. Just lateral to the anterior third of the crest a moderately large pterygoid foramen enters the basisphenoid as in most ruminants. The foramen ovale, near the posterior edge of the alisphenoid, is unusually long and slitlike as in *Leptomeryx*.

The basioccipital has a width of 5.0 mm. Its margins are excavated adjacent to the petrosal bones. The posterior region of the basicranium, including the occipital condyles, closely resembles the same region in *Leptomeryx*.

The anteromedial portion of an ossified bulla occupies the right side of the *Archaeomeryx* skull, AMNH 20311. It has a low rounded profile and is hollow inside. The

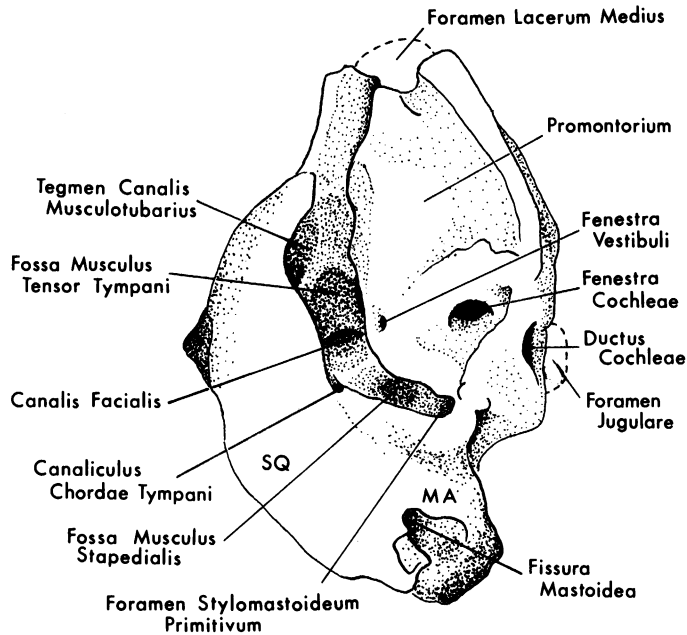


FIG. 2. Ventral view of right petrosal of *Archaeomeryx optatus*, Type, AMNH 20311. Anterior end toward top. Breakage in region of fenestra cochleae and fenestra vestibuli restored by camera lucida reversal from left petrosal. Approximately $\times 8$.

ventral surface bears a posterolateral-trending crest; a depression near the center represents the anterior edge of the stylohyoid cavity. If correctly interpreted, the bulla of *Archaeomeryx* is weakly inflated, non-cancellous, with a nearly central groove for the tympanohyal. In all of these features it resembles the bulla of *Leptomeryx*.

A portion of the right mastoid bone and an adjacent part of the squamosal are present also. The squamosal bears a strong, nearly horizontal crest representing the posterior end of the zygomatic arch as it turns medially to join the lambdoid crest. The mastoid was evidently exposed only on the occipital surface, since its anterior end is covered by the posterior end of the zygomatic crest. This posterior exposure of the mastoid in *Archaeomeryx* closely resembles that of *Leptomeryx* (Whitmore, 1953, p. 150). The anterior part of the mastoid-squamosal suture is marked by a fenestra 3 mm. long, much like that in *Leptomeryx* (Scott, 1940, p. 542).

PETROSAL (FIGS. 2 AND 3): The petrosal of

Archaeomeryx is well represented in AMNH 20311. The ventral face (fig. 2) is described before the endocranial face (fig. 3). (What is here termed the "ventral" surface actually faces anteroventrolaterally.)

The thick posterior portion of the petrosal has fused broadly with the exoccipital near the root of the paroccipital process, although that bone was subsequently crushed. The medial wall of the petrosal is also thick, the dorsoventral dimension ranging from 4 mm. posteriorly to 2 mm. at the anteromedial corner. The thick medial wall of the petrosal closely resembles that in *Leptomeryx*; it is similarly grooved for the median branch of the internal carotid artery. The position of the jugular foramen is marked by a shallow concavity just anterior to the thickest and most prominent projection of the medial wall. This foramen was obviously narrow, being confined anterolaterally by the thickened petrosal and posteromedially by the basioccipital and exoccipital at their junction, much as in *Leptomeryx*. The cochlear

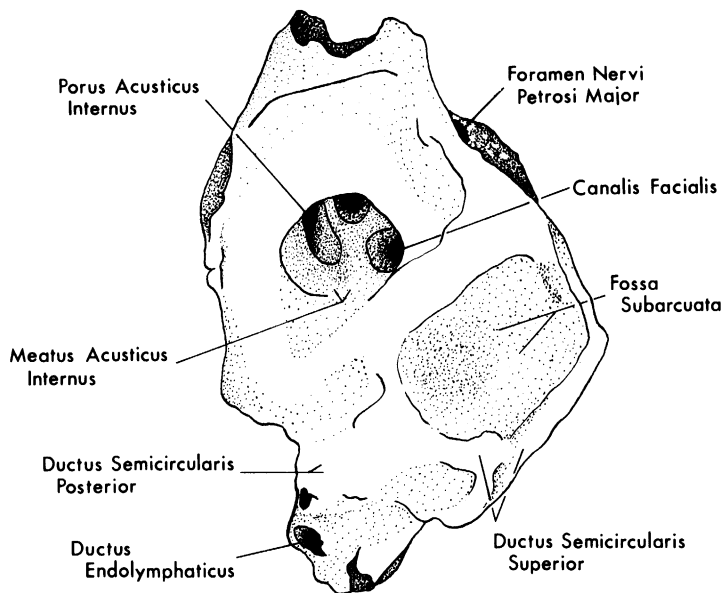


FIG. 3. Endocranial view of right petrosal of *Archaeomeryx optatus*, Type, AMNH 20311. Anterior end toward top. Approximately $\times 8$.

duct enters the thick petrosal through the same posteromedial concavity, but lies nearer the endocranial face, and passes laterally in the direction of the cochlea. Anterior to the jugular foramen the medial wall of the petrosal forms a gentle convexity. Two thin processes from the anterior end of the petrosal help enclose the median lacerate foramen. The anteromedial process touches or nearly touches the basioccipital bone and the anterolateral process overlaps the alisphenoid bone in the region of the eustachian canal.

The promontorium is a long subtriangular surface that dominates the ventral aspect of the petrosal. A broad groove borders the convex medial edge of the petrosal; it is diagnostic of *Archaeomeryx* and *Leptomeryx*; laterally it gives way to the elevated portion of the promontorium. The cochlear whorls above this surface are masked by the subdued slopes of its thickened bone.

The presence in *Archaeomeryx* of a promontory artery with a stapedia branch is highly probable but not proved. In low-angle light a groove for the promontory artery is evident

near the middle of the promontorium of the right petrosal, but the rest of the surface is too poorly preserved to follow it in either direction. Although the area anterior to the fenestra ovale is moderately well preserved on the left petrosal, no trace of a stapedia artery can be found. The courses of both arteries are well marked in specimens of *Leptomeryx*, which encourages the supposition that they would be visible in more favorable material of *Archaeomeryx*.

The fenestra cochleae enters the posterior end of the promontorium. Its thickened ventral margin covers the first cochlear whorl. This ventral margin is retracted anteriorly so that the aperture appears to face ventrally as well as posteriorly. It has a similar arrangement in *Leptomeryx* and *Hypertragulus*. A subtriangular tuberosity descends from the petrosal near the posteromedial edge of this aperture. Presumably it buttresses the basioccipital at its contact with the petrosal. A similar feature occurs in *Hypertragulus*, but is more subdued in *Leptomeryx*.

In *Archaeomeryx* the chamber for the stapedia muscle is long and narrow and main-

tains a nearly uniform tubular cross-section as it curves around the posterior side of the fenestra cochleae. A minor constriction near the middle of the chamber results from encroachment by the posterior wall of the petrosal. A closely similar constriction occurs in *Leptomeryx*. In *Archaeomeryx*, as in *Leptomeryx*, the stylomastoid canal continues on essentially the same course that the facial nerve and vessels take through the stapedial muscle chamber. A moderate-sized foramen for the chorda tympani nerve pierces the wall of the stapedial muscle chamber near its anterior end and proceeds posterolaterally in the mastoid bone. *Archaeomeryx*, like *Leptomeryx*, has a small fenestra vestibuli, its long axis attaining only about one-sixth the diameter of the fenestra cochleae.

The facial canal emerges through the roof of the middle ear just lateral to the fenestra vestibuli as in other ruminants. The epitympanic recess lies lateral to the facial canal opening and at a lower elevation, separated from it by a bony step as in *Leptomeryx*. The chamber for the tensor tympani muscle is elongate, reaching along the lateral wall to about the anterior third of the promontorium. This chamber does not encroach medially into the promontorium, but is deeply excavated into the lateral wall of the petrosal. The chamber fades out gradually in the vicinity of the fenestra vestibuli.

The endocranial face of the petrosal consists of the anterior (cochlear) portion and the posterior (pyramidal) portion (fig. 3). The internal auditory meatus (meatus acusticus internus) is a large basin anteromedial to the center of the internal face. It is divided by a

low bony ridge into a lesser dorsolateral fossa and a greater ventromedial fossa. The major opening of the ventromedial fossa is the internal acoustic pore (porus acusticus internus) by which the acoustic nerve enters the spiral of the cochlear whorls. The large fallopian aqueduct (canalis facialis) opens within the dorsolateral fossa, proceeds ventrally most of the way through the petrosal, and then turns posteriorly to emerge in the roof of the tensor tympani chamber. A smaller passage representing the major petrosal nerve joins the facial canal within the petrosal bone. It enters the tympanic cavity from the pterygoid region, plunging through the slitlike fallopian hiatus on the lateral edge of the petrosal. The passage for the major petrosal nerve is identical in *Leptomeryx*.

The thick posterior (or pyramidal) portion of the petrosal is remarkably plain in *Archaeomeryx*. In *Leptomeryx*, by contrast, a large tuberosity covers the ampulla of the superior semicircular canal lateral to the common root of the superior and posterior semicircular canals. A deep subarcuate fossa lies posteromedial to it, under the arch of the superior semicircular canal. While these same features may be recognized in *Archaeomeryx*, they are more subdued, seemingly covered by thicker bone. The position of the subarcuate fossa, facing posterolaterally, is the same in *Archaeomeryx* as in *Leptomeryx*. A very faint concavity appears on the occipital edge of the petrosal, medial to the posterior semicircular canal. In the posterodorsal corner of the pyramidal region is the opening of the endolymphatic duct.

OSTEOLOGICAL COMPARISONS

In this section we survey the osteological features in representatives of each of the five families of hornless ruminants. We divide the survey into three major sections: (1) cranial data; (2) dental data; and (3) postcranial data. These basic data are selected from an extensive survey of comparative collections and the literature. Within each section of osteo-

logical data, we make comparisons and form phylogenetic hypotheses.

CRANIAL COMPARISONS

The cranium of *Archaeomeryx* is closely comparable to that of *Leptomeryx* in most features. Among the shared derived charac-

ters are the long slitlike foramen ovale, the large mastoid fissure, the oblique subcentral tympanohyal groove on the moderately inflated bulla, and the medial groove on the ventral face of the petrosal. The genus *Archaeomeryx* possibly included the ancestors of *Leptomeryx*. In any case it may be placed in the family Leptomerycidae.

More surprising is the dearth of primitive characters in *Archaeomeryx* in comparison with most other hornless ruminants. Both the extinct Hypertragulidae and the living and extinct Tragulidae have more primitive basicrania. We commence therefore with a brief consideration of the two more primitive families. Some of the key cranial characters for phylogenetic interpretations are summarized in table 1.

The cranium of *Hypertragulus* appears more primitive than that of any other ruminant we have studied. Unfortunately, it has not received such thorough morphological description as Whitmore (1953) devoted to *Leptomeryx*. We here note only a few of its diagnostic characters. *Hypertragulus* is the only ruminant with an incomplete postorbital bar (Scott, 1940). The mastoid bone is extensively exposed on the lateral wall of the skull. The triangular lower half of the mastoid lies immediately posterior to the external auditory meatus and forms a weak mastoid process on the dorsolateral side of the paroccipital process, as observed by Scott (1940). A long dorsal tongue of the mastoid extends two-thirds of the way to the nuchal eminence, separating the squamosal from the exoccipital bone. As shown by Pearson's (1927) wide-ranging studies of artiodactyls, extensive exposure of the mastoid is a primitive feature of the artiodactyls. In the Leptomerycidae, by contrast, the mastoid has shifted to a posterior position on the occiput, and an enlarged mastoid foramen has opened above the base of the paroccipital process.

In the basicranium of *Hypertragulus* the lateral half of the postglenoid process is pressed against the external auditory meatus, thus enclosing the postglenoid foramen laterally. The bulla is hollow and flask-shaped, with a low but broadly expanded body and an elongate meatus which extends

laterally beyond the weak zygomatic crest of the squamosal. The tympanohyal vagina is small and confined to the margin of the bulla immediately anterior to the paroccipital process. In *Leptomeryx* and *Archaeomeryx*, on the other hand, the tympanohyal concavity is larger, and approaches the center of the bulla. Radinsky (personal commun.) has pointed out that a marginal tympanohyal, as noted in hypertragulids, is the primitive condition among ruminants. (Camelidae, but not Protoceratidae, have a different derived condition in which the tympanohyal is deeply implanted between two parts of the bulla.)

The petrosal of *Hypertragulus* is also primitive in many respects. In figures 4 and 5 the petrosals of various lower ruminants are compared. The facial canal in *Hypertragulus*, unlike other ruminants, is disrupted anteriorly by the posttympanic neck which requires the facial canal to arch dorsally and posteriorly around it. Thence the facial canal passes ventrally and emerges via the stylo-mastoid foramen at the anterior end of the paroccipital process. In *Leptomeryx*, by contrast, the facial nerve course is largely uninterrupted by the posttympanic neck and passes more smoothly on a posteromedial course. In its final exit, moreover, it does not turn so sharply ventrad, and so the stylo-mastoid foramen emerges near the posterior edge of the paroccipital process. In these features the facial canal of *Hypertragulus* resembles that of *Dacrytherium* (Beaumont, 1963) and probably represents the primitive condition for selenodont ruminants.

On the promontorium of *Hypertragulus* shallow grooves mark the courses of the promontorial and stapediaal arteries, as in *Leptomeryx* (Whitmore, 1953). The jugular foramen opens just medial to the stylomastoid foramen and well behind the posterior lacerate foramen; it thus resembles *Dacrytherium* but not other ruminants in which the jugular foramen is confluent with or anterior to the posterior lacerate foramen. The posterior lacerate foramen is correspondingly small in *Hypertragulus*. Most of these distinctive features in the basicranium and petrosal of *Hypertragulus* are primitive with respect to other ruminants.

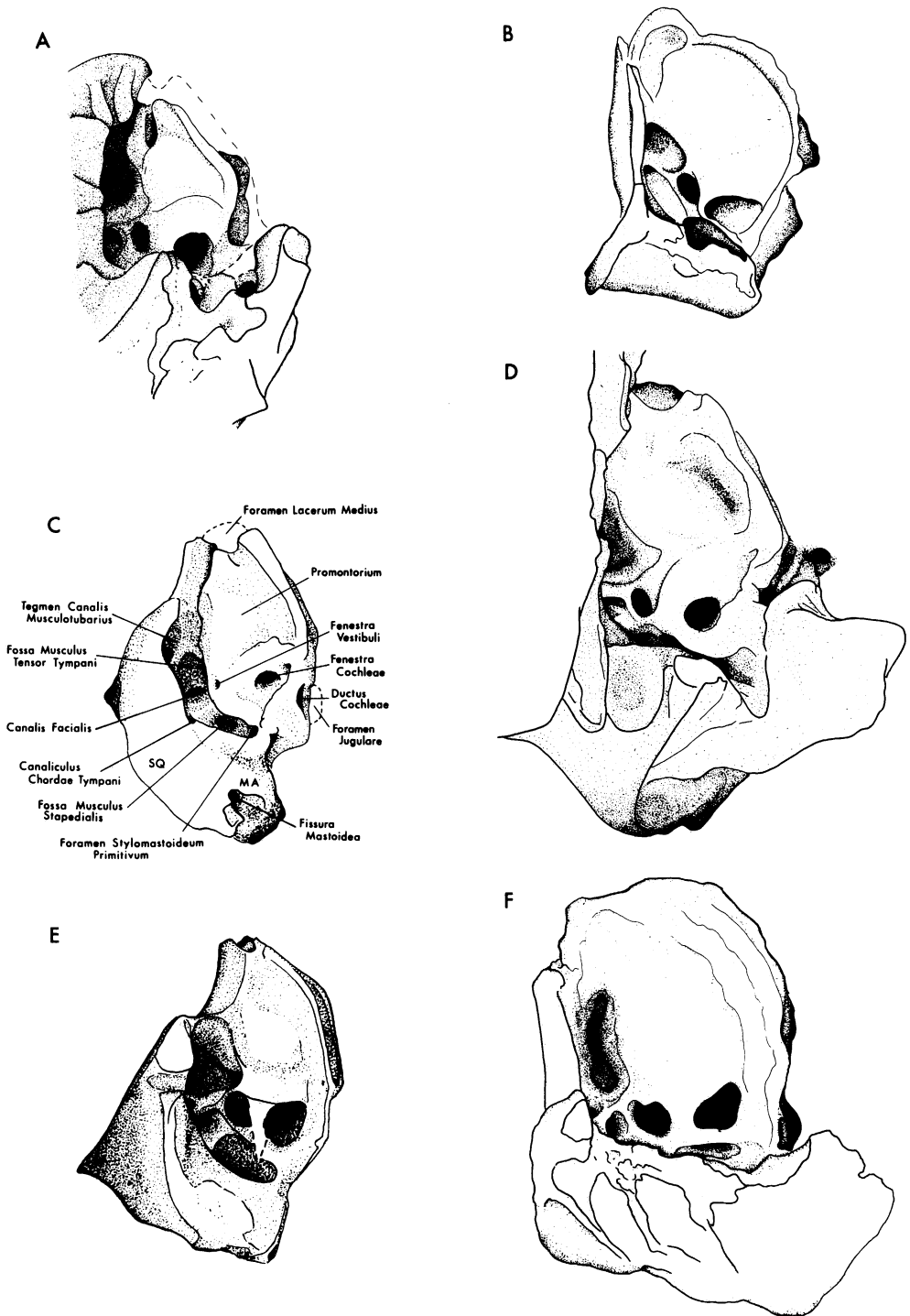


FIG. 4. Ventral views of right petrosals from several hornless ruminants. A. *Hypertragulus* species, F:AM 104867, Orellan of Nebraska. B. *Tragulus javanicus*, Recent of Java, University of Florida Mammalogy Collection. C. *Archaeomeryx optatus*, Type, AMNH 20311, same as figure 2. D. *Leptomeryx evansi*, AMNH 39123, Orellan of South Dakota. E. *Gelocus communis* from Ronzon, early Oligocene of France, Musee Crozatier in Le Puy (reversed). F. *Moschus moschiferus*, USNM 258555, Recent, Szechwan, China. Anterior ends upward.

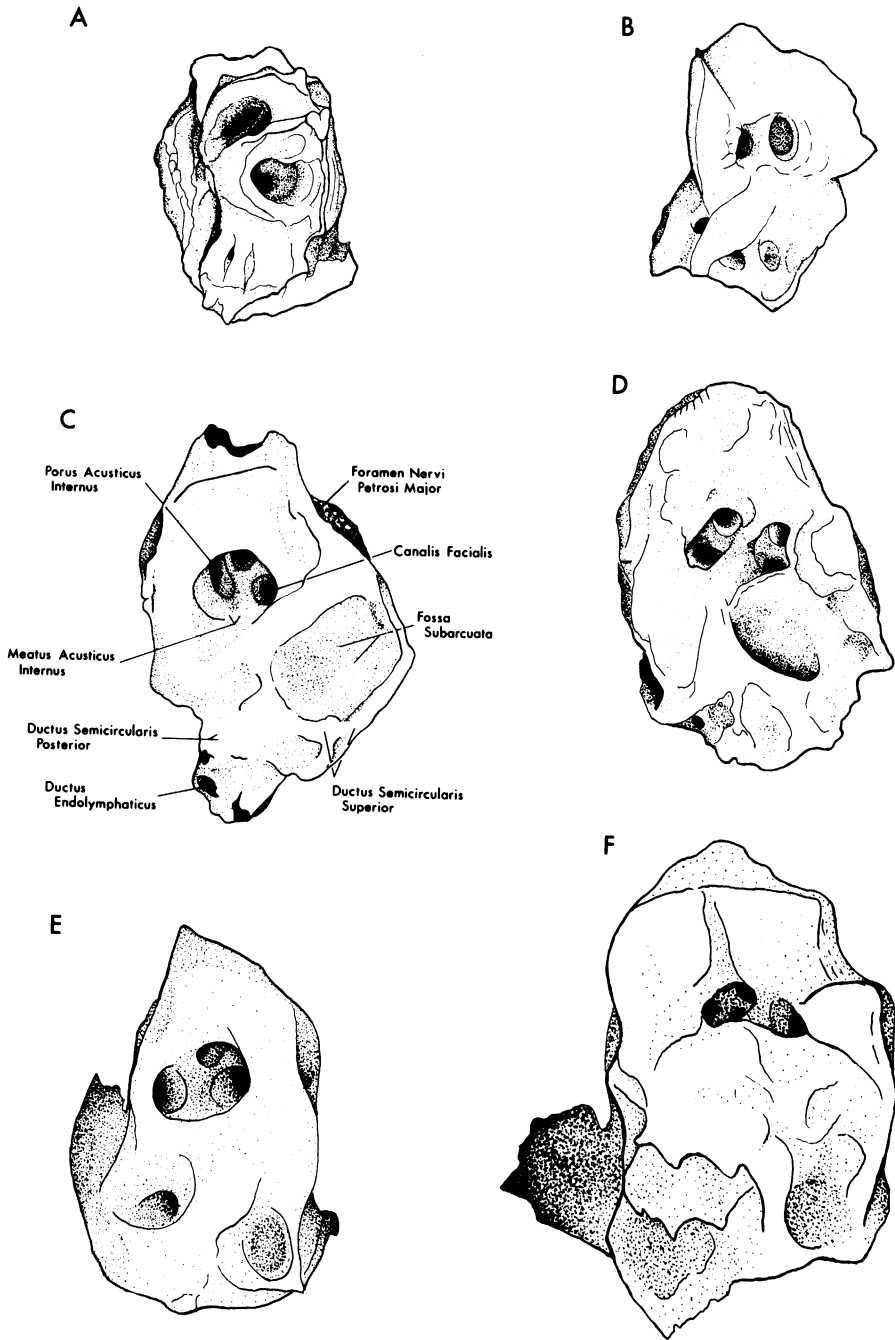


FIG. 5. Endocranial views of right petrosals from several hornless ruminants. Key same as for figure 4.

TABLE 1

Comparison of Selected Cranial Characters in Hornless Ruminants

	Hypertragulidae		Tragulidae		Leptomerycidae	
	Hypertragulus	Tragulus	Hyemoschus	Archaeomeryx		
Postorbital Bar	incomplete	complete, mostly of jugal	same	mostly of frontal		
Mastoid Exposure	broad, lateral	broad, lateral	same	moderate, posterior		
Mastoid Foramen	moderate, lateral	moderate, lateral	same	large, lateral		
Foramen Ovale	small, ovate	small, ovate	same	long, slitlike		
Postglenoid Process and foramen	narrow, foramen small laterally enclosed	absent, foramen small	same	broad, foramen large and laterally open		
Supraglenoid Foramen	absent	absent	same	absent		
Suprameatal Fissure	absent	absent	same	absent		
Tympanohyal Vagina	small, posterolateral	small, posterolateral	same	moderate, subcentral		
Entocarotid Foramen	carotid foramen confluent with posterior lacerate foramen	separate median carotid notches wall of bulla	same	carotid foramen nearly confluent with posterior lacerate foramen		
Entocarotid Branches	promontory and stapedia branches well defined	no branches enter middle ear	same	stapedial artery well defined		
Tensor Tympani Chamber	moderately deeply pocketed in medial and lateral walls	shallow, retracted posteriorly, pocketed in medial wall	same	moderately deep, pocketed mainly in lateral wall		
Stapedial Muscle Chamber	narrow, sinuous	subcircular, deeply pocketed	subcircular	narrow		
Subarcuate Fossa	deep	moderately deep	deep confluent with endo-lymphatic duct	moderately deep		

Dotted Line = Derived Characters; Dashed Line = Shared with Horned Ruminants

The crania of the Tragulidae exhibit an array of primitive and uniquely derived characters. The extensive lateral exposure of the mastoid bone is a primitive character shared only with the Hypertragulidae among ruminants. The small posteriorly positioned stylohyoid vagina is likewise a primitive character.

In addition, the Tragulidae present a re-

markable array of cranial characters that are uniquely derived among ruminants. The secondary palate is considerably extended posteriorly. The postorbital bar, while complete, is narrow and composed principally of the jugal rather than the frontal. The bullae are greatly enlarged, nearly always cancellous, and have long but small-bore auditory meati. The postglenoid process is essentially ab-

Gelocidae		Moschidae		
<u>Leptomeryx</u>	<u>Gelocus</u>	<u>Dremotherium</u>	<u>Blastomeryx</u>	<u>Moschus</u>
same	<u>mostly of frontal</u>	<u>mostly of frontal</u>	<u>mostly of frontal</u>	<u>mostly of frontal</u>
same	<u>narrow, posterior</u>	<u>narrow, posterior</u>	<u>narrow, posterior</u>	<u>narrow, posterior</u>
same	<u>small, posterodorsal</u>	<u>small, posterodorsal</u>	<u>small, posterodorsal</u>	<u>small, posterodorsal</u>
same		<u>large, ovate</u>	<u>large, ovate</u>	<u>large, ovate</u>
same		<u>broad, foramen</u> <u>large, laterally</u> <u>enclosed by bulla</u>	<u>broad, foramen</u> <u>large, laterally</u> <u>open</u>	<u>broad, foramen</u> <u>large, laterally</u> <u>enclosed by bulla</u>
same	<u>present</u>	<u>present</u>	<u>present</u>	<u>present</u>
same	absent	absent	<u>large</u>	<u>large</u>
same		subcentral with lateral wall	posterior with lateral wall	subcentral with lateral wall
same		carotid foramen confluent with posterior lacerate foramen	carotid foramen confluent with posterior lacerate foramen	separate median entocarotid foramen
promontory and stapedial well defined	promontory artery defined	<u>absent</u>	<u>absent</u>	<u>absent</u>
same	<u>deep, elongate,</u> <u>pocketed mainly</u> <u>in lateral wall</u>	<u>shallow, narrow,</u> <u>pocketed in</u> <u>lateral wall</u>	<u>shallow, pocketed</u> <u>mainly in</u> <u>lateral wall</u>	<u>shallow, pocketed</u> <u>mainly in</u> <u>lateral wall</u>
narrow	<u>deep, transversely</u> <u>elongate</u>	<u>large, transversely</u> <u>elongate</u>	<u>large, transversely</u> <u>elongate</u>	<u>large, transversely</u> <u>elongate</u>
deep	<u>shallow</u>	moderately deep	<u>shallow</u>	<u>shallow</u>

sent, having been overridden by and fused into the wall of the auditory bulla.

Several uniquely derived characters of tragulid petrosals may be related to their enlarged bullae. For example, the petrosal has a narrow medial edge in contrast with all other ruminant groups, including Hypertragulidae. The medial branch of the internal carotid artery, instead of contacting the

petrosal, traverses the medial wall of the bulla (Van Der Klaauw, 1931). The tensor tympani fossa in the Tragulidae is very small, posteriorly retracted, and encroaches medially upon the promontorium. The superior semicircular canal rises prominently above the endocranial surface of the petrosal, reflecting a very different orientation of the semicircular canal system from that in other

ruminants. A narrow but deep subarcuate fossa is present in *Hyemoschus*; it faces posteromedially rather than posterolaterally as in *Hypertragulus* and the Leptomerycidae. Unlike other ruminants, the fossa in *Hyemoschus* also transmits the endolymphatic duct. In *Tragulus* the subarcuate fossa is moderately deep.

One of the few derived cranial characters that the Tragulidae share with the Leptomerycidae and most higher ruminants is the confluence of the jugular foramen with the posterior lacerate foramen.

Archaeomeryx and *Leptomeryx* share several derived characters with the Gelocidae, Moschidae, and horned ruminants but not with the Hypertragulidae or the Tragulidae. One such feature is the retreat of the mastoid bone to the posterior surface of the skull and its compression into a narrow exposure marked only by a narrow mastoid foramen. Possibly correlated with this altered mastoid architecture is the more direct posteromedial course of the facial canal through the middle ear. The long tubular chamber of the stapedial muscle in the Leptomerycidae may be transitional to the more expanded chamber found throughout the higher ruminants. (The relatively enlarged stapedial muscle in higher ruminants often includes a heterotopic bone [Wilkie, 1936].) A tympanohyal depression which passes obliquely toward the center of a moderate-sized bulla closely resembles the condition found in most Cervidae and is evidently derived with respect to the marginal posterior position found in the Tragulidae and Hypertragulidae. These shared features tend to link the Leptomerycidae with Gelocidae, Moschidae, and horned ruminants.

The Gelocidae exhibit several derived cranial structures in addition to those found in the Leptomerycidae. An undescribed petrosal of *Gelocus* from the collection in Le Puy reveals several derived characters not found in *Archaeomeryx*. These include shorter proportions, thinner bone over the promontorium, loss of the stapedial artery (though the promontory artery is retained), enlarged stapedial muscle fossa, deeply pocketed in the lateral wall, and on the endocranial side a very shallow subarcuate fossa.

In *Prodremotherium* and other gelocid basicrania one notes other derived characters shared with the Moschidae and horned ruminants. These include a broadened basioccipital with strong flexion stops on the condyles; a laterally enclosed postglenoid foramen (convergent with hypertragulids but differing in details); a deep groove bordering the medial side of the glenoid fossa; a foramen ovale that is large, ovate, and far posterior; and the presence of a supraglenoid foramen above the posterior end of the zygomatic arch.

The Moschidae have progressed beyond the Gelocidae in only a few derived cranial characters. (This may suggest that these two families are parts of one close-knit adaptive radiation of Eurasian Oligo-Miocene ruminants.) One derived feature of the Moschidae is the loss of the promontory artery. In *Moschus moschiferus* a carotid foramen 2 mm. in diameter enters the tympanic chamber 5 mm. anterior to the posterior lacerate foramen, but no branch of the internal carotid artery crosses the promontorium. This condition in adult *Moschus* resembles that in fetal and occasionally juvenile specimens of *Bos* and *Ovis*, in which the median branch of the carotid passes forward in the petrobasilar space above the bulla, makes a characteristic curl, enters the braincase by way of the median lacerate foramen and enters the rete mirabile. In adults of *Bos* and *Ovis*, however, only the anterior end of the internal carotid artery remains functional, serving as a trunk to the rete near the median lacerate foramen (Tandler, 1889; Schmidt, 1910; Baldwin and Bell, 1963; Baldwin, 1964). Thus, in the presence of the median branch *Moschus* is primitive, but in the loss of the promontory branch it is derived.

A second derived character of the Moschidae is the enlarged suprameatal fissure. This fissure provides a broad passage for venous drainage from the braincase above the external auditory meatus and below the zygomatic crest of the squamosal. It is shared with nearly all higher ruminants.

The Moschidae also have several unique cranial characters. These include a shallow tensor tympani fossa and strong lateral en-

closure of the subcentral tympanohyal vagina. In comparison with higher ruminants, the Moschidae are, of course, primitive. Absence of horns and antlers is an obvious feature. Retention of a subarcuate fossa on the endocranial side of the petrosal and a median branch of the carotid artery are other primitive features of moschid crania.

DENTAL COMPARISONS

The presence of a moderately procumbent incisiform (or premolariform) lower canine is characteristic of all ruminant families, and makes a useful distinction from the Camelidae, which usually have sharp upright lower canines. The non-caniniform canine, however, is shared by several other early selenodont artiodactyl groups, including oreodonts, dacrytheres, and protoceratids and may be the primitive condition for all artiodactyls as Stehlin (1906–1910, p. 937) has suggested. It is therefore not a reliable derived character, diagnostic of ruminants.

The shape of the first lower premolar (probably DP_1) and its position with respect to the principal diastema are often cited as key characters to understanding selenodont relationships (e.g., Scott, 1940; Colbert, 1941). We previously contrasted the anterior and caniniform P_1 of the Leptomerycidae with the posterior and premolariform P_1 of the Gelocidae and Blastomerycinae (Taylor and Webb, 1976). (This latter feature is illustrated for *Gelocus communis* in fig. 6.) Also P_1 is a tall anterior caniniform tooth in Hypertragulidae, but a posterior premolariform tooth in such Tragulidae as *Dorcatherium*.

Before relying on the character of P_1 for cladistic analysis, however, we must determine its evolutionary polarity. In such early selenodonts as *Dacrytherium* all the teeth from I_1 to P_2 are leaf-shaped (i.e., roughly premolariform) and in continuous series. Evidently caniniform teeth with separating diastemata are subsequently derived within various progressive selenodont taxa. In groups wherein the major diastema arose in front of P_1 , the tooth remained leaf-shaped or premolariform, as in the Tragulidae and Gelocidae. But this is a primitive, not a de-

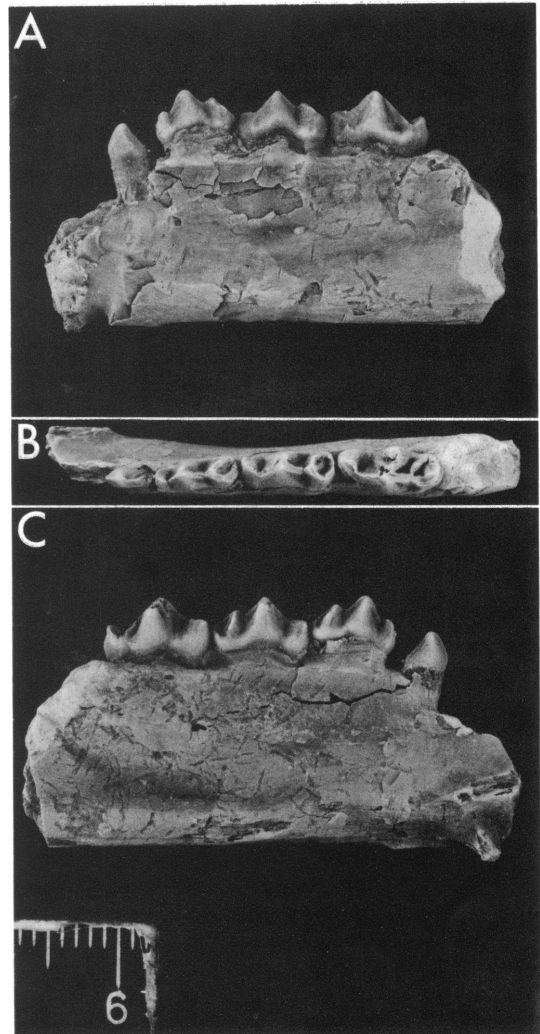


FIG. 6. Lower premolars of *Gelocus communis*. Left mandible in Basle Naturhistorisches Museum, Switzerland, from Ronzon, early Oligocene of France. A. Labial view. B. Occlusal view. C. Lingual view. Approximately $\times 2$. (Photos courtesy of Dr. B. Engesser.)

derived resemblance between these two groups. In other groups P_1 occluded with an enlarged upper canine, and therefore tended to become caniniform. For example, a caniniform P_1 appears in the Protoceratidae and independently again within most later Camelidae; it also appears in *Eotylopus*, but not in *Poebrotherium*. The caniniform P_1 in the Hyper-

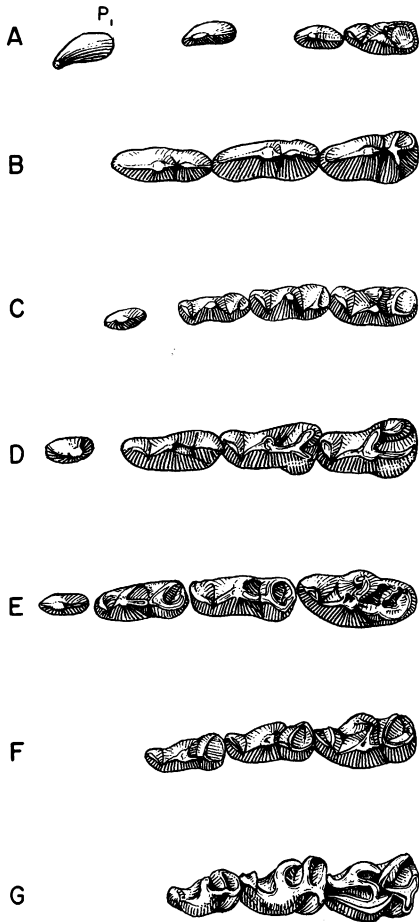


FIG. 7. A. *Hypertragulus calcaratus*, referred, P_1 - P_4 from mandible, AMNH 39410. B. *Tragulus javanicus*, Recent, P_2 - P_4 from left ramus, AMNH (M) 102464. C. *Archaeomeryx opatus*, referred, right P_1 , reversed, from partial skull and mandible, AMNH 20322 and left P_2 - P_4 of partial ramus, AMNH 92308. D. *Leptomeryx evansi*, referred, P_1 - P_4 from left ramus, F:AM 53721. E. *Gelocus communis*, referred, P_1 - P_4 from left mandible of photograph, figure 6. F. *Blastomeryx elegans*, Type, P_3 - P_4 from left ramus, AMNH 14101 and P_2 from referred left ramus, AMNH 17345. G. *Moschus moschiferus*, Recent, P_2 - P_4 from right ramus, reversed, AMNH (M) 17951. All occlusal views. $\times 2$.

tragulidae is taller than and more fanglike than that in *Archaeomeryx* or any other Leptomerycidae, indicating that it may have evolved independently in those two families.

The caniniform condition of the first lower premolar, while derived, apparently evolved independently in several selenodont artiodactyl taxa.

We turn next to comparisons of the closed series of premolars, generally regarded as the most revealing part of the dentition in ruminants (e.g., Loomis, 1925). The key dental characters are summarized in table 2, and a synoptic view of lower premolars is provided in figure 7.

The premolars of the Hypertragulidae are extraordinarily simple. In *Hypertragulus* P^2 and P^3 are simple conical teeth; P^3 is triangular, with a weak protocone and lingual cingulum; and P^4 is wedge-shaped with a narrow heel composed of a very weak metaconid and a weak hypoconid. P^1 and P^4 present much stronger elaborations of the preceding premolars. P^4 adds a small paraconid to the weak metaconid and hypoconid.

Hypertragulus premolars may be deceptively simple, for many non-ruminant selenodont artiodactyls have more elaborate premolars than these, particularly P^2 and P^3 . Emry's (1978) description of *Parvitrágulus*, a new early Oligocene hypertragulid supports this view, for in it P^2 has a protocone and P^3 a narrow heel; P^3 has a paraconid and a stronger basined heel; P^4 has a more crescentid protocone; and P^4 has a more distinct metaconid and hypoconid than in *Hypertragulus*.

In the Tragulidae, including the living *Tragulus* and *Hyemoschus*, the premolars are also relatively simple. P^2 consists of three labial cusps but no protocone and P^3 consists only of three cusps connected by longitudinal crests. On P^3 the protocone is weak in *Hyemoschus* and very weak in *Tragulus*. P^3 and P^4 of *Hyemoschus* have an arrangement not much different from that of *Parvitrágulus* with an inflected paraconid, a protoconid (possibly bearing a very weak metaconid on its flank), a large hypoconid, and a small entoconid and entostylid. Thus, the Tragulidae have long, simple premolars much like hypertragulid premolars may have been before they became peculiarly acuminate.

Regarding the premolar series in *Archaeomeryx*, Colbert (1941, p. 5) stated that the

“premolars on the whole closely resemble those of the New World hypertragulids.” Presumably Colbert referred principally to the close resemblance between the premolars of *Archaeomeryx* and those of *Leptomeryx*, which was then included in the Hypertragulidae. His statement clearly does not apply to *Hypertragulus* and its immediate allies. In *Archaeomeryx* and *Leptomeryx* P² has three labial cusps (a large paracone and smaller anterior and posterior cusps); P³ has a strong protocone in addition to the three labial cusps, and on P⁴ the protocone forms a crescent. P₂ and P₃ of *Leptomeryx* and P₃ of *Archaeomeryx* have three longitudinal crests connecting a paraconid, a tall protoconid, and a small hypoconid. These three crests are well developed on P₄ of *Leptomeryx* and *Archaeomeryx* and both taxa also have a strong metaconid lingual to the protoconid. *Leptomeryx* premolars are constructed on the same plan as those of *Archaeomeryx*, but are more progressive in such features as the presence of a protocone on P², lingual strengthening of the paraconid and hypoconid on P₂, and the presence of a distinct metaconid on P₃. In general, the Leptomerycidae share the tendency toward more submolariform premolar patterns found in more derived lower ruminants.

The premolars of *Gelocus* present an even more elaborate set of lingual cusps and cuspids than in the Leptomerycidae. The upper premolars are not advanced beyond *Leptomeryx* premolars in development of the protocone, but in P³ that cusp is set posteriorly, a unique derived condition among ruminants. The lower premolars of *Gelocus communis* from the early Oligocene of Ronzon in France are indicated in figure 6. P₄ has four strong lingual crests, including paraconid crest, metaconid crest, entostylid crest, entoconid crest; and similar crests also appear on P₃ and P₂.

The Eurasian Gelocidae, as recognized by Viret (1961), present a nearly continuous progression of lower premolar patterns, ranging from the relatively simple four-crested pattern of *Gelocus* to more complex variations on the same theme. This structural progression also approximates a chrono-

cline, proceeding from early Oligocene *Gelocus* through later Oligocene *Prodremotherium* to early Miocene *Amphitragulus* and *Dremotherium* (see Sigogneau, 1968). In these last taxa, the lower premolars resemble those of the living *Moschus* except for the lack of a markedly elongate metaconid and the lack of an exaggerated labial fold on the hypoconid. From such an array of gelocid and moschid premolar patterns, the more complex patterns of higher ruminants could readily be derived (Loomis, 1925; Hamilton, 1973).

The polarity of ruminant premolar evolution, as we view it, begins with long, narrow premolars, progresses toward wider teeth with increased lingual complexity, and culminates in the great array of complex submolariform premolars observed in the higher ruminants. In contrast, Colbert (1941) regarded the trenchant premolars of tragulids as specialized and derived from a pattern resembling that of *Archaeomeryx*. He may have been influenced by the antiquity of *Archaeomeryx* relative to the Miocene and younger Tragulidae. Since such a difference in the presumed direction of change can turn the phylogenetic relationships topsy turvy, it is essential to determine this polarity.

Although it is beyond the scope of this paper to review the premolar patterns of all artiodactyls, a few comparisons will demonstrate the basis for our polarity hypothesis. In the lower premolars of dichobunids and cebochoerids, the only lingual characters are a low cingulum (in some taxa) and a narrow metaconid on P₄ (in most taxa). In camelids a narrow heel with a posterolingual flexid (metaconid) is present on P₄ and often P₃, but in nearly all taxa the premolars are long and secant. In xiphodonts and anoplotheres, the long narrow premolars produce a simple posterolingual crest (metaconid) on P₄ but few other lingual features. In all of these early selenodont groups the premolars are at least as long as the molars, and except for the metaconid on P₄ and sometimes P₃ they are all secant and simple.

In summary, the lower premolars of fossil and recent Tragulidae largely conform to the primitive secant pattern with only a weak

TABLE 2

Comparison of Dental Characters in Hornless Ruminants

	Hypertragulidae		Tragulidae		Leptomerycidae	
	<u>Hypertragulus</u>	<u>Tragulus</u>	<u>Hyemoschus</u>	<u>Archaeomeryx</u>	<u>Leptomeryx</u>	
Upper						
C	large, fixed	moderately large, fixed	moderately large, fixed	moderately large, fixed	small, fixed	
P ¹	conical, 2-rooted	<u>absent</u>	<u>absent</u>	<u>absent</u>	<u>absent</u>	
P ²	compressed, conical ^a	3 labial cusps, no protocone	3 labial cusps, no protocone	3 labial cusps, no protocone	3 labial cusps, small protocone	
P ³	minute conical protocone and lingual cingulum	3 labial cusps, small conical protocone with weak cingulum	3 labial cusps small conical protocone with weak cingulum	3 labial cusps, strong conical protocone	3 labial cusps, strong conical protocone	
P ⁴	conical protocone with low lingual cingulum	<u>crenate protocone</u>	<u>crenate protocone</u>	<u>crenate protocone</u>	<u>crenate protocone</u>	
M ¹⁻³	mesostyles absent	mesostyles present	mesostyles present	<u>mesostyles strong</u>	<u>mesostyles strong</u>	
Lower						
I ₁₋₃	oblique, spatulate	I ₁ fan shaped	I ₁ fan shaped	procumbent, I ₁ enlarged	procumbent, I ₁ tusklake	
P ₁	large, caniniform	<u>absent</u>	<u>absent</u>	moderate, caniniform	small caniniform	
P ₂	small, conical	minute paraconid, moderate protoconid, and "heel"	minute paraconid, broader protoconid, and "heel"	minute paraconid, moderate protoconid, and hypoconid	small paraconid, large protoconid, wide hypoconid	
P ₃	protoconid with small "heel", no lingual crests	minute paraconid, tall protoconid, hypoconid and incipient entostylid	small paraconid, thick protoconid wide "heel"	inflected paraconid, thick protoconid, incipient entoconid, and distinct hypoconid	inflected paraconid, thick protoconid, posteriorly directed metaconid, hypoconid and entoconid enclosing fossetid	
P ₄	small paraconid, weak metaconid, and hypoconid	minute paraconid, large protoconid, thickened hypoconid, small entoconid, and entostylid	inflected paraconid, thickened protoconid, small entoconid, large hypoconid, and small entostylid	like P ₃ , but with posteriorly directed metaconid	like P ₃ , but more elaborate	

Dotted Line = Derived Character; Dashed Line = Shared with Horned Ruminants

^aIn Parvitrágulus the premolars show some weak lingual features, especially on P² and P₃.

metaconid on P₄. *Hypertragulus* premolars are even simpler, but this probably represents a unique modification toward shorter, more acuminate premolars than in other selenodont artiodactyls. The tendency to shorten and broaden the premolars is first clearly seen in *Archaeomeryx* and other Leptomerycidae (with three lingual crests in the lower premolars) and becomes more pronounced in the Gelocidae (with four lingual crests in the lower premolars). Such complexity is further elaborated in the Moschidae and finally in the great array of submolariform premolars of the higher ruminants.

POSTCRANIAL COMPARISONS

The principal postcranial characters of lower ruminants are listed in table 3. A comparison of these limb characters is made to determine if a character is plesiomorphous or apomorphous as defined by Hennig (1966). The axis and the podial elements in particular show a number of progressive changes that are helpful in determining ruminant relationships.

AXIS: In describing the axis in *Leptomeryx*, Scott (1940, p. 545) stated "the odontoid process is short and peg-like, differing much

Gelocidae		Moschidae	
<u>Gelocus</u>	<u>Dremotherium</u>	<u>Blastomeryx</u>	<u>Moschus</u>
?	moderately large, loose, dimorphic	greatly enlarged, loose, dimorphic	greatly enlarged, loose, dimorphic
<u>absent</u>	<u>absent</u>	<u>absent</u>	<u>absent</u>
3 labial cusps, minute lingual cingulum	3 labial cusps, protocone wearing to lingual crescent	3 labial cusps, small proto- cone with lingual cingulum	3 labial cusps, protocone wearing to lingual crescent
moderate conical protocone, posteriorly situated	<u>crescentic protocone</u>	like P ² with stronger <u>protocone</u>	<u>crescentic protocone</u>
<u>crescentic protocone</u>	<u>crescentic protocone</u>	<u>crescentic protocone</u>	<u>crescentic protocone</u>
mesostyles present	mesostyles present	<u>mesostyles strong</u>	mesostyles present
oblique, spatulate	oblique, spatulate	oblique, spatulate	oblique, spatulate
small premolariform, or absent	<u>absent</u>	small premolariform, or absent	<u>absent</u>
small paraconid, large protoconid, weak metaconid, weak entoconid, hypoconid and entostylid	small paraconid, large protoconid, thick hypoconid	small paraconid, thick protoconid, strong entoconid and hypoconid, weak entostylid	inflected paraconid, strong protoconid, strong posteriorly extended metaconid, strong entoconid, hypoconid and entostylid enclosing fossettid
like P ₂	inflected paraconid, large compressed protoconid, compressed metaconid, distinct metaconid, moderate entoconid, hypoconid and entostylid	inflected, bifurcate para- conid, large protoconid, distinct metaconid, strong entoconid, hypoconid and entostylid enclosing fossettid	like P ₂ , with strong labial ridge on hypoconid
strong paraconid, protoconid elongate and anteriorly narrow, metaconid posteriorly situated, hypoconid, entoconid and entostylid enclosing fossettid	inflected, bifurcate para- conid, protoconid elongate and anteriorly narrow, strong metaconid posteri- orly situated; entoconid, hypoconid (with labial ridge), and entostylid enclosing fossettid	inflected, bifurcate para- conid, large protoconid, strong metaconid, often extended anteriorly, strong entoconid, hypoconid and entostylid enclosing large fossettid	like P ₂ , with very strong metaconid extending forward to join paraconid

from that of *Hypertragulus*, to which I refer the small, isolated axis in the Cope collection (AMNH).” A search of the AMNH Cope collection for the hypertragulid isolated axis on which Scott based the above statement proved to be fruitless. Because of contrary evidence, based on a *Hypertragulus* partial skeleton (F:AM 105303) with articulated skull, jaws and cervical vertebrae, we now believe that the isolated axis described by Scott was not of *Hypertragulus*. The odontoid process of a true *Hypertragulus* axis (F:AM 105303) is shown in figure 8. It is short and peglike, features Scott mistakenly

attributed to *Leptomeryx*. The odontoid process of the axis in a partial skeleton of *Leptomeryx* (F:AM 53571) has a high median dorsal crest with a pronounced concavity on each side of the crest, unlike the nearly flat surface in *Hypertragulus*. The axis of *Leptomeryx* further differs from those of *Hypertragulus* and *Tragulus* in having larger anterior articular processes that extend upward nearly to the top of the neural canal. Thus, as figure 8 indicates, a progressive odontoid process is found in *Leptomeryx*. It generally resembles those of *Protoceras* and *Poebrotherium*, and to a lesser degree *Merycoi-*

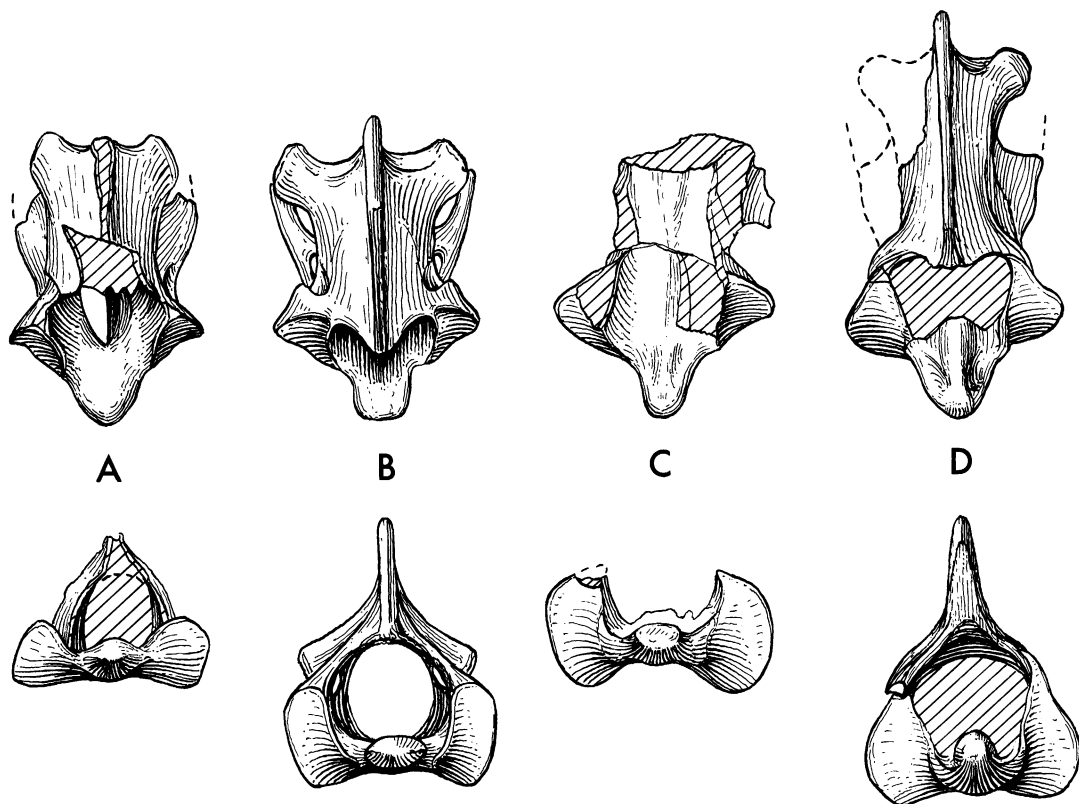


FIG. 8. Axes of several hornless ruminants. Dorsal views above. Proximal views below. A. *Hypertragulus* species, F:AM 105303, partial skeleton, Whitneyan of South Dakota. B. *Tragulus javanicus*, AMNH (M) 90101, Recent, Java. C. *Archaeomeryx optatus*, Type, AMNH 20311, partial skull and mandible, late Eocene of Mongolia. D. *Leptomeryx evansi*, F:AM 53571, partial skeleton, Orellan of Nebraska. All $\times 2$.

dodon and *Agriochœrus* which Scott (1940, p. 545) described as "transitional between the primitive, conical form, which is still retained in Suina—and spout-like shape which is characteristic of Modern Tylopoda and Pecora." In this transitional shape, the dorsal surface of the odontoid process is broad and has a median crest or ridge of varied strength and a concavity of varying degree on each side of the median ridge.

A more primitive odontoid process occurs in *Hypertragulus*, *Tragulus*, and *Archaeomeryx*. The process is relatively short and blunt and its dorsal surface is nearly flat in *Hypertragulus* and *Tragulus*. In *Archaeomeryx* the process is slightly more tapered

anteriorly and shows a hint of a dorsal crest. Likewise the anterior articular processes are very low and weak in *Hypertragulus* and moderately so in *Tragulus*. In *Archaeomeryx* these processes are proportionally larger and deeper.

The axis of *Gelocus* resembles that of *Leptomeryx*. It is transitional both with respect to the spoutlike character of the odontoid process and with respect to the large, deepened atlantal articulation on the anterior face of the axis. The odontoid process in *Gelocus* is outlined in ventral view by Kowalevsky (1876, pl. xxi, fig. 14) and may be seen in the collections at LePuy.

The axis of *Moschus* most nearly ap-

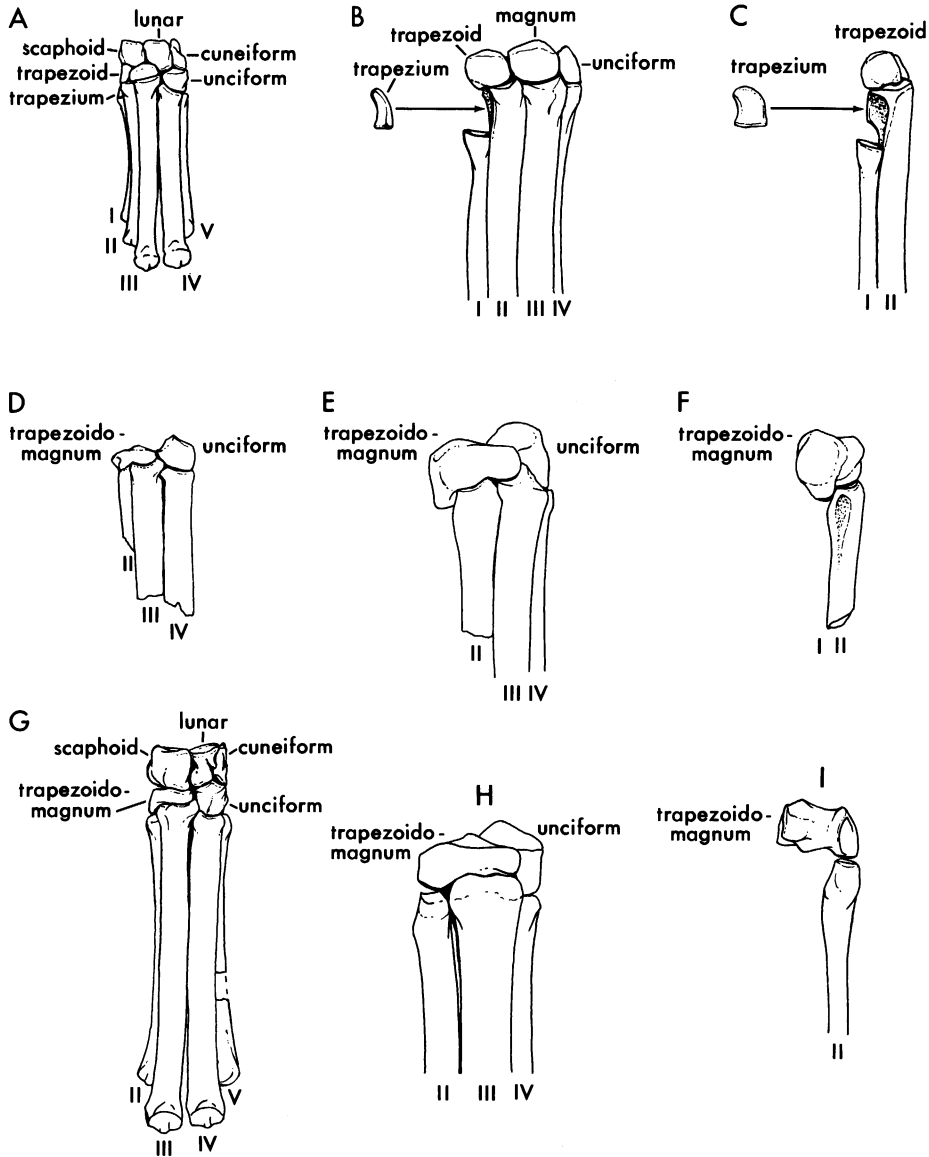


FIG. 9. Front feet of several hornless ruminants. A, D, G. Anterior views of left manus. $\times 1$. B, E, H. Posteromedial views to show position of metacarpal I. $\times 2$. C, F, I. Posterior views of manus. $\times 2$. A, B, C. *Hypertragulus* species, F:AM 53805, partial front limb associated with ramus, Whitneyan of South Dakota. D, E, F. *Archaeomeryx optatus*, AMNH 20322, partial skeleton, late Eocene of Mongolia. G, H, I. *Leptomeryx evansi*, AMNH 38910, partial skeleton, Orellan of South Dakota.

proaches the spoutlike condition present in higher ruminants. As Flower (1875, p. 180) noted, it bears the progressive "crescent hollow above." Thus lower ruminants encompass the whole transformation series of axis

structure from a simple peg in *Hypertragulus* and *Tragulus* to a complex spout in *Moschus*.

LIMB ELEMENTS: The podial elements of *Hypertragulus* have a unique combination of

morphological characters. For example, the magnum and trapezoid of *Hypertragulus* are unfused as in the Tylopoda. This is a primitive character for ruminants found only in *Hypertragulus*; it is found, however, in Tylopoda and all other selenodont groups. The cuboid and navicular are fused in *Hypertragulus*, a derived feature shared with all Ruminantia.

The feet in *Hypertragulus* have a preponderance of primitive features. As observed by Scott (1940, p. 516) *Hypertragulus* has a pentadactyl manus with metacarpal I extremely slender but nearly as long as metacarpal II and complete with phalanges. The trapezium is present in *Hypertragulus*, but with the possible exception of *Archaeomeryx*, is missing in all other Ruminantia (fig. 9).

As observed by Scott (1940, p. 519) the fibula in *Hypertragulus* is extremely reduced but apparently continuous, with both the proximal and distal ends fused. A fused proximal rudiment of the fibula is present in all other ruminants, but the distal end of the fibula is fused only in *Hypertragulus* and *Tragulus*. *Hypertragulus* is the only member of the ruminants with the fibula complete rather than reduced distally to a malleolar bone.

These postcranial characters confirm the position of *Hypertragulus* as the most primitive member of the Ruminantia. In addition, *Hypertragulus* presents two uniquely derived characters in having the distal end of the fibula fused with the tibia and the ulna fully fused with the radius.

The diagnostic postcranial characters (table 3) confirm the close relationship of *Archaeomeryx* with *Leptomeryx*. It is not known whether the trapezium is present in *Archaeomeryx*. The enlargement of the magnum and the relatively small space for the trapezoid in *Archaeomeryx* correspond closely to the arrangement of the carpals in *Leptomeryx* in which the trapezium is missing. In both genera the distal end of the radius does not rest on the cuneiform, and the lunar rests largely on the unciform. Both genera share fusion of the trapezoid and

magnum with all other ruminants except the Hypertragulidae.

A renewed study of the manus of *Archaeomeryx* indicates the possible presence of metacarpal I. Colbert (1941, p. 7) concluded that "the pollux probably was suppressed," but reexamination of the *Archaeomeryx* remains reveals that the proximomedial surface of metacarpal II has a shallow depression that disappears onto the shaft about 5 mm. below the proximal end. The distal articular surface of the trapezoid extends medially (about 0.2 mm.) beyond metacarpal II and might possibly serve as a proximal attachment for a narrow metacarpal I. A broader posterior overhang of the trapezoid, which is about 2.0 mm. in length, is rugose without any articular surface. A slight medial extension of the trapezoid beyond the proximal border of metacarpal II plus a proximal depression on metacarpal II suggests the presence of a rudimentary metacarpal I or even the possibility of rudiments of both the trapezium and metacarpal I, as in *Hypertragulus*. The development of metacarpal I, however, is intermediate between its full development in *Hypertragulus* and the complete loss of this element in *Leptomeryx*.

The limbs of *Leptomeryx* show further advances including reduction of metacarpals II and V, loss of metacarpal I, well-developed malleolar, parallel proximal and distal ginglymi of the astragalus, fused metatarsals III and IV, and the reduction of metatarsals II and V to proximal rudiments. Taylor and Webb (1976) have shown still further advances in the later leptomerycids.

Each of these progressive limb characters in the Leptomerycinae is also found in the Gelocidae and all higher ruminants. *Archaeomeryx*, however, exhibits primitive conditions for each of these characters. Since *Archaeomeryx* is the sister group of the Leptomerycinae (as we shall show) the development of similar progressive features in *Gelocus* and higher ruminants must be the result of parallel evolution. In the case of a character complex so obviously adaptive to cursorial locomotion, such parallelism between leptomerycid limbs and gelocid limbs is to be expected (Taylor and Webb, 1976).

The postcranial elements of the Tragulidae are primitive in appearance. The short proportioned limbs and the unfused, full length, lateral digits II and V resemble those of *Hypertragulus*. Primitive features of the Tragulidae held in common with the Hypertragulidae are relatively short limbs with the radius, tibia, and metapodials especially short; either unfused or partially fused central metapodials; nearly full length lateral digits II and V; an elongate and relatively narrow astragalus with the distal ginglymi medially deflected, and incomplete distal keels on the metapodials. These shared primitive features do not indicate monophyletic relationship between the Tragulidae and Hypertragulidae.

Tragulid limbs further show several derived features that unite this group with the Leptomerycidae, Gelocidae, Moschidae, and higher ruminants. These characters are: (1) fused magnum and trapezoid; (2) absence of trapezium; (3) loss of metacarpal I, and (4) distinct malleolar (separate in *Hyemoschus* but usually fused to the tibia in *Tragulus*). Furthermore, the tarsals of the Recent tragulids are modified in the fusion of the cubonavicular with the ectomesocuneiform. This feature, however, is not present in the fossil genus, *Dorcatherium*.

The derived features shared by the Tragulidae with the Leptomerycidae and all higher ruminants clearly show that the Tragulidae branched from "the main line" after the Hypertragulidae. However, it is not clear from most of the limb evidence whether the separation occurred before or after *Archaeomeryx*. The development of a spoutlike odontoid process in the Leptomerycidae is the most convincing derived character in the postcranial skeleton shared with higher taxa but not the Tragulidae. In addition, the distinctive malleolar articulation of the calcaneum (table 3) helps resolve the problem. In *Hypertragulus* that surface is a simple convexity; in the Tragulidae it is a simple concavity; in the Leptomerycidae (including *Archaeomeryx*) and all higher ruminants, it consists of a proximal convexity and a distal concavity. These features of the axis and the calcaneum thus confirm the cranial and den-

tal evidence indicating that the Tragulidae separated from "the main line" of ruminant phylogeny before *Archaeomeryx*.

The limb features of *Gelocus*, for the most part, are more derived than those of the Hypertragulidae and bear a closer resemblance to those of the Leptomerycidae. Primitive characters shared by *Gelocus* and *Leptomeryx* are unfused metacarpals III and IV, complete lateral digits II and V, and an incomplete keel on the distal end of the metapodials. Derived characters shared by *Gelocus* with the Moschidae and higher ruminants are forelimb relatively long and nearly equal in length to the hind, metapodials relatively elongate in comparison with those of other primitive taxa, and a shorter more symmetrical astragalus. The metatarsus of *Gelocus* as figured by Kowalevsky (1876, pl. 2, fig. 18) is elongate and intermediate in length between that in the Leptomerycidae and the longer proportioned limbs of the Moschidae.

On the basis of the limbs, it is difficult to distinguish the Moschidae from Gelocidae. The morphocline of character states seems to trace the steps by which the limbs evolved. And this morphocline is in accord with the known temporal record of extinct forms from the early Oligocene *Gelocus* through later Oligocene *Prodremotherium*, to early Miocene *Amphitragulus* and *Dremotherium* and finally the early to late Miocene Blastomerycinae of North America. The early Miocene postcranial elements of *Dremotherium* and *Amphitragulus* are relatively longer and more specialized for running than those of *Gelocus*. The limb characters of *Dremotherium* closely approach those of *Blastomeryx* and the Recent *Moschus*. Limb characters of *Dremotherium* that are derived with respect to *Gelocus* but shared with the Blastomerycinae and *Moschus* are fusion of metacarpals III and IV and completion of the distal keels of the metapodials.

A comparison of the whole array of morphological features in lower ruminant limbs (table 3) reveals evolutionary trends toward lengthening the limbs, especially the metapodials, reducing the ulna and fibula, losing and fusing carpals and tarsals, and completing and strengthening the distal metapodial

TABLE 3

Comparison of Postcranial Characters in Hornless Ruminants

	Hypertragulidae		Tragulidae		Leptomerycidae	
	<u>Hypertragulus</u>	<u>Tragulus</u>	<u>Hyemoschus</u>	<u>Archaeomeryx</u>		
Axis	odontoid process short and peglike with dorsal surface nearly flat; anterior articular surfaces small and low	odontoid process short and peglike; anterior articular surfaces higher	odontoid process short and peglike; anterior articular surfaces higher	odontoid process slightly narrowed anteriorly with a hint of dorsal crest; anterior articular surfaces larger and higher		
Forelimb						
Ulna and radius	ulna relatively light and fully fused with radius	ulna relatively strong and usually separate from radius (distal end sometimes partially fused to radius)	ulna moderately strong and separate from radius	ulna strong and separate from radius		
Distal end radius	with articular facet for cuneiform	with articular facet for cuneiform	with articular facet for cuneiform	lacks articular facet for cuneiform		
Magnum and trapezoid	separate	<u>fused</u>	<u>fused</u>	<u>fused</u>		
Trapezium	present	<u>missing</u>	<u>missing</u>	?present		
Lunar	rests almost equally on magnum and unciform	lunar on both magnum and unciform but more so on unciform	rests mostly on unciform	lunar rests mostly on unciform		
Metacarpals III and IV	separate	<u>fused</u>	separate (united in old age, Walker, 1975)	separate		
Metacarpals II and V	separate near full length with metacarpal II more robust than V, both with 3 phalanges	separate very slender near full length, with only 2 phalanges	separate relatively strong near full length, with 3 phalanges	separate relatively strong near full length, with 3 phalanges		
Metacarpal I	vestigial, extremely slender with 2 minute phalanges	<u>lost</u>	<u>lost</u>	?proximal rudiment		
Distal keel on metapodials	incomplete	incomplete	incomplete	incomplete		
Hind Limb						
Fibula	reduced but complete; both ends fused with tibia	incomplete; fused proximal and distal rudiments	incomplete; fused proximal rudiment and separate malleolar	probably incomplete; proximal rudiment fused, separate malleolar		
Shape of fibular facet of calcaneum	large convexity only	simple concavity	simple concavity	large proximal convexity and small distal concavity		
Cuboid and navicular	<u>fused</u>	<u>fused with the ectomesocuneiform</u>	<u>fused with the ectomesocuneiform</u>	<u>fused</u>		
Metatarsals III and IV	separate	<u>fused</u>	<u>fused</u>	separate		
Metatarsals II and V	separate, very slender with 3 minute functionless phalanges	separate, very slender with only 2 phalanges	separate, relatively strong with 3 phalanges	separate, slender with 3 phalanges		

Dotted Line = Derived Characters; Dashed Line = Shared with Horned Ruminants

^aFused on basis of Webb's notes for Amphitragulus.^bMetacarpals figured by Kowalevsky (1876, pl. 2, figs. 24 and 25) and refigured in the *Traite de Paleontologie* (Viret, 1961) are from the Quercy Phosphorites and do not represent Gelocus. We suspect, however, that future evidence will show that Gelocus had complete lateral metacarpals.

	Gelocidae		Moschidae	
Leptomeryx	Gelocus	Dremotherium	Blastomeryx	Moschus
odontoid process with high dorsal crest and concavity on each side; anterior articular surfaces large and dorsally approach top of neural canal	odontoid process semi-spool-like and transitional as in Leptomeryx; anterior articular surfaces high		odontoid process spoutlike; anterior articular surfaces approach top of neural canal	odontoid process spoutlike; anterior articular surfaces approach top of neural canal
ulna strong and separate from radius	ulna relatively light and separate from radius	ulna moderately strong and separate from radius	ulna relatively light and separate from radius	ulna relatively light and separate from radius
lacks articular facet for cuneiform	with articular facet for cuneiform	with articular facet from cuneiform (AMNH 10345)	with articular facet for cuneiform	with articular facet for cuneiform
<u>fused</u>	<u>fused</u>	<u>fused</u> ^a	<u>fused</u>	<u>fused</u>
<u>missing</u>	<u>trapezoid lacks facet for trapezium</u>		<u>missing</u>	<u>missing</u>
lunar rests mostly on unciform	lunar rests on both unciform and magnum		lunar rests on both unciform and magnum	lunar rests on both unciform and magnum
separate	separate	fused with weak line of fusion (AMNH 10345)	fused with very weak line of fusion	fused with weak line of fusion
separate, slender, near full length, with 3 phalanges	separate, represented by distal fragments ^b	fused short proximal splints with distinct sutures (Filhol, 1879, p. 41)	separate, complete, slender with 3 phalanges	presumably proximal rudiments of II and V fused; shaft incomplete, unfused distal rudiments with 3 phalanges
<u>lost</u>	<u>lost</u>	<u>lost</u>	<u>lost</u>	<u>lost</u>
incomplete	incomplete	<u>complete</u> (AMNH 10345)	<u>complete</u>	<u>complete</u>
<u>incomplete; proximal rudiment fused and separate malleolar</u>	<u>incomplete; proximal rudiment fused and separate malleolar</u>	separate acc. to Filhol tibia shows distal articular facets for malleolar (AMNH 10345)	<u>incomplete; proximal rudiments fused and separate malleolar</u>	<u>incomplete; proximal rudiments fused and malleolar separate</u> (?occasionally fused)
large proximal convexity and small distal concavity	large proximal convexity and small distal concavity	small proximal convexity and small distal concavity (AMNH 10345)	proximal concavity and distal concavity subequal	large proximal convexity and small distal concavity
<u>fused</u>	<u>fused</u>	<u>fused</u> (AMNH 10345)	<u>fused</u>	<u>fused</u>
<u>fused</u>	<u>fused and elongate</u>	<u>fused and elongate</u>	<u>fused and elongate</u>	<u>fused and elongate</u>
reduced to fused proximal rudiments	proximal rudiment of II fused; proximal rudiment of V indicated by depression on IV	fused short proximal splints with distinct sutures (Filhol, 1879, p. 41)	proximal rudiment II partially fused; proximal rudiment V generally free	presumably proximal rudiments II and V fused; shaft incomplete

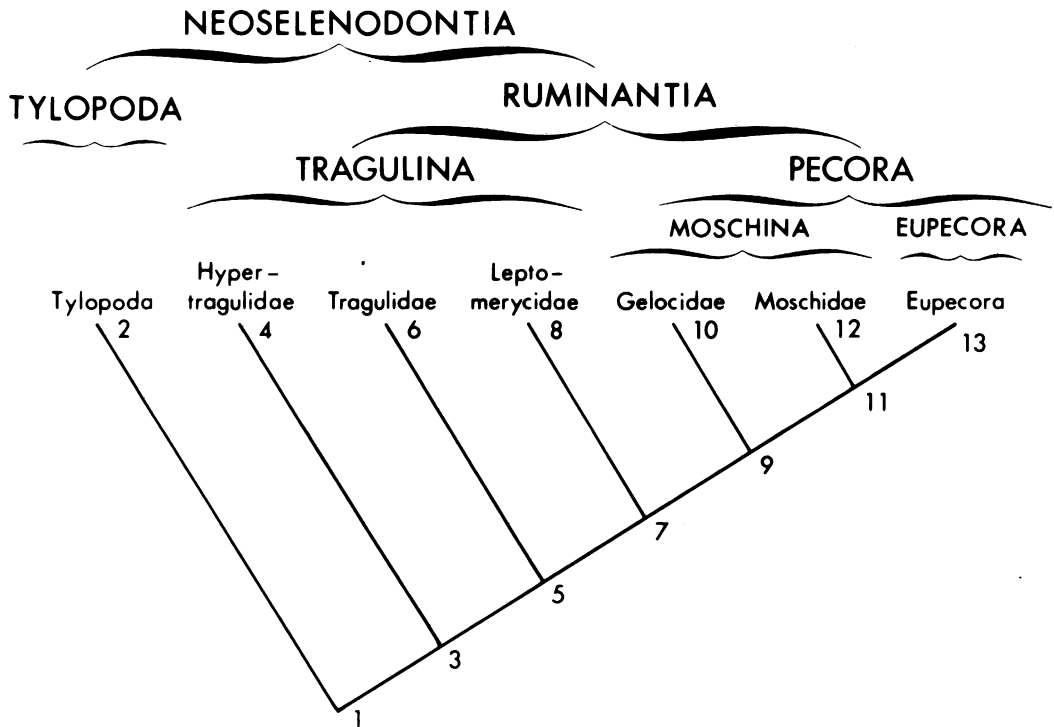


FIG. 10. Cladogram of Neoselenodontia. This hypothesis emphasizes the branching sequence of living and extinct families of hornless ruminants. The horned ruminants (Eupecora) are to the right. The Tylopoda are regarded as the sister group of the Ruminantia. The numbers (1–13) refer to apomorphic characters summarized in table 4.

keels. The axis and limbs of *Hypertragulus* are the most primitive of all the lower ruminants. The evolutionary trends to develop a spoutlike odontoid process and to reduce and lose lateral limb elements while fusing and lengthening others is first strongly evi-

denced in *Leptomeryx* and *Gelocus*. From the limb characters of *Gelocus* relatively minor transformations are necessary in *Dremotherium*, *Blastomeryx*, and *Moschus* to attain the derived conditions of higher ruminants.

PHYLOGENETIC CONCLUSIONS

From such sets of data we have analyzed character differences and attempted to determine their evolutionary polarities. The polarity of a given character is usually evident by comparisons between higher ruminants on the one hand and more remote selenodonts on the other. Whenever there has been a question we have discussed the detailed basis for our determinations in the text. Thus our method of phylogenetic analysis is a cladistic one.

Such a cladistic approach may lead to dif-

ferent conclusions from a stratophenetic approach. The latter approach has been well advocated by Gingerich (1976) and is followed, more or less consciously, by many paleontologists. The efficacy of the stratophenetic approach depends upon a nearly perfect fossil record. As the fossil record improves, the method becomes more reliable. Unfortunately, the fossil record is flimsy in its sampling of biotic diversity through time and space, as pointed out most recently by Simpson (1978). Furthermore, stratophenet-

icists have not clearly set forth the proprietary limits of their method. Hence it is all too easy for the method to be applied too optimistically. For example, major morphological gaps (and stratigraphic lacunae) in the record of early selenodont artiodactyls from western North America have not prevented Black (1978) from postulating continuous local but separate origins for late Eocene Camelidae, Oromerycidae, and Leptomerycidae. As noted above, this picture is considerably complicated by consideration of Old World selenodonts.

In a broad study, such as ours, of a diverse and scattered group, such as the ruminants, a phylogenetic (or cladistic) approach is preferred. The Tragulidae exemplify this point. The living members of the Tragulidae are relicts in the Old World tropics, as emphasized by Thenius (1969); and prior to the Miocene they left little or no fossil record. On the basis of morphological comparisons, however, it is now evident that the Tragulidae are even more remotely related to higher ruminants than is *Archaeomeryx* from the late Eocene of Mongolia. This example does not disprove the usefulness of the stratophenetic method in appropriate applications, but it does emphasize the preeminence of the phylogenetic method for groups broadly scattered through space and time.

Our conclusions as to phylogenetic relationships among the lower ruminants and related taxa are summarized in figure 10. Osteological characters that support these hypotheses are summarized in table 4. Most separate analyses of the cranial, dental, and postcranial characters yielded similar conclusions. However, the reduction of distal limb elements in various groups seems to have undergone much parallel evolution. For example, the distal end of the fibula has apparently been reduced to a malleolar bone separately in the Tylopoda and in the Ruminantia (as evidenced by a complete fibula in the Hypertragulidae). Similarly, many parallel progressions are found in the limbs of the Leptomerycidae and Gelocidae. In such cases, the weight of several lines of evidence is necessary to demonstrate the probability that parallelism has occurred.

The sister group of the Ruminantia is to be

TABLE 4
Key Characters of Hornless Ruminants
(See figure 10.)

- | |
|--|
| 1. NEOSELENODONTIA: Upper incisors reduced or absent. Ectocuneiform fused with mesocuneiform. Molars lack paraconule. Ruminating stomach. |
| 2. TYLOPODA: Vertebral artery passes through neural arch pedicels of cervical vertebrae. Three-chambered stomach lacking reticulum. |
| 3. RUMINANTIA: Cuboid and navicular fused. Three-chambered stomach including reticulum. |
| 4. TRAGULINA: HYPERTRAGULIDAE: Postglenoid foramen laterally enclosed. Mesostyle lost. P ₁₋₃ simplified, acuminate. P ₄ metaconid weak or absent. Radius fused to complete ulna. Complete fibula fused proximally and distally with tibia. |
| 5. Jugular foramen confluent with posterior lacerate. Postorbital bar complete. P ¹ lost. Trapezoid and magnum fused. Fibula reduced to malleolar bone. |
| 6. TRAGULIDAE: Palatine bones extended posteriorly. Postglenoid process reduced and overridden by expanded bulla. Tensor tympani chamber posteriorly restricted. <i>Dorcatherium</i> -fold ^a in lower molars. Malleolar articulation of calcaneum concave. |
| 7. Mastoid restricted to occipital region. Lower premolars with paraconid, metaconid, entoconid lingually projected on at least P ₄ . Malleolar articulation of calcaneum concavo-convex. |
| 8. LEPTOMERYCIDAE: Large mastoid fissure. I ₁ enlarged, tusk-like. |
| 9. PECORA: Stapedial artery lost. Subarcuate fossa reduced. Lower premolars with paraconid bifurcated making four lingual crests. Forelimbs relatively long, nearly equal hindlimb in length. Astragalus short, with parallel ginglymi. Trapezium absent. |
| 10. MOSCHINA: GELOCIDAE: Elongate P ² and P ³ with posterior protocone. |
| 11. Large suprameatal fissure. P ₁ lost. P ² and P ³ triangular. P ₄ metaconid flattened and projecting anteriorly. Metacarpals 3 and 4 fused. Metapodial keels complete. Cotyledonous placenta. Four-chambered stomach including omasum (psalterium). |
| 12. MOSCHIDAE: Laterally enclosed subcentral tympanohyal. Upper canines sabre-like (especially in males) and set loosely in enlarged alveoli. |
| 13. EUPECORA: Frontal appendages (ossicones, antlers, and horns). Upper canines reduced or absent. Subarcuate fossa absent. |

^a*Dorcatherium*-fold is actually a pair of folds normally occurring on each lower molar of this and most other tragulid genera. It consists of an enamel fold on the posterior slope of the protoconid and another similar fold on the posterior slope of the metaconid, which together resemble an anteriorly directed letter M. In the course of tragulid evolution this fold tends to become more strongly developed (Mottl, 1961).

found somewhere within the great late Eocene radiation of selenodont artiodactyls, but at present its identity is unclear. Of living selenodont groups, the Camelidae are the obvious (indeed, the only) choice. When one considers the 10 or more extinct selenodont families, however, the problem is far more difficult. Among North American selenodont families, the Protoceratidae have been allied closely with the Leptomerycidae by many students including Scott (1899, 1940, 1945), Gazin (1955), Golz (1976), and Black (1978). Gazin's recognition of the Leptotragulinae as early Protoceratidae rather than early Leptomerycidae helps clarify the postulated relationship without greatly altering it.

The Camelidae and Protoceratidae have been supposed to be closely related by many students of North American late Eocene artiodactyls, including Gazin (1955), Stirton (1967), Patton and Taylor (1973), Wilson (1974), and Golz (1976). Continuity of Uintan records provides some stratophenetic evidence of possible relationship. And shared derived characters that impress us are some details of their precociously elongated limbs and especially passage of the vertebrarterial canal through the neural arch pedicels rather than through the transverse processes of the cervical vertebrae, as noted by Flower (1885) and Scott (1895) and confirmed by direct examination of *Protoceras* skeletons. Thus the Tylopoda, comprised of the Camelidae and Protoceratidae in North America, are the probable sister group of the Ruminantia.

In Europe the Amphimerycidae and the Xiphodontidae require careful investigation as possible sister groups of the Ruminantia. Their relationships with the Camelidae and Protoceratidae also require review. The presence of lingual cingula in the upper molars and precociously elongate limbs may be derived features shared with the Protoceratidae and (or) Camelidae. Further investigation of this interesting problem is beyond the scope of this paper. Tentatively, we suggest that these four families be grouped together as the Tylopoda, although their interrelationships remain in doubt. For purposes of this analysis we then regard the Tylopoda as the unresolved sister group of the Ruminantia (fig. 10).

The most primitive branch of the ruminants is undoubtedly the Hypertragulidae. They share fusion of the cuboid and navicular with all other ruminants. Discovery of *Parvitrágulus* by Emry (1978) indicates that the peculiarly modified premolars of *Hypertragulus* had origins more directly comparable to those of the Tragulidae. In most respects, however, Hypertragulidae are primitive ruminants, for example in retention of P¹, an open orbit, and a complete fibula.

The phylogenetic position of the Tragulidae near the base of all Ruminantia may seem more surprising to paleontologists than to neontologists. In any event the logic of character analysis demonstrates that the Tragulidae are a lower branch of the phylogenetic tree of ruminants than *Archaeomeryx* and the other Leptomerycidae. The most revealing shared-derived character, linking Tragulidae with higher taxa, is fusion of the trapezoid with the magnum in the carpus. Other derived features such as the reduction of the fibula to a malleolar bone may well result from parallel evolution. Also, the closure of the postorbital bar, while apparently a shared-derived feature, differs in important details from that structure in the Leptomerycidae and higher ruminant taxa. The Tragulidae are characterized by a remarkable array of uniquely derived characters, of which we cite only a few (table 4). The fossil record of the Tragulidae does relatively little to reduce the degree of uniqueness; indeed, *Dorcatherium*, the best known fossil tragulid, closely resembles *Hyemoschus* in most of its features. Major differences between *Tragulus* and *Hyemoschus*, comparable to those between the Gelocidae and Moschidae, for example, further emphasize the long distinct evolutionary history of the Tragulidae. Only the extinct Hypertragulidae can claim a more primitive phylogenetic position within the Ruminantia than the Tragulidae.

The Leptomerycidae are considerably advanced over the Hypertragulidae and the Tragulidae, and share important derived cranial, dental, and podial characters with the Gelocidae and higher ruminants. Such advanced characters include a closed postorbital bar, posterior restriction of the mastoid bone, lingual elaboration of the lower pre-

molars, and a concavo-convex articulation between the calcaneum and malleolar bones. Thus the Leptomerycidae represent a major step in the evolution of ruminants. Nonetheless, most if not all known members of this family are uniquely specialized in their tusk-like first lower incisors and in the modest enlargement of the first lower premolar (Taylor and Webb, 1976).

The next family is the Gelocidae, primitive sister group of the Moschidae and higher ruminants. As Kowalevsky (1876) emphasized long ago, the feet of *Gelocus* have such derived characters of higher ruminants as a compact, parallel-sided astragalus. As we have illustrated (fig. 6), the lower premolars with four lingual crests are also an important derived character.

The relationships of the Moschidae are problematical because of their broad continuity (on the primitive side) with the Gelocidae. A number of important derived characters may be cited, but in many instances the distinctions are blurred by transforma-

tion series in the rich Miocene record from Europe. Among these progressions are shortening the premolar series, further complicating the lingual crests of the lower premolars, fusing the metacarpals, and developing fully keeled metapodials. Progressive features of moschid soft anatomy are a cotyledonous placenta and a four chambered stomach. A large suprameatal fissure characterizes the Moschidae and most higher ruminants. Loosely implanted large upper canines and a laterally enclosed tympanohyal are unique distinctive features of the Moschidae.

From the Moschidae it is not difficult to progress to *Eupecora* or higher ruminants. The principal innovation is the development of frontal appendages, including horns, antlers, and ossicones. Loss of the subarcuate fossa on the endocranial side of the petrosal is another progressive character. Analysis of the origins of higher ruminants from the Moschidae lies beyond the scope of this paper.

CLASSIFICATION

In broadest terms our analysis supports the view of the great comparative anatomists of the last century. We still find Flower's studies (e.g., 1867, 1875) particularly cogent. We therefore do not propose any fundamental reclassification of the Ruminantia or related stocks. We continue to regard the suborder Ruminantia as the ultimate branch of the order Artiodactyla, and we find Tylopoda an appropriate subordinal term for the sister-group of the Ruminantia (see upper part, fig. 10).

The taxa to be included in the Tylopoda remain uncertain. We do not believe the group should include all early selenodonts, as Romer (1966) proposed. As discussed above, we tentatively recommend that, besides Camelidae, Tylopoda include Procercatidae, Xiphodontidae, and Amphimerycidae, pending resolution of their interrelationships. We follow Wilson (1974) in placing the Oromerycidae of Gazin (1955) as a primitive subfamily of the Camelidae.

We doubt the contrary suggestion of Golz (1976) and Black (1978) that the Oromerycidae evolved separately out of the Dichobunidae, and cite as evidence the probably shared-derived enlargement of the third upper incisor in *Eotylopus*.

We find no taxonomic term available for the combined Tylopoda and Ruminantia. Such a concept has great utility as it represents an important natural (monophyletic) group of living selenodont artiodactyls, united (among other features) by ruminating stomachs and by the reduction or loss of upper incisors. Although such a grouping has sometimes been achieved by forcing Camelidae into the Ruminantia, it seems preferable to have a distinct name. We therefore propose the name Neoselenodontia which will stand hierarchically above the subordinal level and will include the suborders Tylopoda and Ruminantia.

Flower (1883) divided the Ruminantia into the infraorders Tragulina and Pecora, the lat-

ter name being restricted from Linnaean usage. Although our analysis reveals a more complicated progression of ruminant phylogeny than Flower could have known, we find no compelling reason to abandon his terms *Tragulina* and *Pecora*. We, like Simpson (1945), accept Flower's basic division of the *Ruminantia*, but alter the contents of these two infraorders to incorporate new evidence. We follow Simpson (1945) in placing the most primitive fossil ruminants along with the *Tragulidae* in the *Tragulina*. Our classification, however, excludes three extinct families included by Simpson in the *Tragulina*. We remove the *Amphimerycidae* and *Protoceratidae* to the *Tylopoda*, as discussed above. We also remove the *Gelocidae*, as explained below, to the *Pecora*. A further difference from Simpson (1945) is our recognition of the *Leptomerycidae* as a distinct family, not within the *Hypertragulidae*.

As one traces morphological changes from modern horned ruminants (the essence of *Pecora*) back into hornless ruminants, the first and greatest gap occurs between the *Gelocidae* and *Leptomerycidae*. In his penetrating studies of *Gelocus*, Kowalevsky (1876, p. 145) reached the following conclusion: "Der *Gelocus* ist das erste Beispiel eines derartig völlig angepassten Paarhufers, welche auf der Erde erschienen ist, und dessen Nachkommenschaft eben in Folge diesen völlständigen, obwohl nur einseitig entwickelten Organisation, eine der wichtigsten Rollen in der Bevölkerung unserer Erde spielt."

Our observations and a century of paleontological advances merely reinforce this view that *Gelocus* is the first fully progressive artiodactyl and lies close to the roots of the higher ruminants. In recognition of this continuity we recommend including the *Gelocidae* and *Moschidae* in the *Pecora* along with the familiar horned, antlered, and ossicone-bearing ruminants.

Transfer of the *Gelocidae* to the *Pecora* properly reflects our phylogenetic conclusions. It is also practical to ally the *Gelocidae* with the *Moschidae*, as the two groups are difficult to separate in their Miocene diversification. We also recognize a special alliance between the *Moschinae* and *Blasto-*

merycinae. Simpson (1945) placed the *Blastomerycini* as a tribe of *Palaeomerycinae* outside of the *Moschinae*. For the families *Gelocidae* and *Moschidae*, primitive hornless *Pecora*, we propose the Division *Moschina*. The rest of the *Pecora*, Simpson's *Pecora* minus *Moschina*, probably represent a monophyletic grouping of ruminants, characterized by horns, antlers, or ossicones. For this group, we propose the Division *Eupecora*. Our suggested hierarchy is indicated in the upper part of figure 10.

Thus, the infraorder *Tragulina* of Flower (1883) may be retained for the non-pecoran ruminants. In the present analysis that definition encompasses three paraphyletically related families, namely *Hypertragulidae*, *Tragulidae*, and *Leptomerycidae*.

STRATIGRAPHIC PATTERNS

Figure 11 summarizes the known stratigraphic ranges of hornless ruminants and related groups. The most striking gap is the apparent absence of Eocene and Oligocene *Tragulidae*. Some possible Eocene and Oligocene records from Europe and Asia have been noted above. Our phylogenetic hypothesis implies that the *Tragulidae* should have been in existence at least as early as the earliest known *Leptomerycidae*, that is in late Eocene time. The *Hypertragulidae* (namely *Simimeryx*) are known from the very late Eocene, but not as yet before Duchesnean age.

The *Leptomerycidae* and *Gelocidae* appeared in the late Eocene and were the prominent ruminants during the Oligocene epoch. By the end of the early Miocene, however, the *Gelocidae* in Eurasia had given way to the *Moschidae*. In turn the *Moschidae* were soon supplanted by the adaptive radiation of the *Eupecora* which was well under way by the medial Miocene.

ZOOGEOGRAPHIC PATTERNS

Known occurrences of hornless ruminant families may provide an approximate history of their geographic distribution. The *Hypertragulidae*, the most primitive ruminants, are

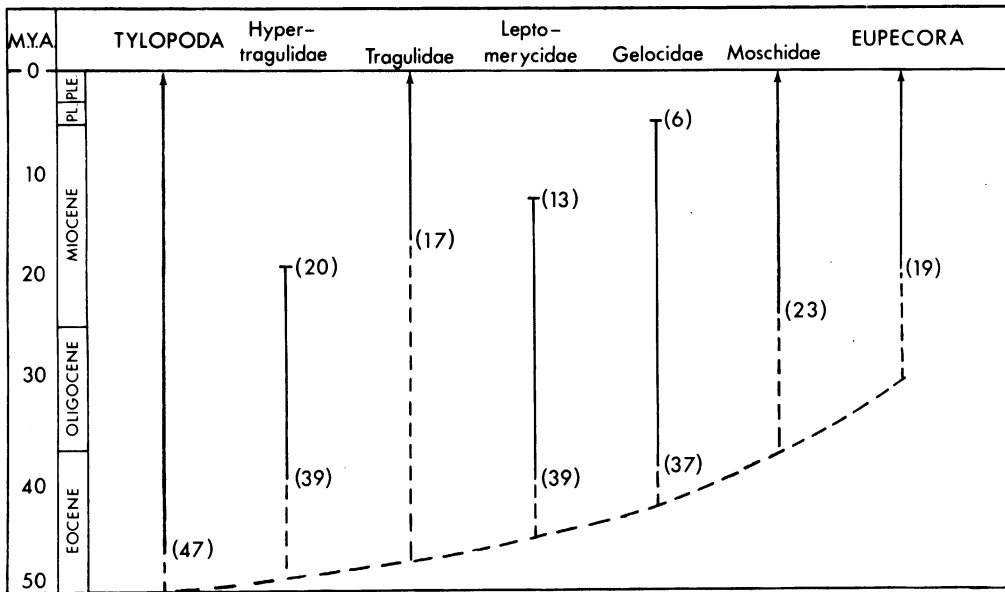


FIG. 11. Stratigraphic ranges of hornless ruminant families. (See text for discussion.)

known exclusively from North America. It may be relevant to note that the tylopodan families Camelidae and Protoceratidae also were exclusively North American during the late Eocene and subsequently through most of the Tertiary. If either or both of these families are the sister group of the Ruminantia it suggests an apparent origin of the most primitive Ruminantia in the late Eocene of North America.

The hypothesis that Ruminantia originated in North America is not as yet a strong one. If the Xiphodontidae and (or) Amphimerycidae were the sister group of the Ruminantia, a possibility that remains to be developed, then an Old World origin for the Ruminantia would appear more probable.

The Tragulidae occur exclusively in the Old World, especially at subtropical latitudes. This low latitude pattern may help explain their obscurity or absence in the early Tertiary, when most Old World fossil samples are from temperate latitudes. We speculate that Tragulidae originated when some late Eocene traguline stock from the New World distributed to the Old World and differentiated there.

The Leptomerycidae have a Holarctic distribution in the late Eocene and thereafter, although some North Americans (e.g., Patton and Taylor, 1973) have claimed the family as exclusively theirs. *Archaeomeryx* in Mongolia, *Xinjiangmeryx* in Sinkiang, and *Hendryomeryx* in the western United States together constitute the earliest Holarctic distribution for one family of ruminants. During the Oligocene and early Miocene two genera (*Bachitherium* and *Miomeryx*) are recognized in Eurasia by Lavocat (1951) and Viret (1961), and three genera (*Leptomeryx*, *Pronodens*, and *Pseudoparablastomeryx*) are recognized in North America by Taylor and Webb (1976).

The primary center of pecoran evolution appears to have been in the Old World, whereas North America was a secondary center. The origin and radiation of the Gelocidae evidently took place in Europe and Asia as did the subsequent diversification of the Moschidae. The Moschidae reached North America late in the early Miocene, where they are distinguished as *Blastomerycinae* (but have not been assigned previously to the Moschidae). The Gelocidae, not previously

recognized in North America, are now believed to be represented by the late Miocene Pseudoceratinae (Frick, 1937; Webb, MS).

The Eupecora likewise had their primary center of evolution in the Old World. Giraffoids, cervoids, and bovoids all seem to have their greatest continuity and diversity in Eurasia and Africa. Nonetheless every major group reached North America. Dromomerycidae (from cervoid or giraffoid stock) appear in the late early Miocene; Antilocapridae (from giraffoid or bovoid stock) reached North America still later in the early Miocene. Finally representatives of both the Cervidae and the Bovidae (*Neotragoceras*) first reached North America from Asia in the

late Miocene and then again, by means of other immigrant taxa, during the Pleistocene. Thus, although much of the history of the Ruminantia took place in the Old World, many of its chapters have a Holarctic setting.

ADDENDUM

After this manuscript was completed, a new genus, *Xinjiangmeryx*, which we believe belongs to the *Leptomerycidae*, was described from the late Eocene of the Tufan Basin in Sinkiang, China (Zheng, 1979, p. 120). This evidence further confirms our statement (p. 123) that the study of early ruminants must not be confined to North America.

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