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The Interrelationships of Higher Ruminant Families with Special Emphasis on the Members of the Cervoidea

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ABSTRACT

We analyze the interrelationships of the higher (Pecoran) ruminants, and suggest possible relationships between these families and the various genera of the polyphyletic assemblage “Gelocidae.” We also review the developmental processes of the cranial appendages of the living horned ruminant families, and conclude that giraffid ossicones, bovid horns, and cervid antlers cannot be considered to be homologous with each other. The characters that have been used in the past and in this paper to distinguish pecoran families are discussed and evaluated.

Within living pecoran families the Giraffidae are the most primitive, and the Moschidae and Antilocapridae are conjoined with the Cervidae in the superfamily Cervoidea, with antilocaprids being closer to cervids than are moschids. The Moschidae includes *Moschus*, the extinct European genera *Dremotherium*, *Micromeryx*, and *Hispanomeryx*, and the North American blastomer-

ycids. The Cervoidea includes the primitive extinct Eurasian genera *Eumeryx* and *Rutitherium*, and (more closely related to the other cervoids) the extinct African genus *Walangania*. The grouping Eucervoidea is proposed for a clade within the Cervoidea containing the Antilocapridae, the Cervidae, and the extinct families Palaeomerycidae and Hoplitomerycidae (which are deemed as closer to the Cervidae than are the Antilocapridae). The Palaeomerycidae contains the Old World genera *Palaeomeryx*, *Amphitragulus*, possibly also *Prolibytherium*, and the North American dromomerycids. The Hoplitomerycidae contains the European genera *Hoplitomeryx* and *Amphimoschus*. The European genus *Triceromeryx* remains as cervoid incertae sedis. A superfamily Giraffoidea is proposed to include the Giraffidae, the extinct family Climacoceridae, and possibly also the extinct African genus *Propalaeoryx*.

INTRODUCTION

The Ruminantia is a suborder of the order Artiodactyla, or even-toed ungulates, and in Neogene and Recent times has represented the most ecologically and geographically diverse group of living ungulates. Ruminants are divided into the more primitive tragu-

loids, and the more derived pecorans, or “higher ruminants,” which are characterized by larger body size and possession of cranial appendages (i.e., horns or antlers) in most living species. Traguloids were more diverse during the early Tertiary (Eocene and Oligo-

cene), and today only one family, the Tragulidae (mouse deer or chevrotains), survives in the tropical regions of the Old World. In contrast, the Pecora had their main evolutionary radiation in the late Neogene, and today comprise between three and five families (depending on taxonomic opinion), although a number of original families are now extinct. Today, the families Cervidae (deer) and Bovidae (antelope, sheep, and cattle) represent the greatest degree of taxonomic and geographical diversity among the Pecora. Despite the evolutionary success and ecological importance of the Pecora, the subject of the interrelationships of the living families, and of the relationship of fossil taxa to living forms, has remained little studied, and what is known about the subject remains an area of controversy and confusion.

The standard opinion on ruminant evolution for the last few decades has been that the extinct Gelocidae are the basal group from which the families of horned ruminants, i.e., the pecoran ruminants, can be derived (Simpson, 1945; Viret, 1961; Romer, 1966). More recently, Webb and Taylor (1980) have proposed that the gelocids should be included in the Pecora, comprising the sister group to the horned ruminants or "Eupecora," with the implication that the presence of horns, or other forms of cranial appendages, is a synapomorphy uniting the Eupecoran families. However, a number of recent papers have shown that horns have evolved more than once within the Ruminantia (e.g., Janis, 1982; Leinders, 1983; Scott and Janis, 1987). Moreover, recent work by Janis (1987) has shown that the gelocids represent a polyphyletic assemblage rather than a distinct clade. Therefore the origin of horned ruminants and their interrelationships must be sought among the different genera within the gelocid assemblage.

This paper is a preliminary analysis of the characters which can be used to define the higher ruminant families and to ally them with taxa within the gelocid assemblage, and of the probable relationships among the ruminant taxa. It is our intention to use a number of limb, dental, and cranial characters to construct a possible cladogram for the interrelationships of the Pecora. We do not see this proposed cladogram as being immutable,

but rather suggest that it should serve as a hypothetical scheme which can be tested by the examination of other characters, either morphological (e.g., basicranial characters, which we discuss in this paper only in the context of the work of Webb and Taylor, 1980) or biochemical (for the interrelationships of living families).

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ABBREVIATIONS

AMNH	Department of Vertebrate Paleontology, American Museum of Natural History
AMNH(M)	American Museum of Natural History, Modern Mammals

BMNH	Department of Paleontology, British Museum of Natural History.
F:AM	Frick American Mammals, Department of Vertebrate Paleontology, American Museum of Natural History
MCZ	Museum of Comparative Zoology, Harvard University
Ph	Naturhistorisches Museum, Basel
PQN	South African Museum (Cape Town)
UCBL	Université Claude Bernard, Lyon

HISTORICAL VIEWS OF LIVING RUMINANT RELATIONSHIPS

Researchers in the past century have recognized between three and five living families of pecoran ruminants. Cervids, bovids, and giraffids have always been accorded family status. Antilocaprids have usually been accorded family status as the Antilocapridae (e.g., Simpson, 1945), although some workers have placed them within the Bovidae (e.g., O'Gara and Matson, 1975). Moschids (represented by the living musk deer species of the genus *Moschus*) have traditionally been regarded as a subfamily Moschinae within the Cervidae (e.g., Simpson, 1945), but a number of authors (e.g., Gray, 1821; Brooke, 1878; Flerov, 1952; Bubenik, 1966; Webb and Taylor, 1980; and Groves and Grubb, 1987) have suggested that *Moschus* should be placed in its own family within the superfamily Cervoidea.

The five living families are clearly distinguishable from each other on the basis of characters of the cranial appendages, limbs, and dentition. They are unified as "higher ruminants," or pecorans, distinguishing them from tragulids by the following characters: possession of cranial appendages, usually only in the male of the species (although cranial appendages are lacking both in *Moschus* and the cervid genus *Hydropotes*); fully selenodont cheek teeth with the absence of a lingual cingulum in the upper molars (as opposed to bunoselenodont cheek teeth with a lingual cingulum in tragulids); elongated, fused metapodials possessing complete distal articular keels; a compact, parallel-sided astragalus; and a four-chambered, ruminant type of stomach, with a fully formed omasum and a large rumen (in contrast to the small rumen

and poorly defined omasum of tragulids) (see Webb and Taylor, 1980; Scott and Janis, 1987).

The five living families have generally been characterized by the following distribution of characters.

CERVIDAE: Deciduous, branched cranial appendages without a keratin cover (antlers); brachyodont (low crowned) to mesodont (moderately high crowned) cheek teeth; limbs without pronounced elongation of the metapodials, with partial retention of metapodials II and V (i.e., the "side toes").

MOSCHIDAE: Absence of cranial appendages; brachyodont to mesodont cheek teeth; moderately elongated metapodials with retention of the side toes.

GIRAFFIDAE: Nondeciduous, unbranched cranial appendages, covered with skin (ossicones); brachyodont cheek teeth; elongated metapodials with complete loss of the side toes.

BOVIDAE: Nondeciduous, unbranched cranial appendages, covered by a nondeciduous, unbranched keratin sheath (horns); mesodont to hypsodont (high crowned) cheek teeth; metapodials may or may not be elongated, but side toes are invariably absent.

ANTILOCAPRIDAE: Nondeciduous, unbranched cranial appendages, covered by a deciduous forked keratin sheath (horns); hypsodont cheek teeth; elongated metapodials with loss of the side toes.

Hydropotes, the only antlerless cervid, can be allied with the Cervidae on the basis of soft anatomy features, detailed in the next section, which are lacking in *Moschus*. *Moschus* also has a less convoluted brain and a less complicated omasum than is typical of both cervids and bovids (i.e., resembling the more primitive pecoran condition seen in giraffids) (Garrod, 1877). *Moschus* has generally been allied with the Cervidae, if not included in the family, on the basis of the brachyodont dentition, retention of the side toes, and possession of a saberlike upper canine in males, resembling the condition seen in *Hydropotes*, but absent in any other living pecoran genera. Webb and Taylor (1980) have shown that *Moschus* can be grouped with other fossil pecoran genera into the family Mos-

chidae on the basis of autapomorphic features. They consider the Moschidae to be the sister group to the other living pecorans, which they place in the Eupecora. They consider the Eupecora to be united by the presence of frontal appendages, reduced or absent upper canines, and loss of the subarcuate fossa.

Antilocaprids have been allied with the Bovidae on the basis of the similarity of the horns, despite the difference of the deciduous, forked horn sheath as opposed to the non-deciduous, unbranched sheath in the bovids (see O'Gara and Matson, 1975, and later discussion in this paper, for discussion of periodic flaking of the bovid horn sheath). O'Gara and Matson (1975) also ally *Antilocapra* with the Bovidae based on possession of hypsodont cheek teeth, long limbs with the complete loss of the side toes, and retention of the gall bladder.

Giraffids have traditionally been allied with cervids in the superfamily Cervoidea (Simpson, 1945; Romer, 1966; Thenius, 1969) because both groups share possession of brachydont cheek teeth with many accessory styles and ribs, in contrast to the more simplified, hypsodont cheek teeth of bovids and antilocaprids. Hamilton (1978a) has restated the significance of the autapomorphic feature of the Giraffidae of the possession of a bilobed lower canine.

More recently, various workers have pointed out that the different types of cranial appendages in ruminants are not homologous in their mode of development. Cervid antlers are formed from an outgrowth of the frontal bone, whereas bovid horns and giraffid ossicones are said to be formed by the fusion of separate dermal ossification centers with the skull, although the developmental condition in the Antilocapridae has not been determined (see review in Goss, 1983, and discussion later in this paper). Frechkop (1955) and Hamilton (1978a) have regarded this similarity between bovids and giraffids as a synapomorphy uniting these two families, a view which appears to be generally accepted at the present time. However, Todd (1975) presents chromosomal evidence to suggest that the Giraffidae are more primitive than any other pecoran family (but see discussion of this paper in Scott and Janis, 1987).

Leinders (1979) and Leinders and Heintz (1980) have pointed out two morphological features of *Antilocapra* which they consider link the Antilocapridae more closely with the Cervidae than the Bovidae; these are: the presence of a closed metatarsal gully (see fig. 7) and the possession of two lacrimal orifices situated on the orbital rim (see fig. 4). These similarities led them to conclude that the horns of *Antilocapra* had a separate evolutionary origin from bovid horns, although they do not regard them as homologous with cervid antlers, but assume that they represent an independent evolutionary event within the Antilocapridae. They also point out that the genus *Moschus*, while resembling cervids in the presence of a closed metatarsal gully, is less like cervids than *Antilocapra* in the retention of the primitive pecoran condition of a single lacrimal orifice situated within the orbit on the ventral anterior orbital wall. Figure 1 summarizes the different evolutionary viewpoints held over the past few decades of the interrelationships of the living pecoran families.

The cladograms presented in figure 1 illustrate the differential value placed on various character states in assessing the interrelationships between living pecoran families. (The numerical characters listed on the cladograms are consistent throughout the text and the figures in this paper, and are referenced in table 1.) The "traditional" view (fig. 1A) regards the characters of the height of the cheek teeth (character 12) and the condition of the metapodials (character 29) as being critical in determining family relationships. Cranial appendages are considered a synapomorphy linking all pecoran families, implying that they were secondarily lost in the genera *Moschus* and *Hydropotes*.

Both present-day views (fig. 1B, 1C) recognize the fact that brachydont cheek teeth and retention of the side toes are primitive characters for the Ruminantia (indeed for all tetrapods!), and cannot be used as synapomorphies to unite families within the Pecora. They also both acknowledge the fact that cervid antlers are not homologous with the cranial appendages of the other pecoran families, and thus that cranial appendages cannot be held to be a primitive pecoran character.

TABLE 1
Characters Used in Text and Cladograms

1. "Ruminant" character suite: Fusion of cuboid and navicular in tarsus Upper incisors reduced or lost Lower canine incisiform (Latter two characters also evolved in parallel within the Protoceratidae)	7h. Cranial appendages supposedly secondarily lost
1a. Suite of characters uniting members of Ruminantia above the level of the Hypertragulidae: Amastoid condition of skull Jugular foramen confluent with posterior lacrimate foramen Loss of trapezium Fusion of magnum and trapezoid Metacarpal I lost Reduction of fibula to malleolar bone P1 lost Mesostyles in upper molars and ectostylids in lower molars "Dorcatheirium fold" in lower molars	7i. Presence of median occipital cranial appendages
2a. "Higher ruminant" features (uniting ruminants above the level of the Tragulidae): Postorbital bar formed from frontal bone Axis with odontoid process possessing high dorsal crest with high anterior articulatory surfaces Calcaneum with fibular facet with large proximal concavity and small distal convexity	8. Presence of lacrimal fossa
2b. Anterior cingulum present on lower molars	9. Double lacrimal orifice on dorsal rim of orbit
3. Lower premolars with small metaconid, without posterior extension of metaconid forming posterolingual wall to tooth	10. Laterally enclosed, subcentral tympanohyal vagina: 10a. Partially formed 10b. Fully formed
4. Characters of p1: 4a. p1 large and caniniform 4b. p1 small and premolariform, separated from p2 by small diastema 4c. p1 lost	11. Upper canine characteristics: 11a. Moderately elongated ("traguloid" type) 11b. Sabrelike ("moschid" type) 11c. Secondarily reduced or lost
5. Compact, parallel-sided astragalus	12. Crown height of cheek teeth: 12a. Brachydont 12b. Hypsodont
6. Pecoran basicranial character suite: Loss of promontorium on petrosal Enlarged fossa for stapedial muscle on petrosal Shallow subarcuate fossa on petrosal Broadened basioccipital with strong flexion stops on condyles Laterally enclosed postglenoid foramen	13. Characters of cingulum on upper molars: 13a. Present 13b. Reduced 13c. Absent
7. Characters of cranial appendages: 7a. Unbranched ossicones preformed in cartilage (nondeciduous) 7b. Unbranched horns (nondeciduous) with unbranched (?) nondeciduous keratin sheath 7c. Branched or unbranched nondeciduous appendages with deciduous branched or unbranched keratin sheath 7d. Branched deciduous antlers on top of nondeciduous pedicle 7e. Branched appendages of uncertain developmental origin (nondeciduous) 7f. Unbranched appendages of uncertain developmental origin (nondeciduous) 7g. Appendages formed with fusion of dermal elements with skull	14. Condition of protocone on P3: 14a. Posteriorly situated and directed 14b. Centrally situated and lingually directed
	15. Presence of entostyle formed from anterior wall of metaconule: 15a. Small, incipient entostyle 15b. More prominent entostyle
	16. Characteristics of metastyle: 16a. Large 16b. Small
	17. Characteristics of P4 metacone: 17a. Large 17b. Small
	18. Characteristics of M3 metaconule: 18a. Small 18b. Large
	19a. Bifurcated posterior wing of protocone on molars
	19b. Bifurcated posterior wing of metaconule on molars
	20. Presence of "Palaeomeryx fold" on molars of brachydont taxa
	21. Metastylids on lower molars
	22. Condition of postentocristid on molars: 22a. Incomplete 22b. Complete
	23. Bilobed lower canine
	24. Paraconid on p4 forming lingual wall to tooth
	25. Vertical groove on posterolingual region of p4
	26. Double posterior lobe on m3: 26a. Closed posteriorly 26b. Open posteriorly
	27. Complete distal metapodial keels
	28. Fusion of metapodials: 28a. Fused with open gully 28b. Fused with closed gully 28c. Secondarily open gully (from closed gully) 28d. Metapodial fused and elongated over traguloid condition. (Metacarpals similar length to metatarsals)
	29. Condition of side toes: 29a. Complete side toes retained 29b. Side toes partially lost (proximal or distal ends)

TABLE 1—(Continued)

	29c. Side toes completely lost, metapodials further elongated
30.	Pattern of fusion of remnants of lateral metatarsals:
	30a. Metatarsal II remnant fused proximally
	30b. Metatarsal V remnant fused proximally
31.	Posterior tuberosity on metatarsus
32.	Condition of cubonavicular facet on proximal metatarsus:
	32a. High and pointed
	32b. Very flat and broad
	32c. Somewhat flattened
	32d. Raised, but not as sharply as in 32a
33.	Stomach characters:
	33a. Three-chambered stomach with rumen
	33b. Four-chambered stomach with omasum
34.	"Cervid" features of soft anatomy, especially absence of gall bladder

By implication, pecoran cranial appendages must have evolved in parallel at least once, and the genera *Moschus* and *Hydropotes* may be assumed to be primarily without cranial appendages.

The view expressed in figure 1B relies heavily on the assumption that the similarity in the mode of formation of bovid horns and giraffid ossicones is a true synapomorphy. Hamilton (1978a) did not specifically address the problem of the position of the Antilocapridae and, as previously mentioned, the mode of formation of their horns is as yet unknown. However, other recent workers (e.g., O’Gara and Matson, 1975) have considered that the similarities between *Antilocapra* and bovids justify the consideration of *Antilocapra* as at least the sister taxon to the Bovidae, although not all present-day proponents of this view would go so far as O’Gara and Matson in placing *Antilocapra* within the Bovidae. In this scheme, the Antilocapridae and the Bovidae are usually united in the superfamily Bovoidea (which may sometimes be expanded to include the Giraffidae).

The view of Leinders and Heintz (1980), represented by figure 1C, takes into account a cervid feature originally noted by Milne-Edwards (1864), a double lacrimal orifice on the orbital rim (character 9); and a cervid feature recognized by Heintz (1963, 1970), a closed metatarsal gully (character 28b). Leinders and Heintz point out that these features can be used to place *Antilocapra* as the

sister taxon to the Cervidae, relegating *Moschus* to the position of the sister taxon to the Cervidae plus the Antilocapridae. They consider that the derived features that *Antilocapra* shares with the Bovidae, such as the elongation of the metapodials, the loss of the side toes, and the hypsodont cheek teeth, were derived in parallel as the result of a similar evolutionary ecological preference for an open habitat and a fibrous diet. (The development of similar characters can be seen in the evolution of the Camelidae and the Equidae). They also point out that the retention of the gall bladder (see O’Gara and Matson, 1975) is a primitive character that cannot be used to specifically unite *Antilocapra* with the Bovidae, or to exclude the genus from the position of the sister taxon to the Cervidae, and consider that the cranial appendages of *Antilocapra* evolved in parallel with bovid horns. While Leinders and Heintz consider that the Bovidae and the Giraffidae may be united by the synapomorphies of a metatarsal with an open gully, and the development of cranial appendages from dermal ossicones, they point out that this condition of the metatarsals is probably the primitive condition for the Pecora (as exemplified by the fossil primitive pecoran genus *Gelocus*). Further, since there are obviously only two ways to form a cranial appendage (i.e., outgrowth from the frontal bone, or fusion of a dermal ossicone), similarity in development may not necessarily be indicative of a close relationship.

Finally, the view presented by Webb and Taylor (1980) (fig. 1D) provided a basis for the definition of the discrete characters that characterize all the ruminants, and also those which characterize the Pecora within the Ruminantia. They also showed that a number of fossil taxa of previously dubious taxonomic affinities could be included in the living family Moschidae on the basis of apomorphic characters of the auditory bulla (character 10). However, we disagree with their assertion that the presence of cranial appendages can be used as a synapomorphy to unite the other pecoran ruminant families into the “Eupecora,” and while we are in agreement with their inclusion of taxa into the family Moschidae, do not consider the Moschidae to represent the sister-group to the other pecoran ruminants.

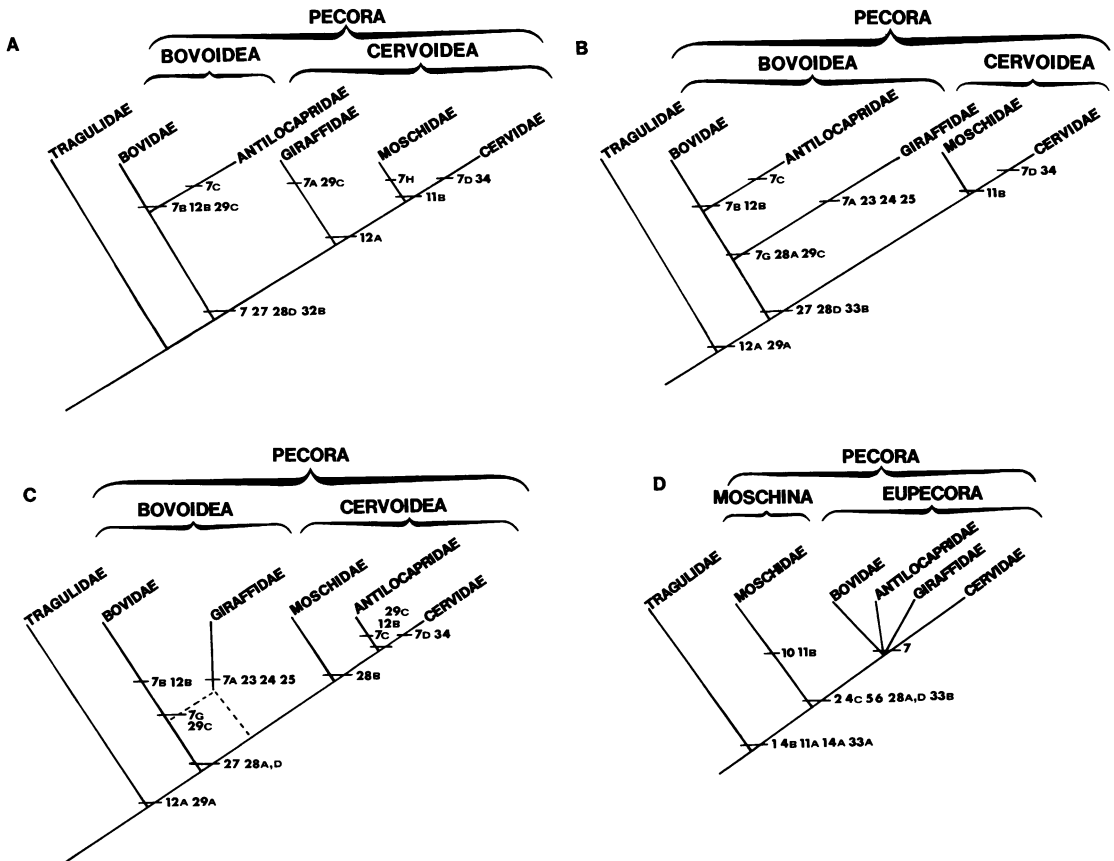


Fig. 1. Historical views on the phylogenetic position of the different living pecoran families. See table 1 for characters. **A.** "Traditional view," espoused by Stirton (1944) and Romer (1966). **B.** Present-day view, espoused by Hamilton (1978a). **C.** Alternative present-day view of Leinders and Heintz (1980). **D.** View of Webb and Taylor (1980).

Our interest in ruminant taxonomy stems not only from a wish to clarify the interrelationships of the living pecoran families, but also to understand the relationships of fossil genera and families within this scheme, and to ascertain which fossil taxa may represent the sister taxa to the living and fossil families. We feel that an evaluation of the status of the character states held by various authors to be synapomorphies linking various pecoran lineages can only be obtained by an examination of the distribution of these states in both living and fossil taxa, and that any scheme which proposes to satisfactorily classify living pecorans in a cladistic fashion must also be amenable to the classification of fossil genera within the same parameters. We propose in

this paper to initially describe and evaluate the various characters that have been used by different authors in pecoran systematics, and to discuss additional characters stemming from our own observations which we feel are of classificatory importance.

CHARACTERS DEFINING MAJOR GROUPS WITHIN THE RUMINANTIA

RUMINANTIA

The defining characters which unite the Ruminantia are the fusion of the cuboid and navicular bones in the tarsus, and the presence of an incisiform lower canine (although an incisiform lower canine was evolved in

parallel in the Protoceratidae, the pecoran-mimicking tylopod family; Patton and Taylor, 1973). Ruminants are also characterized by the reduction or loss of the upper incisors, although upper incisors are present in early fossil taxa such as *Archaeomeryx* (Webb and Taylor, 1980) (character suite 1 on cladograms). The Ruminantia above the level of the Hypertragulidae (the most primitive ruminant family) can be distinguished by the following suite of characters (character suite 1a on the cladograms): amastoid condition of the skull; jugular foramen confluent with the posterior lacerate foramen in the basicranium; loss of the trapezium and fusion of the magnum and trapezoid in the manus, with loss of metacarpal I; reduction of the fibula to a malleolar bone; upper P1 lost; presence of a mesostyle and (primitively) of an internal cingulum in the upper molars; presence of an ectostylid and (primitively) of a "*Dorcatherium*" fold in the lower molars (see figs. 5, 6) (Webb and Taylor, 1980; Janis, 1987).

RUMINANTIA ABOVE LEVEL OF TRAGULIDAE

Webb and Taylor (1980) list a number of characters that unite the extinct Leptomerycidae with the Pecora, distinguishing them from the living family Tragulidae (character suite 2a on cladograms). Janis (1987) has shown that these features occur in the known material of the traguloid genera *Bachitherium* and *Lophiomeryx*. These are: a complete postorbital bar, composed primarily of the frontal bone (in contrast to the absence of a postorbital bar in the Hypertragulidae and the presence of a postorbital bar composed primarily of the jugal in the Tragulidae); an axis with an odontoid process possessing a dorsal crest with high anterior articular surfaces (in contrast to the peglike odontoid process in tragulids); and a calcaneum in which the fibular facet has a large proximal convexity and a small distal concavity (as opposed to a simple concavity or convexity in tragulids and hypertragulids; character suite 2a on cladograms).

The traguloid genera *Lophiomeryx* and *Bachitherium* can be united with the Pecora, above the level of the other traguloids, by the presence of an anterior cingulum on the lower

molars (character 2b, see fig. 5). Two additional characters can unite *Lophiomeryx* and related genera (*Cryptomeryx* and *Iberomeryx*) with the Pecora: the reduction of the primitively caniniform p1, widely separated from the other premolars, to a peglike premolariform tooth (when present), separated from p2 by only a small diastema (character 4b); and the advanced ruminant type of p4, in which the metaconid is small, and does not extend backward to form a posterolingual wall to the tooth (character 3) (see Janis, 1987).

PECORA

The Pecora (sensu Webb and Taylor, 1980) are characterized postcranially by the loss of the trapezium in the manus and the possession of an astragalus with short, parallel sides (character 5), as opposed to the elongated astragalus with nonparallel sides seen in the tragulids (Webb and Taylor, 1980). Janis (1987) notes a tragulid type of astragalus in material referred to the problematical tragulid genera *Lophiomeryx* and *Bachitherium*. A problem with use of astragalus characteristics is that a "pecoran" type of astragalus has evidently been evolved in parallel in the supposedly leptomerycid genus *Pseudoparablastomeryx* (Taylor and Webb, 1976), and in *Pseudoceras*, a genus of uncertain taxonomic affinities, possibly a "gelocid" (see Webb, 1983a). However, Janis (1987) points out that the former genus was a survivor in the late Miocene of North America, where there would be strong environmental pressure to develop a more cursorially adapted type of hind limb in parallel with the pecorans. The same argument would also apply to *Pseudoceras*, should this taxon prove to be nonpecoran on other morphological criteria.

Characters of the petrosal that characterize the Pecora, seen also in the most primitive pecoran, *Gelocus*, are the loss of the promontorium, an enlarged fossa for the stapedial muscle, and a shallow subarcuate fossa. Other basicranial features of the Pecora are a broadened basioccipital with strong flexion stops on the condyles, and a laterally enclosed postglenoid foramen (Webb and Taylor, 1980) (character suite 6).

RELEVANT CHARACTERS IN PECORAN PHYLOGENY

CRANIAL APPENDAGES

Webb and Taylor (1980) assume the higher ruminant families to be united into a distinct clade, the Eupecora, characterized by the possession of cranial appendages, or hornlike organs (character 7), and regard the Moschidae (comprising the living hornless genus *Moschus*, and the fossil genera *Blastomeryx*, *Amphitragulus*, and *Dremotherium*) as the sister-group of the Eupecora. Earlier authors such as Pilgrim (1941, 1947) also regarded cranial appendages as homologous within the Pecora and considered that the skin-covered ossicones of giraffids represented the plesiomorphous condition for higher ruminants (see also Coope, 1968; Hamilton, 1978a). However, as will be discussed below, there is clear developmental and paleontological evidence that cranial appendages have evolved at least twice among the ruminants, and possibly in three or more instances. Possession of cranial appendages therefore cannot be regarded as a synapomorphy which unites higher ruminants.

Roth (1984) has pointed out that the sharing of common developmental pathways, which presumably are governed by the same batteries of genes, is a necessary condition for homology. If cranial appendages are to be used in assessing relationships within ruminants, assumptions of homology must therefore be based on details of ontogeny as well as adult structure. One might take into account the suite of developmental characters which include mode of development, tissues contributing to the formation of the appendages, and tissues actually inducing formation of the appendages, as well as shape, placement on the skull, and the nature of the covering. We propose here to review both the formation of cranial appendages to emphasize the developmental differences, and to review the characteristics of the cranial appendages in the living and fossil pecoran lineages.

DEVELOPMENT OF HORNS AND ANTLERS

Bovidae

The cranial appendages of the Bovidae are termed horns, and are postorbital in position.

The bony horn core is frequently described as developing from a dermal ossicone which fuses with the frontal bone (Frechkop, 1955; Bubenik, 1966) without further explanation. However, this description is somewhat misleading as it implies that at some point in the development of bovid horns a separate ossicone (or *os cornu*) is present and should be observable, as is known to be the case in living giraffids. A number of authors have indeed reported the presence of such an ossicone in domestic sheep, goats, and cattle (see review in Dove, 1935). However, Dove (1935) clearly demonstrates that although suprapariosteal tissues induce and contribute to horn core formation, no separate ossicone is normally found in bovid horn development.

Dove (1935) performed a series of tissue transplants from the horn site of newborn calves and kids. He found that development of a horn core is induced by the connective tissue and dermis superficial to the periosteum of the frontal bone in the horn bud (which he collectively terms the *os cornu*) and that the periosteum and frontal bone in this region are unable to form even a raised boss without the inductive action of the *os cornu*. On the other hand, the connective tissue and dermis will induce horn formation if they are transplanted elsewhere on the skull; transplanted periosteum from the horn bud develops into normal, flat frontal bone.

Early in development the *os cornu* (as yet unossified) causes the underlying periosteum to break down and "draws up" the frontal bone to form the boss, or the base of the horn. The connective tissue and dermal portions of the *os cornu* ossify to form the core proper at the same time that the boss forms from the frontal, and no demarcation or suture is seen in normal development. The entire horn core becomes surrounded by a membrane continuous with the periosteum, which Dove (1935) believes forms from the connective tissue layer. Dove further showed that where the *os cornu* does ossify separately it is the result of abnormal development in animals heterozygous for normal and polled horns, a conclusion also reached by Fambach (1909). Such separate ossification generally results in a "scur," a horn which does not fuse with the skull. We have noted one case of naturally occurring bilateral scurs in a wild *Cephalo-*

phus monticolor. In this species females are polymorphic for the presence of horns, suggesting that this individual was probably heterozygous for the horned/hornless alleles.

Although Dove's (1935) study clearly establishes that it is the suprapariosteal tissues which induce horn core formation, and which ossify to form the core, he does not discuss further growth of the core itself. We feel that it is important to describe this process, since it is widely stated in the literature that both horn cores (e.g., Solounias, 1981) and horn sheaths (e.g., Webb, 1973) grow from the base. In fact, neither the core nor the sheath grow from the base. The bony core grows both from the tip and by appositional growth over the surface (Dürst, 1902a, 1902b, 1926), and the sheath is continually produced over the entire surface of the core (Goss, 1983; Dürst, 1902a). The long-standing but erroneous contention that horn cores grow from the base may in fact be based on Dürst's rather confusing summary, which states that "horn cores grow from the tip downwards," although he clearly states (and describes) elsewhere that growth is from the tip. Bohlin's (1935) description of horn growth in the Miocene bovid *Miotragocerus* may also have popularized this belief. However, his statement is based solely on the fact that there is an area at the base of each horn core which is rich in foramina, and he believes that this indicates a zone of growth. He indicates the position of this zone on a photograph of a *Miotragocerus* skull; it seems clear to us that what he indicates is the boundary between the sheath-covered part of the core and the skin-covered boss or pedicle.

Dürst's (1902a) detailed histological studies of a growth series of domestic calves forms the basis for the description presented here. The 63 specimens that he described ranged in age from fetuses of 4–5 months gestational age to approximately 9 months; he also included histological comparisons of wild bovids of various species and ages. In the earliest fetuses the area destined to give rise to the horn presents a normal appearance. The overlying skin consists of an outer epidermis and an inner dermis, and apparently contains normally developing anlagen of hair follicles. Between the skin and the underlying frontal bone is a layer of connective tissue. The frontal is bounded by an outer periosteum; be-

neath the periosteum is a layer which Dürst refers to as the "preosseous substance," produced by the fibroelastica. The "preosseous substance" described by Dürst (see also Brandt, 1928) is clearly the osteoid tissue or prebone of modern histological terminology. Osteoid tissue consists of the organic matrix of bone which is laid down as the first step of osteogenesis (Ham and Cormack, 1979). Thus the location of the preosseous tissue in histological sections is a clear indication of the region where new bone is being formed. Deep to the preosseous substance is a layer of newly formed bone, and deep to that older, cancellous bone.

Since the processes which lead to horn formation are a slight modification of the processes of normal growth of the skull bones, we will review the mechanism by which the roofing bones of the skull grow and change shape. The roofing bones are formed by intramembranous ossification: that is, bone is deposited within a connective tissue layer, and not in preformed cartilage. Ossification begins from a central point, and bone is added to this center only by appositional growth, which occurs in two places: at the edges, through which the bone increases in size; and on the surface, through which the bone becomes thicker and changes in shape can be brought about. Interstitial growth does not occur in intramembranous bone formation (Ham and Cormack, 1979). Bone added at the surface is produced directly under the periosteum, and is deposited in horizontal layers. These layers of bone may then be reworked or resorbed from their inner surface. Change in the angle of curvature of the bones of the skull is brought about by differential deposition over the outer surface and differential resorption from the inner surface of the bone (Ham and Cormack, 1979).

The first sign of the appearance of the horn core is the establishment of a connection between the connective tissue layer and the preosseous substance, and a thickening of the preosseous substance, which was observed in a week-old calf. At about 4 weeks of age a section of the area shows a mound-shaped elevation of the frontal, which is clearly the beginning of the horn core. Dürst notes at this stage that the building of the horn core now differs significantly from that of the frontal in one important aspect: the surface la-

mellae are now oriented vertically rather than horizontally. These lamellae of differing orientation merge at the base of the developing horn core.

Dürst describes the vertical lamellae as initially forming superficial to the periosteum of the frontal (see illustrations in Dürst, 1902a, 1902b, 1926), and gradually elongating. These vertical lamellae then fuse with the horizontal lamellae of the frontal. Although Dürst's work preceded that of Dove (1935), we believe that what Dürst described is the ossification of the dermal/connective tissue *os cornu*, and the simultaneous dissolution of the periosteum described by Dove. Dove's (1935) transplantation studies clearly showed that the dermal portion of the *os cornu* formed the tip of the initial core, and the connective tissue portion formed the base of the spike, with their inductive effect on the frontal causing it to form the boss. Dürst's histological descriptions are thus consistent with Dove's experimental results, as far as the two can be compared, since Dove did not describe later growth.

Throughout the remainder of the growth series described by Dürst (1902a) the preosseous substance is found on the surface and tip of the horn core, forming a continuous, cone-shaped layer over the surface of the growing horn core. New bone is thus added appositionally in two places: at the tip (that is at the edges of the vertically oriented lamellae), and on the surface of the growing core. Dürst clearly states that the core grows in length through deposition at the tip, and in thickness through deposition of new bone along the sides. As it is laid down the bone is reworked internally, forming diploë and allowing expansion of the frontal sinuses into the core.

Deposition of bone is intramembranous and there is no preformation of the core in cartilage (Dürst, 1902a; Brandt, 1928). The mechanism of growth described by Dürst for the horn cores is consistent with the growth mechanisms of the membrane roofing bones of the skull: appositional growth over the surface and at the edges (here at the tip). Neither the roofing bones of the skull (Ham and Cormack, 1979) nor the growing horn core (Dürst, 1902a) exhibit interstitial growth. There is thus no mechanism by which horn cores can

grow from the base. The process of horn core growth appears to be a variation of that of the other membranous bones of the skull, but involving ossification of suprapariosteal tissues.

Dürst's descriptions of horn core growth are entirely consistent with our observations on growth series of horn cores. If horns grew from the base, the tip of the core would not grow after the first appearance of the core, but rather would be pushed outward by bone being added proximal to it (see fig. 32 in Solounias, 1981). One would expect that the tip of a young horn core would have the same size and taper as that of an adult core. Instead, young horn cores are thicker at the tip and not as finely tapered as adult cores, clearly indicating that they are not equivalent structures.

The permanent bony core is covered by a nondeciduous keratin sheath, which is formed from the basal layers of the epidermis of the horn bud. Dove's (1935) transplantation experiments indicate that the epidermis does not induce horn core formation; rather keratinization of the epidermis of the horn bud is induced by the underlying *os cornu*. However, both Dürst (1902a) and Brandt (1928) found that histological changes occur in the epidermis of the horn anlagen before birth, suggesting that the epidermis might have an inductive effect prenatally. In any case, this epidermis is evidently "preprogrammed" to become keratinized, as the *os cornu* is unable to induce keratinization in epidermis transplanted from other areas of the head.

When the first clearly recognizable keratinous horn substance appears at 3–4 weeks postnatally, it is a round disc situated above the tip of the growing horn core (Dürst, 1902a). As the horn core beneath expands, the original disc gradually grows downward to cover the entire core (Dürst, 1902a). The horn-producing basal epithelium is now a cone-shaped layer, covering the entire horn core and lying parallel to its surface. Successive layers of keratin are produced by this epithelium over the entire core. Each new layer is internal to the last, producing a series of nested keratin cones, with the oldest cone on the outermost surface, at the tip (see fig. 2). The horn sheath thus does not grow from the base, although new growth would only be

visible at the base, and alterations in rate of growth at the base produce annual growth rings (Dürst, 1926).

Although this sheath is never shed completely or on a regular basis, it may be subject to periodic flaking and renewal (exfoliation) in certain bovids, e.g., *Bison*, *Cephalophus*, *Kobus*, *Oryx*, *Bos*, *Boselaphus*, *Rupicapra*, and *Antelope* (O'Gara and Matson, 1975). This procedure would seem to involve flaking off, in most cases caused by rubbing, of the outermost layers of the sequentially laid down lamellar keratin. With respect to these phenomena, it is important to realize that although the keratin sheath is produced continuously by the germinal layer as described above, two different types of keratinous tissue are produced, usually referred to as young horn ("Jugendhorn") and permanent or adult horn ("Dauerhorn") (Dürst, 1902a, 1926; Fambach, 1909; George, 1956). Young horn is softer than permanent horn and the nature of the horny fibers of the intertubular horn differs (George, 1956). It is produced until the animal is 4–6 months old (Dürst, 1902a; George, 1956). The layers of young horn are, of course, located on the outer surface of the sheath, near the tip, and it gradually flakes off as the animal becomes older (George, 1956). This softer keratin tissue would seem to function as a flexible protective coating for the growing horn core, which can easily be split as the core of permanent horn grows up beneath it. Although the outer layers are removed, exposing shiny new permanent keratin, this process never results in shedding of the entire keratin sheath, nor is the horn ever left without a functional sheath, as is the case in antilocaprids. "Exfoliation" in bovids is clearly growth related and is neither seasonal nor associated with rut-related hormonal changes, as it is in *Antilocapra*.

In living bovids the sheath generally follows the shape of the underlying bony core, but may extend considerably beyond the core, as for example in the Caprini or musk oxen, *Ovibos moschatus* (Dürst, 1926). This growth beyond the core is largely produced at the tip (Dürst, 1902a). The permanent horn core and its sheath may be straight, curved, or spiraled, but are never branched or forked. The mechanism of growth of the horn core and the horn sheath would appear to make it me-



Fig. 2. Growth of the keratinous horn sheath in bovids. (Modified from Goss, 1983)

chanically difficult for the bovid horn to branch (P. Grubb, in litt.); in order for a branched sheath to grow, it would have to be able to spread outward over the fork, which clearly is not possible for a sheath formed from inflexible keratin. However, it is possible for the core to split along all or part of its length, producing two parallel horns. Dürst (1926) figures the skull of an ibex with two entirely separate horn cores on one side, and the other horn double in the distal third. Dürst (1926) was able to show experimentally that such split cores could be produced by artificially dividing the horn anlagen. Depending on the degree to which the parts of the anlagen are separated, only part of the core may be split, or four separate horns may be produced, as in the relatively common four-horned mutants of domestic sheep and, in its most extreme form, in the four-horned antelope *Tetracerus quadricornis*.

Although true branching is unknown in any living bovid horn core or sheath, either as a normal or abnormal condition, some authors have suggested that certain fossil species may have had a forked horn sheath. It has been noted for the fossil genera *Miotragocerus* (Bohlin, 1935; Solounias, 1981), and *Mesembriportax* (Gentry, 1974), that the shape of the horn core is similar to that of *Antilocapra americana*. These authors have suggested that the horn sheath may also have been similarly

forked and possibly deciduous. Development of such a forked sheath would require a modification of the bovid sheath building mechanism; in *Antilocapra*, the upper prong is almost fully formed before the cornification of the anterior prong and proximal part of the sheath begins (O'Gara and Matson, 1975). Since the sheath does not cornify over its entire surface, formation of a prong does not cause the mechanical problems which would arise in the formation of a bovid sheath. We consider the evidence for a forked sheath in fossil bovids to be questionable at best.

In some specimens of *Miotragocerus* the anterior surface of the horn core has a stepped profile, which Solounias (1981) suggests may have had a multi-tined sheath. Bohlin (1935) believed that the core morphology resulted from the addition of a series of platelike anterior placations, presumably in conjunction with growth at the base. Solounias (1981) suggests that this method of growth sets *Miotragocerus* apart from other bovids. However, since Bohlin's reconstruction is largely hypothetical, and since bone is normally added to all surfaces of a bovid horn, there is no reason to believe that the growth mechanism of this genus was any different from other bovids, past or present, although the final core shape is different.

We do not accept Solounias' (1981) suggestion that the stepped horn core of *Miotragocerus* may have been associated with a multi-tined sheath. Since the small points on the core are superficial, they must have been deposited late in horn core development, after the bulk of the core was laid down. This means that the normal, smooth sheath would have been forming over the core during development. Even if the sheath-forming epithelium did follow the shape of the steps on the core, any shape change would be under the old core, and would not be visible. We think that it is more likely that the fairly small anterior tuberosities on the core are merely slight irregularities in the horn core that were not reflected in the overlying sheath, especially as they are not present in all specimens. There is some experimental evidence for this. Dürst (1926) produced a line of moorland sheep by inbreeding in which the tip of the horn core was notched or bilobed. He states that the notches presumably are produced by

infolding of the covering skin, but the sheath was apparently normal externally. In one case a separate "horn core," consisting of an ovoid core of poorly defined matrix surrounded by concentric layers of horny material, was formed in the cleft at the tip within the normal sheath. It thus seems from Dürst's work that the horn sheath is not likely to reflect superficial surface irregularities added late in development, and thus that Solounias' (1981) suggestion of a multi-tined sheath is unlikely to be correct.

Cervidae

The cranial appendages of cervids are termed antlers, and are found in all living genera with the exception of *Hydropotes*, which is assumed to primitively lack cranial appendages, rather than to have lost the antlers secondarily (see Leinders, 1983; Scott and Janis, 1987). Antlers are postorbital in position, forked, branched, or palmate, and are developed as outgrowths of the frontal bone (Frechkop, 1955; Bubenik, 1966; and numerous other references summarized below). Antlers are covered with skin during the growth phase, but the main portion of the antler consists of nonliving bone when growth is complete. Antlers are unique among the diversity of cranial appendages in living and fossil ungulates in the fact that the bony portion of the appendages is deciduous, and is shed and regrown annually (see Goss, 1983).

Cervid antlers have long been accepted as outgrowths of the frontal bone, but a more detailed description of their development will point out how different this process is from that which results in horn formation. Development of cervid antlers is induced by the periosteum in the antler bud; the overlying connective tissue and dermis do not have any role. This has been shown conclusively in a series of experiments (Goss, 1983). Excision of the periosteum from the presumptive antler site prevents antler formation; transplantation of this periosteum, without the overlying connective tissue and skin, to other parts of the body will induce ectopic antler formation (Goss et al., 1964; Hartwig, 1967; Hartwig, 1968; Hartwig and Schrudde, 1974; Goss, 1983).

Before antler development begins, the site

where the antler will form is marked by thickening of the frontal bone and its overlying periosteum. The area which will give rise to the antler differs from the rest of the skull in being composed of spongy rather than compact bone (Goss, 1983). New bone is deposited by the periosteum, and the pedicle grows up out of the skull. As the pedicle enlarges, chondrogenesis begins at the tip, and the remainder of the antler is preformed in cartilage before it ossifies (Goss, 1983). Tines form from bifurcations of the growing tip, with the two parts of the bifurcation elongating in different directions. Growth in the tines eventually decelerates and then ceases, while that in the main beam continues at a constant rate (Goss, 1983).

Cervid antlers consist of two portions: a nondeciduous pedicle and a deciduous distal antler; both are derived from the frontal bone without contribution from the overlying tissue (Goss et al., 1964; Hartwig, 1967, 1968; Hartwig and Schrudde, 1974; Goss, 1983). During initial antler growth, it is evidently not possible to distinguish between the pedicle and the antler proper (i.e., the deciduous part). During initial growth both the pedicle and the antler proper are covered by skin, which is later shed from the deciduous portion. The pedicle remains skin covered throughout life. Commencing with the formation of the second deciduous antler, the pedicle is separated from the deciduous portion by a bony burr, which is part of the deciduous portion and is shed with it (Goss, 1983). The primitive cervid condition, seen in the earliest fossil genus *Dicrocerus*, and retained in the living genera *Muntiacus* and *Elaphodus*, is for the antler to possess a long pedicle and a short antler proper. Additionally, in primitive cervids the entire structure is probably permanent, with later development of the shedding of the distal portion. This was evidently the case in the fossil cervid genera *Lagomeryx* and *Dicrocerus* (Chow and Shih, 1978; Bubenik, 1982), and in the living *Muntiacus atherodes* (Groves and Grubb, 1982). Cervids with this type of antler also retain large upper canines. The derived cervid condition is for a short pedicle, and for a long deciduous antler of increasing complexity in the number of branches and the extent of palmation.

Although skin is necessary for full differentiation of antlers, its involvement is secondary (Goss, 1983). Development of the overlying dermis and epidermis into velvet is induced by the periosteum; transplanted antler bud periosteum can induce formation of velvet by integument from other areas of the body (Hartwig and Schrudde, 1974; Goss, 1983). The integument is evidently not "pre-programmed" to produce velvet, as bovid epidermis is to produce a keratinized horn sheath. Velvet is a highly specialized type of integument which is capable of extremely rapid growth. It is unique especially with regard to the constant regeneration of new hair follicles at the growing tips of the antlers, and in the absence of erector pili muscles (Goss, 1983). In giraffes, the only other living ruminants with skin-covered cranial appendages, the skin is thickened and highly cornified with only a few scattered hairs (Spinage, 1968), but otherwise shows no striking specializations.

HOMOLOGIES OF HORNS AND ANTLERS

The development of horns and antlers thus differs in a number of important ways. Antler growth is induced and controlled by the periosteum, and no suprapariosteal tissue contributes to bone formation, while horn growth is induced by the overlying connective tissue and dermis, both of which form bony tissue. Growth in antlers is primarily through endochondral ossification, while in horns it is by intramembranous ossification. As Goss (1983) points out, the developmental processes which result in antler formation on the one hand and horn formation on the other are different in all respects and are clearly not homologous. This developmental evidence, together with the existence of the antlerless deer *Hydropotes*, clearly demonstrates that cervid antlers and bovid horns are not homologous structures.

Given the existence of two nonhomologous types of cranial appendages with different ontogenies, it would be of interest to determine the method of development in other ruminants. However, it should be made clear that cranial appendages should not be homologized on the basis of broad similarities in mode of development. As Leinders (1983)

has pointed out, there are only two ways to form a cranial appendage: either as an outgrowth of the frontal bone, involving ossification only of subperiosteal tissues, or from a dermal ossification center, that is, involving ossification of suprapariosteal tissue. No matter how many times bony appendages may have evolved independently, each evolutionary event must have resulted from one of these basic developmental pathways. Clearly, cranial appendages have evolved at least twice in ruminants and once in protoceratids, indicating that this character can arise convergently. As Janis (1982) has pointed out, there are good ecological reasons to explain the origin of cranial appendages at certain body sizes. As far as possible, homology of cranial appendages should be based on comparison of the details of the developmental processes and the inducing and contributing tissues; simply homologizing cranial appendages on the basis of development by frontal or suprapariosteal growth as Bubenik (1982) has done may be insufficient. Unfortunately, comparison of developmental processes is clearly impossible in fossil groups, and it is nearly as impossible in living ruminants, although we will summarize the available information below.

One important point should be made regarding the interpretation of the mode of development of the cranial appendages of fossil organisms. In normal development in bovids there is never a separate ossicone (*os cornu*) as there is in giraffids even though the process is induced and regulated by the overlying connective tissue and integument. If one examines museum specimens of nondomestic bovids, even the earliest stages of horn growth (in neonatal and very young animals) will appear as an outgrowth of the frontal bones. We have done this for a series of *Antelope cervicapra* skulls, which includes both newborn and very young animals, in the AMNH; in this series it would not be possible to tell that the developmental stimulus for horn core formation was an *os cornu* rather than a true frontal outgrowth as is seen in cervids. Unless a separate ossicone is normally formed during development, as it is in living giraffids, both frontal outgrowths and appendages that are induced by suprapariosteal ossification centers will appear identical. Although Bube-

nik (1982) states that frontal and suprapariosteal growths can be identified histologically, we question the reliability of this method. Since no other certainly identified frontal outgrowths are available to compare with cervid antlers, it is difficult to say whether their unique histological appearance relates to their mode of development, or to their deciduous nature and rapid growth. This methodology requires further study.

Giraffidae

The cranial appendages of the Giraffidae are termed ossicones. They are postorbital in position, and developed from dermal ossicones which fuse later during development with the frontal or parietal bones (Lankester, 1907a; Frechkop, 1955; Bubenik, 1966). A median nasal ossicone is additionally present in some living subspecies of *Giraffa camelopardalis* (Spinage, 1968). Ossicones are skin covered in living giraffids, and in living and fossil Giraffini and Okapini are straight, unbranched, and nondeciduous. In the fossil subfamily Sivatheriinae the ossicones were branched and palmate, though apparently still nondeciduous (Hamilton, 1978a).

Among members of the extinct giraffoid family Climacoceridae, cranial appendages are known in the genera *Nyanzameris* (see Thomas, 1984), *Climacoceras*, *Injanatherium* (see Heintz et al., 1981), and *Zarafa* (Hamilton, 1973). The cranial appendages of *Climacoceras* were very different in appearance from giraffid ossicones, being more rounded in cross section, supraorbital rather than postorbital in position, and possessing multiple branches (but not palmate like sivatheriine ossicones) (see Hamilton, 1978b). Superficially they bear greater resemblance to cervid antlers or merycodontine cranial appendages than to giraffid ossicones, although there is no evidence that they were deciduous (see Goss, 1983), and Bubenik (1982) suggests histological similarities with frontal outgrowths. In fact, *Climacoceras* was originally described by MacInnes (1936) as a cervid. There is no apparent line of fusion with the skull at the base of these appendages, as is evident in giraffid ossicones. The cranial appendages of *Nyanzameris* appear to be similar to those of *Climacoceras* (Thomas,

1984). In the genus *Zarafa*, the ossicones are short, supraorbital, and dorsolaterally projecting (Hamilton, 1978a). A skull of a medium-size giraffoid with cranial appendages similar to those seen in *Zarafa* has been described from the late Miocene of Iraq (*Injanatherium hazami*, Heintz et al., 1981). This animal may well be closely related to *Zarafa/Canthumeryx*. The situation in *Canthumeryx* is not clear. No cranial appendages can clearly be ascribed to *Canthumeryx*, unless Hamilton (1978b) is correct in synonymizing *Zarafa* with *Canthumeryx*, which we question (see below).

Giraffid ossicones are widely considered homologous with bovid horns (e.g., Hamilton, 1978a), although the supposed homology is based largely on the erroneous assumption that a separate ossified *os cornu* is routinely formed in bovids. The development of cranial appendages in giraffids is not as well understood as in bovids and cervids, since no experimental evidence exists. Nevertheless, it is clear that in living giraffids a separate ossicone is formed in the integument overlying the frontal bone. The ossicone is evidently preformed in cartilage, with subsequent endochondral ossification (Lankester, 1907a; Spinage, 1968), in contrast to the bovid condition where ossification is intramembranous (Dürst, 1902a; Brandt, 1928). Ossification proceeds from the tip of the ossicone ventrally toward the skull, with growth occurring in the zone of cartilage between the ossicone and skull in the nature of a true epiphysis. In neonatal animals there is no corresponding boss on the frontal beneath the ossicone (see illustrations in Lankester, 1907a). We could find no histological studies of the bone, so it is not known whether there is any thickening of the periosteum of the frontal, although a section in Lankester (1907a) indicates that the bone in this region is somewhat thicker.

The formation of a boss on the frontal bone is, however, apparent later during development, and the enlarged ossicone eventually comes to articulate with and finally to fuse with this boss. It is not known whether the development of this boss is induced by the overlying ossicone, or whether it develops independently under the influence of the periosteum. The sequence of development sug-

gests that boss formation is induced by the overlying ossicone. However, some of the median bosses which develop in *Okapia* are not associated with an ossicone (Lankester, 1907a), suggesting that some control may additionally reside in the periosteum of the frontal bone. This condition may be secondary, as median ossicones are present in some male *Giraffa* (Spinage, 1968).

Giraffid ossicones thus differ developmentally from those of bovids in the initial formation in cartilage, in the later fusion with the skull, and probably also in the extent to which the periosteum is involved. The process is clearly not homologous with the formation of antlers in cervids. Despite the greater apparent similarity with horn formation in bovids, we do not consider giraffid ossicone formation to be homologous to it, since this would require a shift from an intramembranous to an endochondral form of ossification.

This conclusion is further supported by evidence suggesting that ossicones must have evolved within the Giraffidae. The epiphyseal nature of giraffid ossicones with the zone of growth at the base may preclude the possibility of branching. Although the epiphyseal ossicone might also grow at the tip, it is clear, at least in *Okapia* where the tip is bare, that this is not the case. Excepting sivatheres, no giraffid ossicones branch, although male specimens of *Giraffa* may grow knobs on the side of the horns (Spinage, 1968). Even in sivatheres, the "ossicones" are palmate, with small knobs rather than distinct tines along the edges, and might be produced by the flattening and elongating of the ossicone.

It thus seems improbable that the type of ossicone possessed by living giraffids could develop into a branched structure in the course of evolution. Yet, as previously detailed, branched cranial appendages are present in the giraffoid genus *Climacoceras* and in the giraffid subfamily Sivatherinae. The obvious conclusion is that the "ossicones" of these fossil taxa (or at least of *Climacoceras*) are not homologous with the ossicones seen in other giraffids. This view was also expressed by Geraads (1986), although Solounias (personal commun.) considers that the cranial appendages of sivatheres are not truly "branched" and may be homologous with

those of living giraffids. *Climacoceras* and sivatheres are clearly giraffoids, as evidenced by the possession of a bilobed lower canine (Hamilton, 1978b). Sivatheres are included in the Giraffidae because they possess the giraffid synapomorphous features of a central lingual cuspid on p4 and a vertical groove on the posterolingual region of p4 (Hamilton, 1978a). However, Janis and Lister (1985) have shown that the first character is not unique to the Giraffidae, and we argue later in this paper that the second character cannot be regarded as a unique giraffid autapomorphy either.

Traditional phylogenies of the Giraffidae (e.g., Hamilton, 1978a) place the Okapinae as the most primitive subfamily, with the Sivatheriinae more closely related to the Giraffinae, although Hamilton (1973) originally considered sivatheres to form their own distinct family Sivatheriidae, with an early (late Oligocene) divergence from the Giraffidae. This phylogeny is not compatible with the suggestion that, while the cranial appendage of the living giraffid genera *Okapia* and *Giraffa* are clearly homologous, their ossicones may not be homologous with the cranial appendages of sivatheres. While it is not our intention to revise the phylogeny of the Giraffidae in this paper, we would point out that the characters used by Hamilton (1978a) to unite the Sivatheriinae with giraffids above the level of *Okapia* are all characters that can be functionally related to habitat choice (Scott, unpublished data) or to feeding style (Janis, unpublished data). These characters are listed by Hamilton (1978a) as: further lengthening of limbs; skull flexed; orbits positioned posteriorly; back of skull shortened; and ossicones large. (See also Radinsky, 1984, for discussion of the acquisition of some of these cranial characters in the evolution of the Equidae.) In addition, sivathere "ossicones" are formed of cancellous bone, in contrast to the compact bone seen in the ossicones of living giraffids (Spinage, 1968).

We suggest that cranial appendages were evolved independently three times within the Giraffoidea: in the Climacoceridae, in the Sivatherinae, and in the other Giraffidae. This would imply, accepting Hamilton's placement of the Sivatherinae within the Giraffidae, that sivatheres form the sister-group to

the other giraffids, which all appear to share the type of ossicone seen in the living taxa. Additional evidence for this suggestion comes from the observation that an early member of the Sivatherinae (*Helladotherium*) (Churcher, 1978) apparently lacked cranial appendages. Cranial appendages may also be absent in the climacocerid *Canthumeryx*, although of course this type of negative evidence cannot be taken as conclusive. Although we would speculate that it is possible that the palmated form of cranial appendages in sivatheres could be derived from a giraffid type of ossicone, we cannot see any possible homology between giraffid ossicones and the form of cranial appendages in the Climacoceridae.

The obvious conclusion from this discussion is that if the type of cranial appendage present in living giraffids was developed within the Giraffidae, rather than representing a character shared by all members of the Giraffoidea, it clearly cannot share an evolutionary origin with the bovid type of horn core.

Antilocapridae

Living antilocaprine antilocaprids (genus *Antilocapra*) possess an unbranched, non-deciduous, supraoccipital bony horn core, in combination with a forked, deciduous keratinous horn sheath (see O'Gara and Matson, 1975). The cranial appendages are usually termed "horns." Fossil antilocaprids variously possessed horn cores that were branched (e.g., *Texoceras*) or spiraled (e.g., *Ilingoceros*) (see Frick, 1937). The nature of their covering is uncertain, but at least some genera (*Hexameryx*, *Hexobelameryx*) apparently had keratinous sheaths (Webb, 1973), although it is not clear whether these were deciduous.

It is apparently not known whether antilocaprine horn cores are formed from an outgrowth of the frontal bone, or from a dermal ossification center. If the skulls of a series of young *Antilocapra* are examined, the horn core first appears as a triangular knob over the posterior of the orbit. There is no trace of a separate ossicone but, as previously pointed out, this does not mean that the horn core is a frontal outgrowth, although it has

TABLE 2
Distribution of Cranial Appendages in Ruminant Genera

TRAGULINA	
<i>Hypertragulus</i>	Absent
<i>Tragulus</i>	Absent
<i>Leptomeryx</i>	Absent
<i>Bachitherium</i>	Absent
<i>Lophiomeryx</i>	Absent
"GELOCIDAE"	
<i>Gelocus</i>	Absent
<i>Notomeryx/Gobiomeryx</i>	Absent
<i>Prodremotherium</i>	Absent
<i>Eumeryx</i>	Absent
<i>Rutitherium</i>	?Absent
GIRAFFOIDEA	
<i>Propalaeoryx</i>	?Absent
<i>Climacoceras</i>	Supraorbital, branched, nondeciduous, ?skin-covered
<i>Canthumeryx/Zarafa</i>	Supraorbital, dorsolaterally projecting, unbranched, ?skin-covered
<i>Sivatheres</i>	Postorbital, nondeciduous, may be branched or palmate, ?skin-covered
Giraffines	Postorbital, nondeciduous, unbranched, skin-covered
BOVIDAE	
<i>Eotragus</i>	Postorbital, unbranched, nondeciduous, keratin sheath covering
Other bovids	Similar, may be completely curved, twisted, or spiraled
MOSCHINA	
<i>Walangania</i>	?Absent
<i>Dremotherium</i>	Absent
<i>Blastomeryx</i>	Absent
<i>Parablastomeryx</i>	Absent
<i>Micromeryx</i>	Absent
<i>Moschus</i>	Absent
ANTILOCAPRIDAE	
<i>Paracosoryx</i>	Supraorbital, branched, nondeciduous, ?naked
Other merycodontines	As <i>Paracosoryx</i>
Antilocaprines	Supraorbital, unbranched, branched, or spiraled. Deciduous keratin cover in some
PALAEOMERYCIDAE	
<i>Prolibytherium</i>	Supraorbital, horizontally projecting, flattened and lobate, ?skin-covered
<i>Amphitragulus</i>	Absent
<i>Palaeomeryx</i>	Supraorbital and occipital, unbranched, nondeciduous, ?skin-covered

TABLE 2—(Continued)

Dromomerycids	Supraorbital (and median occipital in some), unbranched, nondeciduous, ?skin-covered
HOPLITOMERYCIDAE	
<i>Hoplitomeryx</i>	Postorbital and nasal, unbranched, nondeciduous, covered with keratin sheath
<i>Amphimoschus</i>	?Absent
CERVIDAE	
<i>Hydropotes</i>	Absent
<i>Dicrocerus</i>	Nondeciduous, skin-covered pedicle. Deciduous, branched naked antler on top of pedicle
Other cervids	Pedicle often shorter, deciduous antler more elaborate

been interpreted as such (Noback, 1932; Solounias, in press). As the core increases in size the area anterior to the developing horn core becomes elevated and a sinus forms in the bone over the orbit. The area of bone and its sinus are incorporated into the horn core, and form its anterior expansion, resulting in the broad horn core spanning the entire supraorbital area in adult animals. The position and shape of the immature horn core are interesting in that the core is similar in position and shape to that of immature merycodontines. Since no developmental evidence exists to suggest that antilocaprine horn cores are either frontal outgrowths or dermally induced ossifications, they cannot be homologized with other living ungulates with any degree of confidence. Bubenik (1982) considers them to be similar in their histology to frontal outgrowths, but is uncertain of their true mode of development.

The fossil subfamily Merycodontinae possessed branched, supraorbital cranial appendages, which were rounded in cross section (as opposed to oval cross section of antilocaprine horns). Many merycodontines have a burr or series of burrs near the base of the cranial appendage, and this was initially interpreted as an indication that the distal portion of the appendage was shed (Cope, 1874, 1877; Matthew, 1904, 1918). However, a number of authors have convincingly demonstrated that these append-

ages were not deciduous (see for example Furlong, 1927; Voorhies, 1969). The burr has been interpreted by various authors as the line of demarcation between the covering of the appendage proper and that of the skull (see for example Furlong, 1927; Frick, 1937). Pilgrim (1941) suggested that the burrs represented the point from which the keratinous horn sheaths were shed annually. However, as discussed earlier, it is not possible to grow a bovid-type sheath over a branched structure, since the sheath grows internally over the entire surface of the core. Neither would it be possible for such a core to be shed entire as is that of *Antilocapra*, or to increase in size. It seems much more likely that the appendage was covered by skin, as is suggested by the smooth surface marked by vascular grooves similar to those of cervids. The burr would then mark the boundary between head and cranial appendage integuments (Furlong, 1927). Frick (1937) suggested that multiple burrs might have been formed by periodic retreat and regrowth of the skin covering, but as Goss (1983) points out, in no living system does skin grow over dead bone. Voorhies (1969) noted that each of the pseudoburrs was associated with a different outer layer of bone. As Voorhies (1969) and Goss (1983) discuss, this is consistent with the hypothesis that these appendages were covered with an integument which laid down successive layers of bone each year, and which retreated proximally each year, with the burr representing the level to which the covering had regressed. An analogous situation exists in the living *Okapia*, where the skin retreats from the tip, leaving a distinct groove in the os-sicone at the level to which it has moved (Lankester, 1907b). The appendage would have been covered with skin as it grew, but when it reached adult size the skin covering would die back, gradually leaving a dead, naked structure (Voorhies, 1969; Goss, 1983). This is supported by the fact that the cranial appendages do not increase in size in older individuals (Voorhies, 1969), as they do in bovids or cervids. Goss (1983) has pointed out that the bony structure of merycodontine appendages, with an inner layer of spongy bone and an outer layer of lamellar bone, is consistent with this hypothesis. This is also supported by the fact that some merycodon-

tine appendages show wear on the tines (Frick, 1937; Voorhies, 1969). On this basis Goss (1983) has termed these appendages "non-deciduous antlers." Although there is no developmental information for merycodontines, Bubenik (1982) has suggested that they are frontal outgrowths based on histological characters and branching patterns.

We consider that there is extremely strong evidence that merycodontine cranial appendages were initially skin-covered during the period of growth, and progressively became naked as the animal aged. Certainly the evidence precludes the possibility that merycodontines had a keratinous horn sheath. This has a number of important taxonomic implications. If we accept, for the moment, the widely accepted belief that merycodontines are ancestral to antilocaprine, then it is clear that the keratinous sheath of antilocaprine (or *Antilocapra*) has evolved independently and cannot be used as a character to link bovids with antilocaprine. This is further supported by differences in formation of the sheath. Conversely, if one accepts the homology of the keratinous sheath in bovids and *Antilocapra*, then merycodontines cannot be ancestral to antilocaprine.

We would also like to stress the other differences between merycodontine and antilocaprine cranial appendages. The cranial appendages of merycodontines are rounded rather than oval in cross section and may have branches with acute angles between shaft and tines. It should be noted that even Frick (1937) remarks on the differences between the appendages of merycodontines and antilocaprine, and he bases his assignment of these two groups to the same family on other characters. There seems little reason to assume the homology of merycodontine antlers with antilocaprine horns, although it is not impossible that such a homology exists. The only morphological similarity between them rests in their supraorbital position, which is shared with the condition in the dromomerycids and in the giraffoid *Climacoceras*.

Dromomerycidae

Dromomerycids possessed supraorbital or postsupraorbital cranial appendages, which were variably round or oval in cross section,

and were straight or curved, or flattened and extended laterally (as in *Dromomeryx*) but never forked or branched. Members of the Cranioceratini also possessed a single median occipital cranial appendage, and *Sinclairiromeryx* possessed paired nasal bosses in addition to the frontal appendages. The texture of the appendages was usually smooth, suggesting a skin cover. In some genera, such as *Dromomeryx*, the appendage surface was more rugose and pitted in places, suggesting a keratinous thickening of the skin cover, although there is no evidence for a bovid or antilocaprine type of horn sheath. The concept of a skin covering (as opposed to the type of naked appendage seen in cervid antlers) is strengthened from the examination of certain specimens of *Sinclairiromeryx* (including the type of *S. sinclairi*, AMNH 33791) where the appendage has clearly suffered pre-mortem breakage and subsequent healing over the tip region. The tips of dromomerycid cranial appendages have a more spongy texture, reminiscent of the surface of the horn cores of *Antilocapra*, and may have been reinforced with keratin at this point. However, as pointed out by Webb (1983b), there is no evidence for the type of forked, deciduous keratinous tips restored to these appendages by Frick (1937). These appendages have been referred to as "ossicones" (e.g., Janis, 1982; Leinders, 1983; Webb, 1983b), because of the superficial similarity to giraffid ossicones. However, there is no direct morphological evidence to suggest that they were formed from giraffidlike dermal ossicones, as there is no apparent line of fusion between the appendage and the skull in young animals. Bubenik (1982) suggests that they were frontal outgrowths on histological grounds.

Hoplitomerycidae

Leinders (1983) described the ruminant *Hoplitomeryx matthewi*, which appears to be a cervoid on other morphological criteria, yet possesses unbranched cranial appendages resembling bovid horn cores. The surface texture of these appendages is heavily ridged, suggestive of a bovidlike nondeciduous keratin sheath. Unlike true bovids, this animal possessed two pairs of suprapostorbital frontal appendages and a single median nasal ap-

pendage. Leinders offered no evidence for their mode of formation, but considers the animal to represent a parallel evolution of at least a superficial bovidlike form of cranial appendage within the Cervioidea.

"Palaeomerycidae"

Ginsburg and Heintz (1966) ascribe an isolated cranial appendage to *Palaeomeryx kaupi*. The appendage appears to be similar in texture and shape to a giraffid ossicone, suggesting a skin cover and a postorbital position, and its isolated occurrence and the appearance of the lower surface suggest that it is a dermal ossicone which would later fuse with the skull. Qiu et al. (1985) recently described a complete skull of *Palaeomeryx tricornis*, which possessed supraorbital giraffidlike cranial appendages, and had in addition a single median occipital appendage, resembling the condition in the cranioceratine dromomerycids.

The genus *Triceromeryx* (Crusafont-Pairó, 1952), which has been linked with the genus *Palaeomeryx* by some authors (e.g., Hamilton, 1973; Leinders, 1983), but with the Giraffidae by other authors (e.g., Crusafont-Pairó, 1952; Churcher, 1970; Hamilton, 1978a), also possessed a pair of postsupraorbital appendages and a single median occipital appendage. The texture of the appendages is smooth, suggesting a skin covering, but there is no evidence as to their mode of formation.

Figure 3 shows in diagrammatic form the different kinds of cranial appendages in living and fossil artiodactyl families.

OTHER SKULL CHARACTERS

Antorbital Vacuity and Lacrimal Fossa

Both an antorbital vacuity, sometimes referred to as the ethmoidal vacuity (e.g., Sigogneau, 1968), and a lacrimal fossa are present in living cervids and were included by Brooke (1878) among his defining characters of the Cervidae (see fig. 4). These characters have been used by several authors as defining cervid characters. For example, Sigogneau (1968) uses them in her discussion of the cervoid affinities of *Dremotherium*, and Ginsburg and Heintz (1966) state that the apparent absence of an antorbital vacuity in *Palaeomeryx* im-

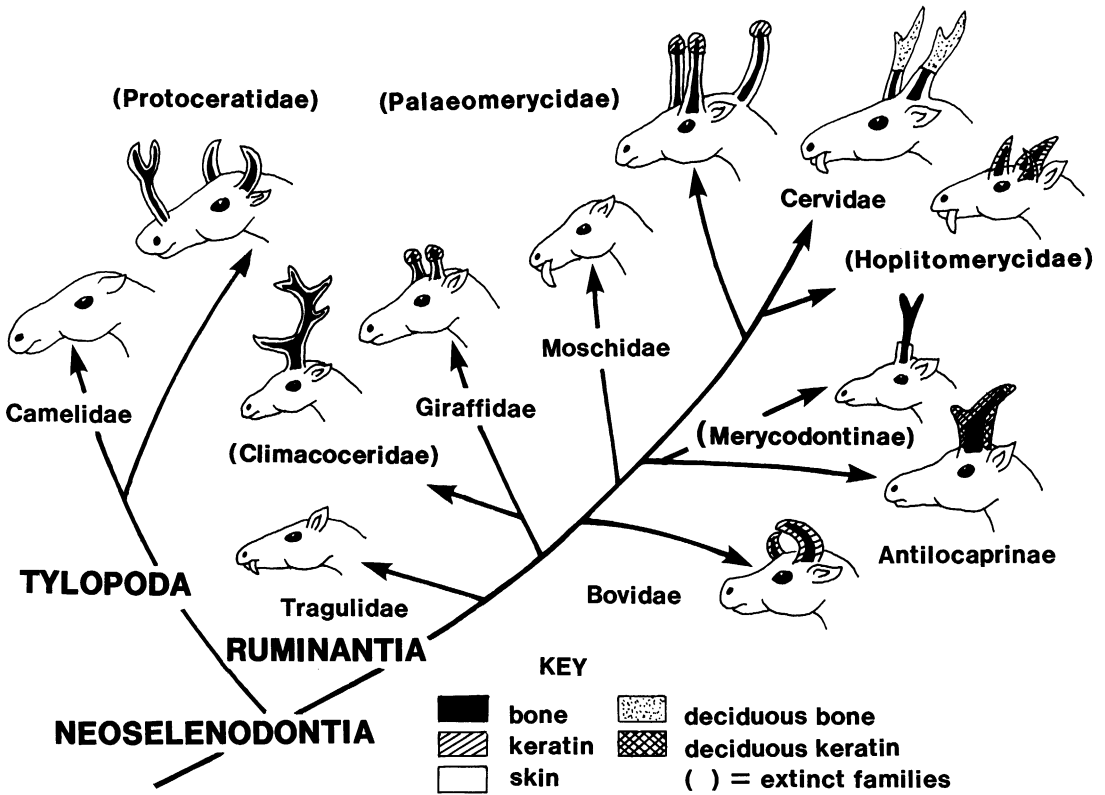


Fig. 3. Types of cranial appendages found in living and fossil families of the Neoselenodontia (sensu Webb and Taylor, 1980).

plies giraffoid rather than cervoid affinities. However, an examination of the distribution of these character states in fossil and living artiodactyls suggests that they cannot be taken as cervid (or cervoid) apomorphies.

The antorbital vacuity forms at the junction of the lacrimal, frontal, nasal, and maxilla in cervids. In defining the Cervidae, Brooke (1878) notes that the antorbital vacuity in cervids is of such dimensions as to exclude the lacrimal from articulation with the nasals. Brooke also notes that an antorbital vacuity of this type is not unique for the Cervidae, as it is also present in the bovid genera *Gazella* and *Oryx*. In addition, an antorbital vacuity is also present in a number of other bovid genera, although in some cases the vacuity is of smaller dimensions and there may be nasal/lacrimal contact. These genera include *Raphicerus*, *Gazella*, *Tragelaphus*, *Neotragus*, *Oreotragus*, *Kobus*, and *Ourebia*. In the Giraffidae, a small fossa is present in the living genus *Okapia* and in the fossil gen-

era *Giraffokeryx* and *Bohlinia* (Colbert, 1933), and may also be present in *Zarafa* (Hamilton, 1973). A small vacuity is also present in the camelid genus *Llama* and has been described in *Prodremotherium* (Jehenne, 1977).

The antorbital vacuity has obviously arisen in parallel a number of times, making its taxonomic value questionable. The character would still be of value if it were possible to distinguish a cervid-type of vacuity from a bovid-type, but this does not appear to be the case. The vacuity always seems to form at the junction between the aforementioned bones; failure of these bones to meet is probably the simplest way, developmentally, to form a vacuity in this area. The position of the vacuity in some bovids may differ because of the differing relationships of the four bones. For example, in *Neotragus batesi*, which lacks an antorbital vacuity, the lacrimal has an anterior extension which blocks the maxilla from contact with the nasal. In the other two species of this genus (*N. mos-*

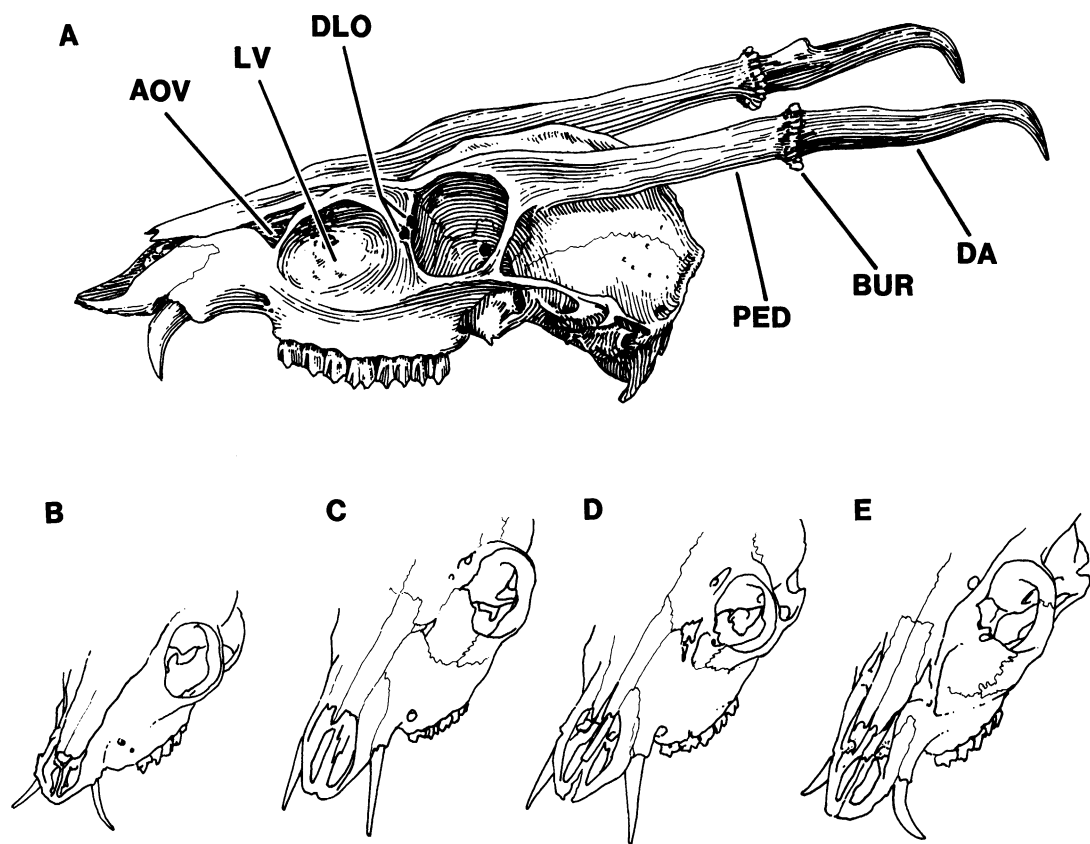


Fig. 4. Skulls of living ruminant taxa, illustrating certain cranial characters (not to scale). A. Lateral view of *Muntiacus reevesi*, MCZ 25858, showing cervoid skull features and primitive condition of cervid antlers with long nondeciduous pedicle. B-E. Anterior views, showing direction of flaring canines: B. *Tragulus memmina*, MCZ 30251. C. *Moschus sifanicus*, MCZ 13272. D. *Hydropotes inermis*, MCZ 11526. E. *Muntiacus reevesi*, MCZ 25885. AOV, antorbital vacuity; DA, deciduous portion of antler; BUR, antler burr; DLO, double lacrimal orifice; LV, lacrimal vacuity; PED, nondeciduous antler pedicle.

chatus and *N. pygmaeus*) which have an antorbital vacuity, it forms at the junction of the nasal, frontal and lacrimal. The vacuity in this genus could thus be distinguished from that of other bovids as well as cervids, but in general there appears to be no way to determine when the vacuity is homologous, and it should therefore not be used as a taxonomic character. Although an antorbital vacuity is characteristic of most extinct cervoid lineages, such as dromomerycids, blastomerycines, antilocaprine, and merycodontines, it has obviously arisen in parallel among other artiodactyl lineages, and cannot be considered diagnostic of cervoids.

The lacrimal fossa (character 8) is a depression in the facial plate of the lacrimal bone

which contains the suborbital gland. In species in which the gland is large, the depression may extend onto the maxilla and may also involve the jugal. A lacrimal fossa is present in *Hydropotes* and all living antlered cervids, but is absent in *Moschus* and most fossil cervoids. This character also appears to have arisen in parallel within the Pecora, as it is present in the dromomerycids *Barbouromeryx*, *Sinclairiomeryx*, and *Dromomeryx* (Frick, 1937), in *Dremotherium* (Sigogneau, 1968), in *Zarafa* and *Prolibytherium* (Hamilton, 1973), in certain bovids, including *Cephalophus*, *Madoqua*, *Neotragus*, *Oreotragus*, and *Ourebia* (personal observ.), in *Dacrytherium*, and in many oreodonts. The lacrimal fossa may well be a symplesiomorphic character

for bovids, lost in more derived taxa (P. Grubb, personal commun.). The lacrimal fossa varies in depth and extent among the species of cervids and bovids in which it occurs. In both bovids and cervids in which the fossa is large the walls of the fossa are very thin, and may become fenestrated. The size and depth of the fossa are clearly related to the degree of development of the suborbital gland, which is in turn related to aspects of social behavior. There is therefore no consistent or taxonomically useful pattern in its distribution, nor are there any characteristics of the fossa which might be used to establish homology. The character should therefore be dropped from taxonomic considerations in distinguishing cervoids from other pecorans, but we consider that it may have some value at the lower taxonomic level of linking *Hydropotes* with antlered cervid genera.

Lacrimal Orifice (character 9)

Flower (1875) and Brooke (1878) first pointed out the significance of the number and placement of the lacrimal orifices, noting that the presence of two lacrimal orifices on or near the rim of the orbit was one of the features which defined the family Cervidae (see fig. 4). Leinders and Heintz (1980) used this character more broadly, to define the superfamily Cervoidea within the higher ruminants. However, as we pointed out elsewhere (Scott and Janis, 1987), there are several problems associated with use of the number of orifices as a taxonomic character, namely that the number of orifices may be individually variable within individuals in a species, and that the character has clearly evolved more than once within the mammals. For example, it is seen in certain suid and kangaroo species.

The primitive condition for the Ruminantia is the presence of a single orifice located within the rim of the orbit. This is the condition seen in all of the Tragulina, the Moschidae, and in *Prodremotherium* (Jehenne, 1977). The lacrimal orifice in giraffids is either single, reduced, or absent. Although a double lacrimal orifice, situated within the orbit, was described for the genera *Zarafa* and *Prolibytherium* by Hamilton (1973), Leinders (1983) decided on reexamining this material

that only a single orifice was present. (The condition of the lacrimal orifice in these two genera will be discussed further in a later section.) The derived double orifice has evidently evolved at least twice among the ruminants, since it is present in the bovid tribes Bovini and Tragelaphini (Leinders and Heintz, 1980), and occasionally in the Alcelaphini, Hippotragini, and Caprini (personal observ.), as well as in the Cervidae. The double orifice has clearly evolved independently in these bovid tribes, since the orifice is single in the more primitive Boselaphini (Leinders and Heintz, 1980); however, the condition in *Eotragus* (the earliest known bovid, considered to be a boselaphine) is not known. The placement of the double orifice in Tragelaphini and Bovini is highly variable, and in some individuals there may be only a single orifice, also variably placed (Leinders and Heintz, 1980).

The cervoid condition is for the dorsal orifice to be situated on the orbital rim, or somewhat inside the rim, and for the ventral orifice to be situated on the external side of the rim. Usually, a small spur of the lacrimal bone juts out laterally from a position within the two orifices (see fig. 4). The condition in *Antilocapra*, and in those fossil antilocaprine taxa in which we have been able to observe this feature, is similar to the cervoid condition (in those instances where a double orifice is present). The condition in bovids is more variable. Individuals of the genus *Tragelaphus* usually have both orifices situated slightly within the orbit, and there is no spur of the lacrimal bone. However, we have observed individuals of the Bovini where the situation is identical to the condition in cervids, despite variability within each species. Thus, the simple presence of the two orifices cannot be assumed to be homologous with the cervoid condition, although the presence of two orifices with the cervoid configuration may be useful as part of a suite of defining characters.

Use of the double lacrimal orifice as a derived character is also problematical since the number of orifices can be variable within a species. This was noted by Leinders and Heintz (1980) for *Tragelaphus scriptus* and by Scott and Janis (1987) for *Antilocapra* and *Moschus*. The character should therefore

be used with caution, especially in fossil groups where only one or a few specimens are known.

Characters of the Auditory Bulla

The primitive condition of the auditory bulla in the Pecora is an unexpanded bulla with a posteriorly positioned, exposed attachment for the tympanohyal. Although expansion of the bulla and changes in the position of the tympanohyal are common with the Pecora, personal observation has shown that, with the exception of the Moschidae, no specializations of the bulla can be found to characterize any one Pecoran family. However, Webb and Taylor (1980) showed that living and fossil moschid taxa can be characterized by a subcentral position of the tympanohyal, with a laterally enclosed tympanohyal vagina (character 10).

GENERAL CHARACTERS OF THE DENTITION

Upper Canines (character 11)

The presence of large upper canines, presumably used in intraspecific combat, has been considered a primitive characteristic among ruminants (e.g., Webb and Taylor, 1980). The presence of large upper canines has been noted in a number of traguloid and pecoran genera and families. However, no previous attempt has been made to distinguish among the types of large upper canines seen among ruminants. While an enlarged upper canine appears to be a primitive character for the Ruminantia in general (see Webb and Taylor, 1980), the primitive type of enlarged upper canine, seen in modern tragulids, which curves laterally, differs markedly from the loose-socketed ventrally projecting canine seen in *Moschus* or *Hydropotes*. In modern and fossil tragulids the canines curve laterally and posteriorly, so that the pointed tips are widely divergent. This type of canine also is found in the fossil traguloid genera *Hypertragulus*, *Archaeomeryx* (Webb and Taylor, 1980), and *Bachiitherium* (Bouvrain and Geraads, 1985).

In contrast, the moschid type of canine is curved slightly posteriorly and laterally, with

the tips directed downward. Viewed anteriorly, the lateral surface appears concave proximally and convex distally. This type of canine is seen in *Moschus*, blastomerycids, *Hydropotes*, *Hoplitomeryx*, *Dremotherium*, *Amphitragulus*, the dromomerycid *Barbouromeryx* (see Frick, 1937), and has recently been described in *Palaeomeryx* (Qiu et al., 1985) and *Lagomeryx* (Chow and Shih, 1978). In these genera, the canine is much larger relative to body size than is the enlarged canine of the tragulid type. The same type of canine is present in *Micromeryx*, but it is smaller relative to body size. Reduction of this type of canine is seen in the dromomerycid genera *Aletomeryx* and *Sinclairiomeryx*. The tragulid type of canine also occurs in living *Muntiacus* and *Elaphodus* and related fossil genera; its occurrence here is presumably secondary (see fig. 4).

Although the differences in canine morphology are not strictly allometric, that is, the size and shape of the canine do not change regularly with body size, the difference in morphology is probably related to the absolute size of the tooth relative to the skull. In those genera with the tragulid type of canine, the tooth is short relative to body size and the tip would have little clearance below the jaws if it were relatively straight as in the moschid type. The outward flare allows the tip to be used more effectively in combat. In the relatively larger moschid type canine, the tip is clear without the lateral flare. In muntjaks, the reduction of the canine in conjunction with the evolution of antlers presumably led to the redevelopment of the laterally flared canine from the reduction of the moschid type of canine.

Large upper canines are absent in all known giraffids and bovids, although small upper canines may be present as an individual variation in some Miocene bovids, e.g., *Protragoceras* (Gentry, 1970: 249). They are also present in a variety of living cervid species, e.g., *Cervus elephas*. We have also observed a small upper canine alveolus in the merycodontine genus *Paracosoryx* (AMNH 31191, *Paracosoryx wilsoni*). The anterior part of the skull is unknown in all Eurasian gelocids, although small, apparently tragulid type canines have been ascribed to *Prodremotherium elongatus* (AMNH 10336) and *Eumeryx culminus*

TABLE 3
Distribution of Other Cranial Characters in Ruminant Genera

	Lacri- mal orifices	Antorbital vacuity	Lacrimal fossa	Auditory bulla	Upper canine
TRAGULINA					
<i>Hypertragulus</i>	?1	Absent	Absent	Unexpanded	Large
<i>Tragulus</i>	1	Absent	Absent	Expanded, cancellous bone	Large
<i>Leptomeryx</i>	1	Absent	Absent	Unexpanded	Large
<i>Bachitherium</i>	?1	?	?	?	Large
<i>Lophiomeryx</i>	?1	?	?	?	Large
"GELOCIDAE"					
<i>Gelocus</i>	?1	?	?	Unexpanded	?
<i>Notomeryx/Gobiomeryx</i>	?1	?	?	?	?
<i>Prodremotherium</i>	?1	Present	?	Large	
<i>Eumeryx</i>	?1	?	Absent	?	Large
<i>Rutitherium</i>	?1	?	?	?	?
GIRAFFOIDEA					
<i>Propalaeoryx</i>	?1	?	?	?	?Large
<i>Climacoceras</i>	?1	?	?	?	Absent
<i>Canthumeryx/Zarafa</i>	1	Present	Present	Moderately expanded	Absent
Giraffids	1	Small or absent	Absent	Expanded in some	Absent
BOVIDAE					
<i>Eotragus</i>	?1	Absent	Absent	Unexpanded	?
Other bovids	1 or 2	Present in some	Present in some	Expanded in some	Small/absent
MOSCHINA					
<i>Walangania</i>	?1	?	?	?	?Small
<i>Dremotherium</i>	1	Present	Present	Less pronounced than other moschids	Sabrelike
<i>Blastomeryx</i>	1	Present	Absent	Laterally enclosed	Sabrelike
<i>Parablastomeryx</i>	1	Present	Absent	Subcentral	Sabrelike
<i>Moschus</i>	1	Present	Absent	Tympanohyal vagina	Sabrelike
<i>Micromeryx</i>	?	Present	?	?	Sabrelike
ANTILOCAPRIDAE					
<i>Paracosoryx</i>	2	Present	Absent	?Somewhat like moschids	Small/absent
Other merycodontines	2	Present	Absent	As <i>Paracosoryx</i>	Absent
Antilocaprines	2	Present	Absent	Moderately expanded	Absent
PALAEOMERYCIDAE					
<i>Prolibytherium</i>	?2	?	Present	?Moderately ex- panded	?
<i>Amphitragulus</i>	2	?	Absent	Unexpanded	Sabrelike
<i>Palaomeryx</i>	?1	Present	Present	?Unexpanded	Sabrelike
<i>Barbouromaryx</i>	2	Present	Present	Unexpanded	Sabrelike
<i>Aletomeryx</i>	2	Present	Absent	Unexpanded	Moderate
Other dromomerycids	2	Present	Present in some	Unexpanded	Mod./absent
HOPLITOMERYCIDAE					
<i>Hoplitomeryx</i>	2	?	Absent	Expanded in unique fashion	Sabrelike
<i>Amphimoschus</i>	?	?	?	Similar to <i>Hoplitomeryx</i>	?
CERVIDAE					
<i>Hydropotes</i>	2	Present	Present	Unexpanded	Sabrelike
<i>Dicrocerus</i>	2	Present	Present	Unexpanded	Large
Other cervids	2	Present	Present	Unexpanded/slightly expanded	Large/absent

(AMNH 19147) in the AMNH collections. A similar type of canine is associated with *Propalaeoryx austroafricanus* from Namibia (BMNH 36963). The North American *Pseudoceras*, which has been referred to the Gelocidae by Webb (1983a), has short upper canines of the tragulid type. This suggests that the tragulid type canine is primitive for the ruminants, that the absence of a canine in bovids and giraffids is a derived condition for these groups, and that the moschid type canine is a derived condition uniting the blastomerycines and various other cervoid genera with the early true cervids.

Height of Cheek Teeth (character 12)

The primitive ruminant condition is for low-crowned or brachydont cheek teeth. High-crowned, or hypsodont, cheek teeth are generally defined as deeper than they are long from root to crown (Janis, 1984; Fortelius, 1985), although many hypsodont mammals have cheek teeth that have exceedingly high crowns in the unworn condition, and the term mesodont is often applied to teeth that are moderately hypsodont. Despite past assertions, as detailed in the previous section, that bovids and antilocaprids can be united by the possession of hypsodont cheek teeth, the character is obviously of no taxonomic value, as it can be shown to have evolved in parallel many times within the Mammalia. Among living ungulate families alone, this has occurred in the Proboscidea, Hyracoidea, Rhinocerotidae, Equidae, Suidae, and Camelidae.

CHARACTERS OF UPPER CHEEK TEETH

Figure 5 depicts the tooth nomenclature used in this paper. Figure 6 shows diagrammatic dentitions illustrating "primitive" and "derived" conditions in pecorans.

Internal Cingulum on Upper Molars

An internal cingulum on the upper molars (see fig. 6) is often considered a diagnostic characteristic of the Tragulidae (see, e.g., Sudre, 1984), and is a common feature of traguloid taxa above the level of the Hystragulidae. Although absent (presumably secondarily lost) in the Leptomerycidae, it is seen

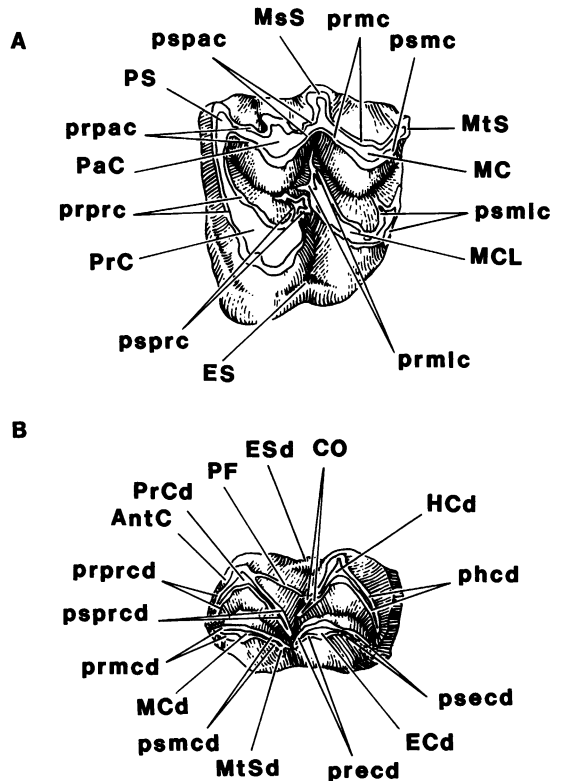


Fig. 5. Guide to dental morphology terms used in this paper: Upper and lower molars of *Dremotherium* (Montaigu, Allier). A. M2, Ph 52933. B. m2, Ph 32488. Abbreviations: AntC, anterior cingulum; CO, cristid obliqua; ECd, entoconid; ES, entostyle; ESd, ectostylid; HCd, hypoconid; MC, metaconid; MCL, metaconule; MsS, mesostyle; MtS, metastyle; MtSd, metastylid; PaC, paracone; PF, *Palaeomeryx* fold; phcd, posthypoconid; PrC, protocone; PrCd, protoconid; precd, preentocristid; prmc, premetacrista; prmcd, premetacristid; prmlc, premetaconule crista; prpac, preparacrista; prprc, preprotocrista; prprcd, preprotocristid; pscd, postentocristid; psmc, postmetacrista; psmcd, postmetacristid; psmic, postmetaconule crista; pspac, postparacrista; pspcr, postprotocrista; pspcrd, postprotocristid.

in the tragulid genera *Lophiomeryx* and *Bachitherium*, and is retained in primitive pecoran genera such as *Gelocus*, *Eumeryx*, and *Prodremotherium*, although it is absent from all living pecoran genera (see Janis, 1987). Traces of this internal cingulum are retained in the extinct higher pecoran genera *Climacoceras*, *Canthumeryx*, *Zarafa*, *Propalaeoryx*, *Walangania*, *Dremotherium*, *Palaeomeryx*, *Barbouromaryx*, and *Dicrocercus* (see table 4).

Posteriorly Situated Protocone on P3 (character 14)

Webb and Taylor (1980) unite the family Gelocidae on the basis of a narrow waisted, posteriorly situated, and posteriorly inclined protocone on P3. While this character is certainly present in all of the gelocids for which the upper dentition is known (see *Prodremotherium*, fig. 11), it is not unique to the gelocids as it is also present in the tragulid genera *Bachitherium* and *Lophiomeryx* (Janis, 1987). However, all other pecorans have P3 with an unconstricted, lingually situated and lingually inclined protocone, with the possible exception of *Walangania* (e.g., BMNH 21364) and *Propalaeoryx* (e.g., BMNH 36962), which show some resemblance to the gelocid condition (see fig. 12). The functional significance of this character is not known. The development of a "normal" pecoran type of P3 might be considered to be a character linking the higher ruminant families, but as certain derived cervoid characters are developed within the gelocids, as will be discussed in a later section, we consider it more likely that the lingually directed protocone was evolved independently in the higher pecoran families.

Entostyle (character 15)

The entostyle in the upper molars (see figs. 5, 6) is a dental character which we consider to be of phylogenetic significance. The functional significance of this character appears to be related to the puncture-crushing of food items with rounded contours, such as seeds and hollow grass stems (Janis, 1979), but its presence is not uniformly distributed throughout the selenodont ruminants. It is absent from the tylopod artiodactyls with the exception of the protoceratids *Pseudoprotoceras* and *Prosynthetoceras* (where it is derived from the posterior face of the protocone, rather than from the anterior face of the metaconule, or from the lingual cingulum, as in the Ruminantia) and is seen as an occasional variant in the living genus *Camelus*. It is also absent from the traguloid ruminants, with the exception of the Hypertragulidae and *Lophiomeryx*. While it is clear that this feature may evolve in parallel among selenodont artiodactyls, as evidenced by its

presence in *Hypertragulus* and *Lophiomeryx*, it is apparently not a character which has evolved numerous times, as evidenced by its absence in most nonruminant selenodonts. Among living pecorans, it is present in cervids, with the exception of the genera *Hydropotes*, *Moschus*, *Capreolus*, and *Pudu*, and in bovids in the tribes Bovini, Cephalophini, Hippotragini, Reduncini, and Tragelaphini, but generally absent among the Giraffidae.

Among fossil pecorans it is present in the earliest bovids and cervids, as well as in other cervoid genera (see table 4), and is also seen in *Prolibytherium*. It is generally absent in antilocaprids, with the exception of the early genus *Paracosoryx*, and is absent in *Propalaeoryx*. The entostyle is absent in all non-giraffoid giraffids, and in giraffids with the exception of its occasional occurrence in certain individuals of the species *Giraffa camelopardalis* and in *Palaeotragus coelophysys* (specimens in the collections of the AMNH), where it is derived from the posterior face of the protocone, as in *Prosynthetoceras*, and so may have evolved in parallel with other pecorans. A small entostyle derived from the anterior face of the metaconule is evident on the unerupted molars of specimens ascribed to *Zarafa* (Hamilton, 1973). Despite Hamilton's later synonymizing of this genus with *Canthumeryx* (1978a), we have never observed this feature in other specimens assigned to *Canthumeryx*, and regard the taxonomic assignation of these Gebel Zelten teeth to be problematical. They are clearly too big to belong to the same species represented by the type of *Zarafa* (and, indeed, are considerably larger than the fragmentary remains of molars on this skull, which clearly show the absence of an entostyle). Moreover, the larger teeth ascribed to *Zarafa* have a very different type of preservation from those on the skull, possessing enamel that is brownish black as opposed to the medium tan color of the enamel on the skull of *Zarafa* and also on the associated dental material ascribed to *Prolibytherium*.

An entostyle is generally absent among primitive Pecora, although an incipient entostyle, formed as a protuberance of the lingual cingulum, is present in the genera *Prodremotherium* and *Eumeryx* (see fig. 11), and a similar condition exists in some specimens

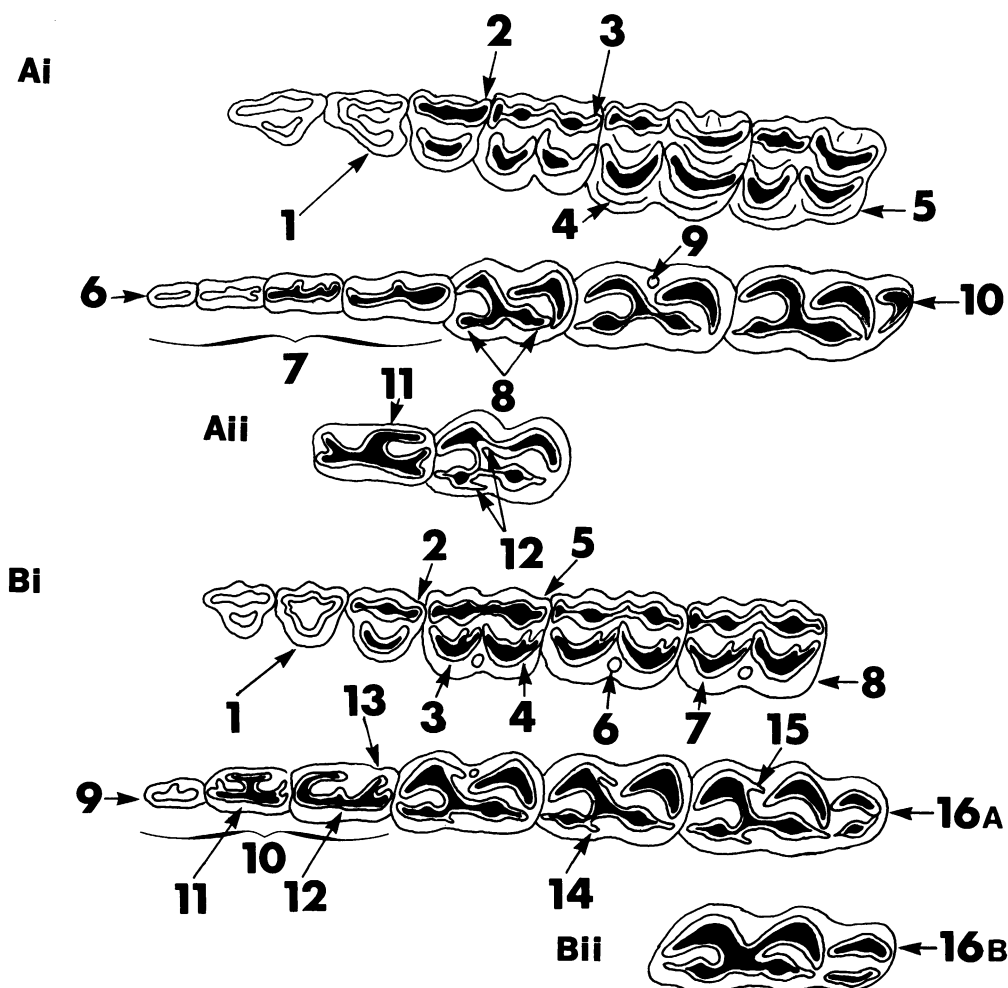


Fig. 6. Diagram of composite ruminant teeth, illustrating dental character: **Ai**. Composite primitive pecoran condition: 1, posteriorly situated and posteriorly directed protocone on P3; 2, large metacone on P4; 3, large metastyle; 4, internal cingulum; 5, small M3 metaconule; 6, p1 present; 7, long premolar row, unmolarized premolars; 8, incomplete premetacristid and postentocristid; 9, ectostylid; 10, simple posterior loop to m3. **Aii**. p4 and m1 in more primitive traguloid condition: 11, p4 metaconid forming posterolingual wall to tooth; 12, "Dorcatherium fold." **Bi**. Derived pecoran condition: 1, lingually directed and centrally situated protocone on P3; 2, attenuated P4 metacone; 3, bifurcated protocone; 4, bifurcated metaconule; 5, reduced metastyle; 6, entostyle; 7, cingulum lost; 8, large M3 metaconule; 9, p1 lost; 10, shorter, more molarized premolar row; 11, "cervoid" type of molarization, with expanded metaconid; 12, "giraffoid" type of molarization, with suppression of the metaconid and posterior extension of the paraconid; 13, vertical groove on posterolingual region of p4; 14, metastylid; 15, "Palaeomeryx fold"; 16, double posterior lobe on m3: A, closed. B, open. Also shows condition in more hypsodont teeth, where metastylids, ectostylids, and "Palaeomeryx fold" tend to be reduced or lost.

of *Walangania* (e.g., BMNH 35251), although it is absent in other specimens. The condition in *Rutitherium* is not known. We assume this incipient condition to be homologous with the more developed entostyle apparent in the bovids and cervoids, and to

represent a precursor of the more derived condition.

A problem using the entostyle as a diagnostic character is that it appears to be a trait that is lost in more hypsodont members of a lineage, presumably correlated with the re-

duction of small, crushable items in the diet when hypsodonty is developed for better mastication of fibrous material (Janis, 1979). For example, an entostyle is present in some specimens of *Paracosoryx minor* but not in the other merycodontines. It tends to be lost in the more hypsodont living cervids and bovids, though it is characteristically present as a pillarlike style in the Bovini and the Hippotragini. Within the dromomerycids, it is greatly reduced in the more hypsodont genera *Aletomeryx* and *Pedionomeryx* (see Frick, 1937).

Thus the absence of an entostyle in a lineage that is initially fairly hypsodont may not be of phylogenetic significance, although we feel that its absence in an initially brachydont lineage, such as the Giraffoidea probably is of phylogenetic significance. Despite the variable presence of an entostyle in ruminants, its distribution among the range of living and fossil pecorans suggests a closer association of the Bovidae with the Cervoidea than with the Giraffoidea.

Reduced Metastyle (character 16)

The presence of a metastyle in the upper molars appears to characterize the pecoran genera, as it is present in all gelocids, although it has also been evolved in parallel in the traguloid genera *Leptomeryx* and *Lophiomeryx* (Janis, 1987). However, certain pecoran genera, namely *Parablastomeryx*, *Amphitragulus*, *Palaeomeryx*, *Prolibytherium*, and all of the dromomerycids with the exception of *Aletomeryx* and *Rakomeryx*, appear to have secondarily reduced the metastyle (figs. 6, 13, 15, and 16, and see table 4). The functional significance of this character state is not clear. However, we believe that this is a derived condition that may be of phylogenetic significance.

Attenuated Metacone on P4 (character 17)

Sigogneau (1968) mentions the presence of an attenuated P4 metacone in the upper dentition of *Amphitragulus* and *Palaeomeryx*. In the primitive pecoran condition, retained in most pecoran genera, the P4 metacone is prominent, forming a posterior ridge on the labial wall of the tooth, and projecting labially from the ectoloph in occlusal view (see fig. 6). In the aforementioned genera, and also

in most dromomerycid genera, *Prolibytherium*, and *Parablastomeryx* (see table 4), the exterior rib is reduced, and there is little labial projection of the metacone in occlusal view (see figs. 13, 15, and 16). This condition seems to accompany the attenuation of the metastyle on the molars, a feature also seen in these genera, and may be taken as a derived pecoran condition, possibly indicative of interrelationships between the genera in which it occurs.

Small M3 Metaconule (character 18)

The presence of a small metaconule on M3 appears to be a primitive ruminant character, seen in traguloids such as *Dorcatherium* and *Lophiomeryx* and is also characteristic of gelocids (e.g., *Prodremotherium*, see fig. 11). The metaconule is the same size as the protocone in the earliest members of the Bovidae, Giraffidae, and Cervidae, but the primitive state is variously retained in other fossil pecorans such as *Paracosoryx* (but not in other antilocaprids), some specimens of *Palaeomeryx*, *Amphimoschus*, and *Dremotherium*. The metaconule is larger in the dromomerycids, blastomerycids, and in *Amphitragulus*, and is also large in the traguloid *Leptomeryx* (see table 4). It is apparent that the larger size metaconule has arisen in parallel among the Pecora several times, as also evidenced by the parallel evolution of the condition in *Leptomeryx*. However, the character is of interest because it may be presumed that an animal with a large metaconule represents a derived condition.

Bifurcated Protocone (character 19a)

Ginsburg and Heintz (1966) state that the bifurcated posterior wing of the protocone is a derived cervid character, which forms part of their argument for the conclusion that *Palaeomeryx* cannot be a cervoid. A bifurcated protocone is present in the earliest antlered cervids such as *Dicrocerus* and *Euprox*, but is not present in any of the other noncervid cervoids except for *Amphimoschus* (Leinders, 1983) (see fig. 6). We consider this to be an advanced cervoid character, possibly linking *Amphimoschus*, and by association *Hoplitomeryx* (see Leinders, 1983), with the

true cervids. To the best of our knowledge, this dental character does not appear as a variant in any other pecoran genera, although it can be seen in the possibly tragulid genus *Dorcabune* and in oromerycid tylopods. However, this character is not universally present among living cervids, being found only in the genera *Odocoileus*, *Blastocerus*, *Alces*, *Mazama*, *Pudu*, and *Capreolus*.

Bifurcated Metaconule (character 19b)

A bifurcated posterior wing of the metaconule is a feature of early giraffids such as *Palaeotragus*, and is occasionally seen in specimens of *Canthumeryx* [e.g., *Canthumeryx sirtensis* from Moruorot, in the collections of the University of California (Berkeley), V 4898/41981]. However, among other African genera, it is present in *Propalaeoryx*, but absent in *Walangania*. The character may be of limited phylogenetic significance, as it has arisen in parallel in other selenodonts; for example, it is seen in the living cervid *Capreolus*, in *Palaeomeryx*, and in many dromomerycid genera [e.g., *Barbouromaryx*, *Bouomeryx*, *Drepanomeryx*, *Dromomeryx*, and *Rakomeryx* (see Frick, 1937), although this character is not invariably present in all specimens of these genera]. However, we believe that it may be of importance in establishing the sister-groups of the Giraffoidea and the Dromomerycinae, as will be discussed later.

CHARACTERS OF LOWER CHEEK TEETH

Palaeomeryx Fold (character 20)

The *Palaeomeryx* fold in the lower molars (see figs. 5, 6) has been generally considered to be a primitive ruminant character (e.g., Hamilton, 1973). This assumption probably stems from the phylogeny of Stirton (1944), where he assumed that the Palaeomerycidae (including *Palaeomeryx* and the North American blastomerycids and dromomerycids) were the basal family for the origin of both cervids and giraffids (see also Matthew, 1934). Hamilton (1973) repeated Stirton's assertion, and claimed that a *Palaeomeryx* fold is irregularly present in the giraffid genera *Palaeotragus* and *Honatherium*. He also described a *Palaeomeryx* fold in *Zarafa* (Ham-

ilton, 1973), but the teeth in question from Gebel Zelten cannot be assumed to belong to the skull of *Zarafa*, as previously discussed. In addition, we have never seen a *Palaeomeryx* fold in other specimens referred to *Canthumeryx*. Further, we have not noticed a *Palaeomeryx* fold in any giraffid genus (an observation confirmed by Solounias, personal commun.), and are dubious as to the homology of such a fold in these giraffids with the typical cervoid condition. Janis (1987) has shown that the *Palaeomeryx* fold quoted by Matthew (1908) as being present in *Lepotomeryx* is actually a remnant of the buccal portion of the traguloid *Dorcattherium* fold, which involves a bifurcation of both the postparacristid and the postmetacristid (see fig. 6). A similar situation may exist in these giraffid genera. Thomas (1984) presents evidence of a "*Palaeomeryx*" fold in the premolars of *Palaeotragus*. However, a *Palaeomeryx* fold is not seen in cervoid premolars, and we are dubious about the homology of this structure in *Palaeotragus* with the condition in cervoid molars. We consider the *Palaeomeryx* fold to be a derived cervoid condition. Among the earliest representatives of the living pecoran families, it is present in early cervids but absent in early members of the other families (see table 5).

The problem with this character is that it is often seen as a primitive feature in certain lineages and is lost in later forms. For example, it is present as a diagnostic character in Miocene cervids, but has been lost in all Recent genera. Among dromomerycids, its presence is apparently linked with tooth crown height. It is present in the brachyodont genera *Barbouromaryx*, *Bouomeryx*, *Procranioceras*, and *Dromomeryx*, variably present in the mesodont genera *Sinclairiomeryx*, *Rakomeryx*, *Drepanomeryx*, and *Cranioceras*, and absent in the more hypsodont genera *Aletomeryx* and *Pediomeryx*, representing parallel loss with increasing hypsodonty in three lineages. It is generally absent in the blastomerycids, but present in the most brachyodont early genus *Problastomeryx* and in the brachyodont *Parablastomeryx*. The *Palaeomeryx* fold is absent in all known antilocaprids, bovids, and giraffids. Among other primitive pecoran genera, it is absent in *Gelocus*, *Notomeryx*, *Gobiomeryx*, and *Pro-*

TABLE 4
Distribution of Upper Dental Characters in Ruminant Genera

	Direction of P3 protocone	P4 meta- conule	Meta- style	M3 metaconule	Lingual cingulum	Entostyle	Bifurcated meta- conule	Tooth height
TRAGULINA								
<i>Hyphantragulus</i>	Lingual	Normal	Present	Small	Slight	Present	No	Low
<i>Tragulus</i>	Lingual	Normal	Absent	Small	Strong	Absent	No	Low
<i>Leptomeryx</i>	Lingual	Normal	Absent	Large	Absent	Absent	No	Low
<i>Bachitherium</i>	Posterior	Normal	Absent	Small	Slight	Absent	No	Low
<i>Lophiomeryx</i>	Posterior	Normal	Present	Small	Strong	Present	No	Low
"GELOCIDAE"								
<i>Gelocus</i>	Posterior	Normal	Present	Small	Mod./strong	Absent	No	Low
<i>Notomeryx/Gobiomeryx</i>	?	Normal	Present	Small	Mod./strong	Absent	No	Low
<i>Prodremotherium</i>	Posterior	Normal	Present	Mod./strong	Slight	Small	No	Low
<i>Eumeryx</i>	Posterior	Normal	Present	Small	Moderate	Small	No	Low
<i>Rutitherium</i>	?	?	?	?	?	?	?	Low
GIRAFFOIDEA								
<i>Propalaeoryx</i>	Somewhat post.	Normal	Present	Moderate	Slight	Absent	Yes	Low
<i>Climacoceras</i>	Lingual	Normal	Present	Large	Slight	Absent	No	Low-Mod.
<i>Canthumeryx/Zarafa</i>	Lingual	Normal	Present	Large	Slight	Absent	Yes	Low
Giraffids	Lingual	Normal	Present	Large	Absent	Occasional	In some	Low-Mod.
BOVIDAE								
<i>Eotragus</i>	Somewhat post.	Normal	Present	Large	Absent	Present	No	Moderate
Other bovids	Lingual	Normal	Present	Large	Absent	Pres./lost	No	Mod.-High

TABLE 4—(Continued)

	P4	Direction of P3 protocone	Meta- style	M3 metaconule	Lingual cingulum	Entostyle	Bifurcated meta- conule	Tooth height
MOSCHINA								
<i>Walangania</i>	Normal	Somewhat post.	Reduced	Moderate	Slight	Small	No	Moderate
<i>Dremotherium</i>	Normal	Somewhat post.	Present	Moderate	Slight	Present	No	Low
<i>Blastomeryx</i>	Normal	Lingual	Present	Moderate	Absent	Pres./lost	No	Low-mod.
<i>Parablastomeryx</i>	Reduced	Lingual	Reduced	Moderate	Absent	Present	No	Low
<i>Moschus</i>	Normal	Lingual	Present	Large	Absent	Lost	No	Moderate
<i>Micromeryx</i>	Normal	Lingual	Present	Moderate	Absent	Small	No	Low-mod.
ANTILOCAPRIDAE								
<i>Paracosoryx</i>	Normal	Lingual	Present	Large	Absent	Small	No	Moderate
Other merycodontines	Normal	Lingual	Present	Large	Absent	Lost	No	High
Antilocaprinae	Normal	Lingual	Present	Large	Absent	Lost	No	High
PALAEOMERYCIDAE								
<i>Prolibitherium</i>	Reduced	Somewhat post.	Reduced	Large	Slight	Present	No	Low-mod.
<i>Amphitragulus</i>	Reduced	Lingual	Reduced	Large	Absent	Present	No	Low
<i>Palaeomeryx</i>	Reduced	Lingual	Reduced	Moderate	Slight	Present	Yes	Low
<i>Barbouromeryx</i>	Reduced	Lingual	Reduced	Large	Slight	Present	Yes	Low
<i>Aletomeryx</i>	Reduced	Lingual	Present	Large	Absent	Small	No	Moderate
Other dromomerycids	Reduced	Lingual	Reduced	Large	Absent	Pres./small	In some	Low-mod.
HOPLITOMERYCIDAE								
<i>Hoplitomeryx</i>	Normal	Lingual	Present	Large	Absent	Lost	No	Moderate
<i>Amphimoschus</i>	Normal	Lingual	Present	Large	Absent	Present	No	Low-Mod.
CERVIDAE								
<i>Hydropotes</i>	Normal	Lingual	Present	Moderate	Absent	Lost	No	Moderate
<i>Dicrocerus</i>	Normal	Lingual	Present	Large	Slight	Present	No	Low
Other cervids	Normal	Lingual	Present	Large	Absent	Pres./lost	No	Low-Mod.

dremotherium, but present in some specimens of *Eumeryx* and *Rutitherium* (see Janis, 1987). It can also be seen in some specimens of the poorly known African taxon *Gelocus whitworthi* (e.g., in the holotype and the paratype from Songhor BMNH. K.Sgr. 365-1949 and K.Sgr. 581-1949). Among more derived extinct pecorans, it is absent in the mesodont taxa *Walangania gracilis*, *Amphimoschus*, and *Hoplitomeryx*, but present in the more brachyodont taxa *Walangania africanus*, *Amphitragulus*, *Dremotherium*, *Micromeryx*, *Palaeomeryx*, and *Triceromeryx*. We would conclude, on the basis of observational evidence, that the presence or absence of the *Palaeomeryx* fold may be considered a diagnostic character for brachyodont taxa, but for lineages where no early brachyodont genera are known (as is the case for the Antilocapridae), its apparent absence in the known hypsodont species cannot be taken as diagnostic.

Metastylids (character 21)

Metastylids in the lower molars (see fig. 5) are present in all pecoran taxa, with the exception of *Gelocus* (although small metastylids are present in the African "*Gelocus*" *whitworthi*), and are not seen in any traguloid genera (Janis, 1987). Metastylids are frequently reduced or lost in more hypsodont taxa, and this reduction has occurred in parallel in the Bovidae, Antilocapridae, Hoplitomerycidae, Cervidae, and Dromomerycinae. In the living genus *Antilocapra*, small metastylids are apparent on newly erupted cheek teeth, but are not apparent on teeth that have started to wear.

Condition of p1 (character 4)

P1 is absent in all the Ruminantia with the exception of the Hypertragulidae (Webb and Taylor, 1980), but p1 is retained, and the primitive condition for the ruminants is apparently for p1 to be large and caniniform (Janis, 1987). p1 is small and premolariform in *Lophiomeryx* and in primitive Pecora with the exception of *Notomeryx* where it is absent (Savage et al., ms). The presence or absence of p1 is a character of similar interest to the condition of the metaconule: p1 has obviously been lost in parallel numerous times, as

evidenced by its absence in the recent Tragulidae, but the retention of the character in certain genera is of interest in that it suggests that they cannot be derived directly from animals which have already lost p1. p1 generally is present in primitive pecorans and in the genera *Propalaeoryx* and *Amphitragulus*, although it is admittedly difficult to distinguish with certainty a p1 from a retained dp1 in fossil taxa. It is generally absent in *Dremotherium*, although it is present in the earliest members of the genus from La Milloque in France (M. Brunet, personal commun.). p1 is generally absent in *Palaeomeryx*, although it is present in early species such as *P. kaupi*, as shown by the presence of an alveolus for p1 in specimens of this species from Artenay (L. Miocene, France) (Basel, 502342). p1 is generally absent in blastomerycids, although it is present in *Problastomeryx*, and in dromomerycids, though a deciduous p1 is present in *Dromomeryx*, *Rakomeryx*, and *Drepanomeryx* (Frick, 1937). However, p1 is completely absent in the earliest antilocaprids (such as *Paracosoryx*), bovids (e.g., *Eotragus*), cervids (e.g., *Dicrocerus*), and giraffoids (e.g., *Climacoceras*). It is also absent in *Hoplitomeryx*. The condition in *Canthumeryx*, *Walangania*, and *Micromeryx* is unknown (see table 5).

Postentocristid (character 22)

The postentocristid (see figs. 5, 6) forms the completion of the posterior lingual selenite in the lower molars, making the tooth fully selenodont. The formation of a completely selenodont lower molar with complete lingual selenites has evidently occurred in parallel among the ruminants many times (Janis, 1987). For example, complete lingual selenites are present in *Hypertragulus*, but not in the tragulids; among the leptomerycids they are present in the Oligocene genus *Leptomeryx*, but not in the Eocene *Archaeomeryx*. Taking *Gelocus* as the sister taxon to the other pecorans (Janis, 1987), the lower molars are very primitive, lacking both the postentocristid and the premetacristid. The premetacristid is present in the other pecoran genera, but the postentocristid is not fully formed in a number of early higher pecorans. As with the presence of a p1, this character is of interest as

the retention of the primitive condition implies that an animal with a fully formed postentocristid cannot be directly ancestral to one in which the postentocristid is not fully formed, although it does not exclude the possibility of their being sister taxa.

A complete postentocristid is absent from all gelocids with the exception of *Prodremotherium*. The postentocristid is also incomplete in the early giraffoids *Canthumeryx* and *Climacoceras*, as well as the other early Miocene African genera *Propalaeoryx* and *Walangania*. It is incomplete in *Amphitragus*, early blastomerycids such as *Problastomeryx*, and early dromomerycids such as *Barbouromeryx*. In contrast, it is complete in early bovids (*Eotragus*), cervids (*Dicrocerus*), giraffids (*Palaeotragus*), antilocaprids (*Paracosoryx*), and also in other cervoid genera (see table 3). This character has been included in our cladistic analysis, but we do not consider it to have a high degree of phylogenetic significance.

Bilobed Lower Canine (character 23)

Hamilton (1978a) unites the Giraffoidea (families Giraffidae and Climacoceridae) on the basis of a bilobed lower canine. We have not observed any instances of the parallel acquisition of this character in any other ruminant taxon, and consider it to be a valid apomorphy of the Giraffidae.

Condition of Paraconid on p4 (character 24)

Hamilton (1978a) asserted that the presence of a posteriorly directed paraconid on p4, forming a lingual wall to the tooth, in combination with the suppression of the metaconid, was a unique feature of the Giraffidae (see fig. 6). Janis and Lister (1985) have shown that, while this feature is not variable among living giraffids, it cannot be taken as diagnostic of the Giraffidae, as it is seen as a variant of premolar morphology in cervids, bovids, and dromomerycids.

Vertical Groove on Posterolingual Region of p4 (character 25)

The presence of a posterolingual groove on p4, dividing the tooth into a posterior third separated from the anterior two-thirds by a

lingual "waist," was also held by Hamilton (1978a) to be diagnostic of the Giraffidae, although he did note in an earlier paper (Hamilton, 1973) that this dental feature was also present in "some palaeomerycids." We have not performed a thorough investigation of the distribution of this trait in all pecoran taxa, but would point out that a similar p4 morphology is present in *Amphitragus* (see fig. 13), *Eotragus*, and *Prolibytherium*, and it appears to the usual form of premolar morphology among the dromomerycids (see fig. 16) and blastomerycids (see Frick, 1937). Thus this character cannot be considered diagnostic for the Giraffidae.

Double Loph on Posterior Lobe of m3 (character 26)

Signogneau (1968) mentions the presence of a double loph on the posterior loph of m3 in *Amphitragus* and *Palaeomeryx*, which she suggests may be indicative of a relationship between these two genera. In the usual pecoran condition, the m3 hypoconulid arises close to the base of the entocristid, frequently forming a closed loop by the traverse of a cristid around the posterior border of the tooth, returning towards the entostyle on the lingual side of the tooth (see condition in *Dremotherium*, fig. 13). In the case of the double lophed m3, the hypoconulid has a double origin, with a distinct cusp arising on the posterolingual margin of the tooth, somewhat posterior to the entostyle, in addition to the more labially positioned "true" hypoconulid. Posteriorly directed cristids extend from both labial and lingual hypoconulids, approaching each other at the posterior border of the tooth to form a closed loop. This morphology of the lower dentition is also seen in most dromomerycids, in *Parablastomeryx*, and possibly also in *Prolibytherium* and the teeth from Gebel Zelten ascribed to *Zarafa* (see table 5). This type of m3 morphology is sometimes also evident in the living giraffid species, though it is not typical of all giraffids. It is a derived condition though evidently not a unique one. A parallel condition, seen in *Amphimoschus* and *Hoplitomeryx*, and used by Leinders (1983) to link these two genera, is for a similarly double condition of the m3 hypoconulid in which the posteriorly extend-

TABLE 5
Distribution of Lower Dental Characters in Ruminant Genera

	Morphology of p1	Palaeo- meryx fold	Ectostylid	Metastylid	m3 type A	m3 type B	Postento- cristid	Postero- lingual groove on p4
TRAGULINA								
<i>Hyphantragulus</i>	Caniniform	No	Small	Absent	No	No	Complete	No
<i>Tragulus</i>	Small/absent	No	Present	Absent	No	No	Absent	No
<i>Leptomeryx</i>	Caniniform	No	Absent	Absent	No	No	Complete	No
<i>Bactitherium</i>	Caniniform	No	Present	Absent	No	No	Incomplete	No
<i>Lophiomeryx</i>	Small	No	Present	Absent	No	No	Absent	No
"GEOCIDAE"								
<i>Gelocus</i>	Small	No	Present	Absent	No	No	Absent	No
<i>Notomeryx/Gobiomeryx</i>	?	No	Present	Present	No	No	Incomplete	No
<i>Prodremotherium</i>	Small	No	Present	Present	No	No	Complete	No
<i>Eumeryx</i>	Small	Yes	Present	Present	No	No	Incomplete	No
<i>Rutithierium</i>	Small	Yes	Present	Present	No	No	Incomplete	No
GIRAFFOIDEA								
<i>Propalaeoryx</i>	Small	No	Present	Present	No	No	Incomplete	No
<i>Climacoceras</i>	Lost	No	Present	Present	No	No	Incomplete	Yes
<i>Canthumeryx/Zarafa</i>	?	No	Present	Present	No	No	Incomplete	Yes
Other giraffids	Lost	No	Present	Present	In some	No	Complete	Yes
BOVIDAE								
<i>Eotragus</i>	Lost	No	Present	Small	No	No	Complete	No
Other bovids	Lost	No	Small/lost	Small/lost	No	No	Complete	No
MOSCHINA								
<i>Walangania</i>	DP1 retained	In some	Small	Small	No	No	Incomplete	No
<i>Dremotherium</i>	Small/lost	Yes	Present	Present	No	No	Complete	No
<i>Blastomeryx</i>	Small/lost	In some	Present	Present	No	No	Incomplete	Yes

TABLE 5 — (Continued)

	Morphology of p1	Palaeo- meryx fold	Ectostylid	Metastylid	m3 type A	m3 type B	Postento- cristid	Postero- lingual groove on p4
<i>Parablastomeryx</i>	Lost	Yes	Present	Present	Yes	No	Complete	Yes
<i>Moschus</i>	Lost	Lost	Small	Present	No	No	Complete	No
<i>Micromeryx</i>	?	Yes	Present	Present	No	No	Complete	No
ANTILOCAPRIDAE								
<i>Paracosoryx</i>	Lost	No/?/Lost	Small	Small	No	No	Complete	No
Other merycodontines	Lost	No/?/Lost	Lost	Lost	No	No	Complete	No
Antilocaprine	Lost	No/?/Lost	Lost	Lost*	No	No	Complete	No
PALAEO-MERYCIDAE								
<i>Prolibytherium</i>	Small	No/?/Lost	Present	Present	Yes	No	Complete	Yes
<i>Amphitragulus</i>	Small/lost	Yes	Present	Present	Yes	No	Incomplete	Yes
<i>Palaeomeryx</i>	DP1 retained	Yes	Present	Present	Yes	No	Complete	Yes
<i>Barbouromaryx</i>	DP1 retained	Yes	Present	Present	Yes	No	Incomplete	Yes
<i>Aletomeryx</i>	Lost	Lost	Small	Small	No	No	Complete	Yes
Other dromomerycids	DP1 or lost	In some	Present	Present	Yes	No	Complete	Yes
HOPLITOMERYCIDAE								
<i>Hoplitomeryx</i>	Lost	No/?/Lost	Lost	Small	No	Yes	Complete	No
<i>Amphimoschus</i>	Lost	No/?/Lost	Present	Present	No	Yes	Complete	No
CERVIDAE								
<i>Hydropotes</i>	Lost	Lost	Present	Present	No	No	Complete	No
<i>Dicrocerus</i>	Lost	Yes	Present	Present	No	No	Complete	No
Other cervids	Lost	In some	In most	Present	No	No	Complete	No

m3 type A = double posterior lobe closed posteriorly.

m3 type B = double posterior lobe open posteriorly.

* Metastylids present in unerupted teeth of *Antilocapra americana*.

ing cristids do not meet at the posterior margin of the tooth, and an open valley extends between the two parallel cristids from the posterior end of the tooth to the twinned hyponulids (see fig. 6).

POSTCRANIAL CHARACTERS

Complete Distal Metapodial Keels (character 27)

In higher ruminants (including the members of the horned ruminant families, the fossil hornless genera which are not included in the *Gelocidae*, and the genus *Pseudoceras*) the distal articular surfaces for the first phalanges have a strongly marked keel which extends completely around the articular surface (see fig. 7 and table 6). In more primitive ruminants, including the traguloids and the genera assigned to the *Gelocidae*, the keels are incomplete, being present only on the posterior part of the articular surface. Completion of the distal keels presumably stabilizes the metapodial-phalangeal joint, preventing dislocation of the phalanges. The development of this character might therefore be expected to arise in conjunction with a more cursorial habit. Although the development of the character itself does not present any direct evidence that it may have evolved more than once, the strong functional basis of the character suggests that it might have done so. Complete distal keels appear independently in equids, suggesting that the character may readily be evolved in parallel. Although the character does have taxonomic significance, we would suggest that when it appears in conflict with other characters it may be assumed to have evolved in parallel.

Fusion of Metapodials and Condition of Metatarsal Gully (character 28)

In ruminants in which the third and fourth metatarsals have fused to form a single cannon bone, the line of fusion on the anterior surface is marked by a groove, the metatarsal gully. This gully may be open along its entire length, as in living bovids and giraffids, or it may be closed at its distal end by a thin bridge of bone, as in living cervids and moschids (see fig. 7). The taxonomic significance of this gully was first pointed out by Heintz (1963,

1970), who noted that the state of the gully could be used to distinguish bovids from cervids in all deposits where they co-occur. Leinders and Heintz (1980) discussed the usefulness of the metatarsal gully as a taxonomic character which distinguished cervoid (as well as cervid) artiodactyls from the bovids. They point out that the character is not known to be variable in any living bovid, cervid, or giraffid, and this invariability makes it appear to be a useful taxonomic character. Although Leinders and Heintz (1980) do not specifically address the point, it is implicit in their discussion that the closed gully is a derived condition for the *Cervoidea* and that an open gully is the primitive condition for the *Pecora*; other authors have also assumed this (e.g., Groves and Grubb, 1987).

The invariability of the character in living ruminants makes it appear to be particularly strong. No variability has ever been reported in living bovids and cervids, and none has been observed in the over 1000 skeletons of living bovids and cervids we have examined. Neither have we observed variation in metatarsals of *Eotragus* or early cervids such as *Euprox*, *Heteroprox*, and *Dicrocerus*, an observation also noted by Heintz (1963). However, the character does show variability in two groups, the *Moschidae* (sensu Webb and Taylor, 1980) and the merycodontine antilocaprids. An open gully was observed in one specimen of *Moschus moschiferous* in the Rijksmuseum von Naturhistorische, Leiden (osteology catalog d, no number) and we have observed both open and closed gullies in the North American genus *Blastomeryx* from the Olcott and Trinity River Formations. Variability is also seen in *Amphitragulus* and *Dremotherium* from San Gerard-le-Puy (Allier, France). Among merycodontines the character is variable in *Paracosoryx*, *Merycodus*, *Ramoceros*, and *Cosoryx*.

The significance of the variability can be understood only in the context of the ontogeny of the character. In living cervids the immature metatarsus consists of a single shaft, or diaphysis, with an open gully on the anterior surface, and two distal epiphyses (see fig. 8). The edges of the distal end of the gully project toward the median axis of the shaft. These ridges begin just distal to the point at which a nutrient foramen passes through the

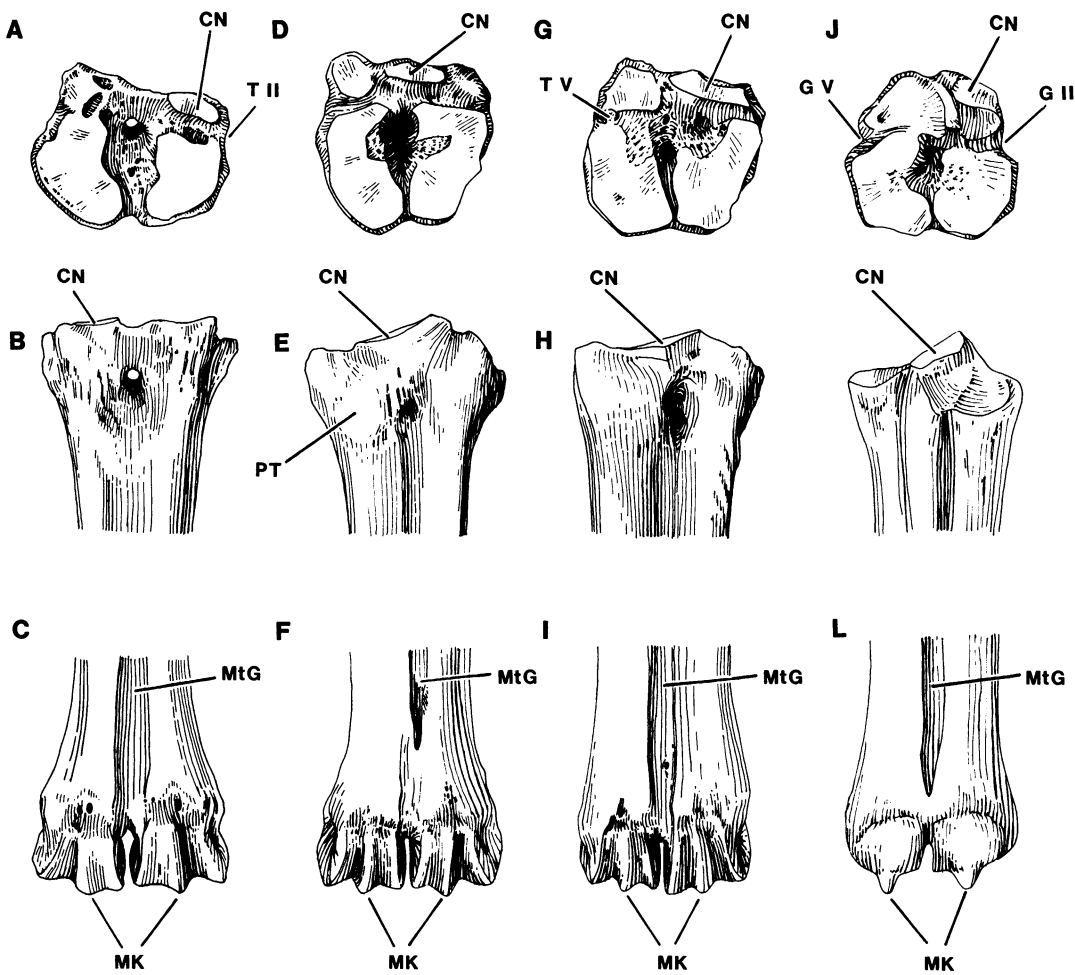


Fig. 7. Morphology of pecoran metatarsals (not to scale). A, D, G, J, proximal views (posterior to top of page). B, E, H, K, posterior views of proximal metatarsus. C, F, I, L, anterior views of distal metatarsus. A–C, giraffid (*Okapia johnstoni*, MCZ 38015). D–H, cervid (*Axis porcinus*, MCZ 1703). G–I, bovid (*Tragelaphus scriptus*, MCZ 14222). J–L, primitive cervoid (*Eumeryx culminis*, type, AMNH 19147). Abbreviations: CN, cubonavicular facet; G II, groove for metatarsal II; G V, groove for metatarsal V; MK, metapodial keels; MtG, metatarsal gully; T II, tubercle for metatarsal II; T V, tubercle for metatarsal V.

bone. As the bone grows, the edges of the gully continue to grow inward until they meet. Initially there is a visible suture where the two sides of the bridge meet, but it is rapidly obliterated. The nutrient foramen is interrupted as growth continues, and is no longer continuous through the bone. A small foramen usually remains on the posterior surface. Anteriorly the foramen is bridged over, and now ends at the distal end of the shaft. The end of this foramen is formed by the epiphyses, and in the adult it terminates between

the two articular condyles. As growth continues at the distal epiphyseal plate the length of the bridged portion increases. The epiphyses also contribute to the bridge as they fuse to the diaphysis. The shorter bridge seen in *Moschus* may result from some minor differences in timing of the developmental process, but the process can be seen to be similar in young moschids we have observed. We will refer to the type of gully formed in this way as the cervid-type gully.

In the *Amphitragulus* and *Dremotherium*

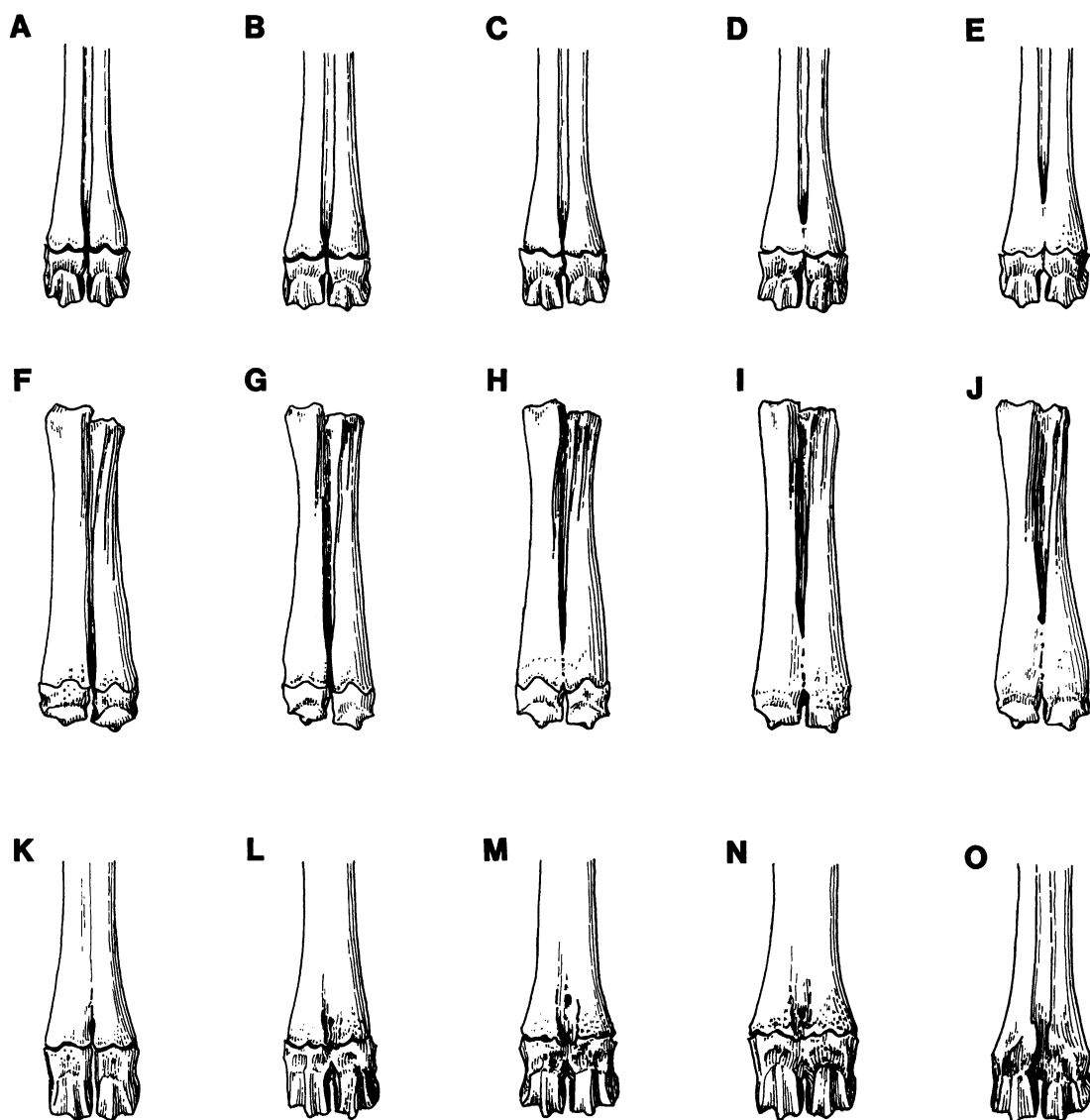


Fig. 8. Developmental stages of the fusion of the metatarsus and formation of the metatarsal gully in bovids, cervids, and tragulids (not to scale). Youngest individuals in each series are on the left. A–E, cervid developmental stages (all of *Odocoileus virginianus*). F–J, tragulid developmental stages (all of *Aepyceros melampus*). K–O, bovid developmental stages (K and N are of *Aepyceros melampus*, L, M, and O are of *Antelope cervicapra*). A, MCZ 50991. B, MCZ 50987. C, MCZ 50985. D, MCZ 51000. E, MCZ 50986. F, AMNH(M) 53601. G, AMNH(M) 53640. H, AMNH(M) 53611. I, AMNH(M) 53617. J, AMNH(M) 53604. K, AMNH(M) 33317. L, AMNH(M) 35218. M, AMNH(M) 54481. N, AMNH(M) 82045. O, AMNH(M) 35957.

specimens from St. Gerard Le Puy with a closed gully (in the collections of the Musée Gimee, Lyon, France) the bridge is relatively low as it is in *Moschus*. In some, there is a visible suture in the ventral midline of the bridge. In specimens with an “open” gully

there is clearly a partial bridge: two thin ridges of bone extend medially from the raised areas on either side of the gully. The bridge is very thin, and some of the “open” specimens may in fact have been closed in life and been broken or worn after preservation. However, not

all of the open metatarsals show signs of wear, and it is clear that some of the variation at least is real. It is possible that in life this gap was bridged by connective tissue or cartilage, and that the extent of ossification is variable.

Metatarsals of *Amphitragulus* and *Dremotherium* were examined from a number of other localities. In only one, La Milloque, a French Chattian locality under study by Y. Jehenne of Poitiers, was any variability seen; the nature and extent of the variability is similar to that at St. Gerard-le-Puy. It is significant that in younger deposits the gully is invariably closed, indicating that this character became more stable over time, although we would still interpret the closed condition of the gully as primitive. It is also clear that continuation of the trend toward incomplete ossification of the edges of the gully in metatarsal development would result in an open gully, probably one with raised edges at its distal end. This is precisely the condition seen in some bovids (i.e., *Gazella*). It thus seems clear that a closed gully in which the degree of ossification of the bridge is variable can give rise to an open gully which would be interpreted as a bovid type gully.

In the merycodontines the character is variable in the earliest genus *Paracosoryx*, and in *Merycodus*, *Ramoceros*, and *Cosoryx*. The nature of the variability is very similar, and, judging from the immature specimens we have observed, the metatarsus develops in the same way. The bridge appears to form in the same way as it does in living cervids, with thin shelves of bone extending toward the midline from either side of the gully on the diaphysis before fusion begins between epiphysis and diaphysis. The extent to which this bridge is ossified evidently remains variable in all genera of merycodontines except *Meryceros*, in which it is consistently open. In *Meryceros* the gully is similar to that of some smaller bovids, with a relatively deep gully bordered at the distal ends by raised ridges which extend slightly toward the midline. Although the gully is variable in the earliest genus of this subfamily, we hypothesize that the primitive condition for the merycodontines is to have a closed gully on the basis of the morphological and developmental similarities with the bridge in the Allier specimens. The fact that the gully has

become permanently open in *Merycodus* further supports our contention that a closed gully can give rise to an open one.

In living *Antilocapra* the gully is closed, and as in cervids the bridge occupies approximately the lower one-third of the metatarsal. In fossil antilocaprine the gully is similar to that of *Antilocapra*. In the earliest material we have been able to examine (*Plioceros* from the Ash Hollow Formation, Cherry County, Nebraska) the gully is always closed, although it tends to be closed more distally than in living cervids, as is more typical of early cervids and the living genus *Moschus*. There is no evidence of variability in any antilocaprine, as one might expect if they were derived from a group like the merycodontines in which variability in ossification seems to be typical. However, it is clearly possible that a variable gully may be fixed in the closed state as well as in the open one.

We have assumed throughout this discussion that there is no functional significance to the closed versus open gullies. Leinders (1979), in his analysis of functional differences in the foot of cervids and bovids, notes that the metatarsal gully contains the dorsal digital artery in both groups; the artery is accompanied by the dorsal common digital nerve (Ghoshal, 1975). Leinders (1979) finds no connection between morphology of the gully and the functional differences he describes between bovids and cervids. It is indeed difficult to postulate any functional significance for the various states of the gully. A deeper gully, with or without a bridge, would provide protection for the artery and nerve and would reduce pressure from the extensor tendons on these structures. The depth of the gully is greatly reduced in the Bovini and the Caprini, which would seem to suggest that this is not an important function of the gully. However, in these groups the metatarsals are strongly compressed in the anteroposterior plane, presumably to counter lateral stresses during locomotion (Scott, 1985). The gully may become reduced as a secondary result of this flattening. Selective pressures for increased transverse diameter of these bones may outweigh any advantage of a deeper gully.

Even if the gully did function to reduce pressure on the artery and nerve, it is difficult

to see why the groove should be more protected in the Cervidae which are less specialized for rapid locomotion. Nor does the loss of the bridge appear to be correlated with more rapid locomotion; if this were the case the gully would be expected to have the same form in the gazelles and in *Antilocapra*, in which the gully is in fact closed. Cervids generally do emphasize the use of the hindlimb in locomotion more than do bovids (Scott, 1987) and this may be the reason why the gully is more protected in cervids. However, none of these suggestions has a strong functional basis and we would agree with Leinders that the gully is essentially a neutral character with little functional significance.

Caution must be used in drawing conclusions based on the presence of a closed gully, since the closed condition has evolved independently in at least one other instance. In the living tragulid *Hyemoschus* the gully is closed in older individuals but both the morphology of the distal end of the bone and the sequence of development of the bridge differ from those in cervids. In young individuals the metatarsals are unfused. Proximally they are closely joined by connective tissue but distally they are separated by a distinct gap. Fusion appears to begin proximally and anteriorly and proceed distally and posteriorly. As the metatarsals fuse anteriorly the edges of the groove grow toward each other and the gap is filled by connective tissue. The epiphyses fuse completely before fusion of the metatarsal shafts is completed. When fusion has been completed along the anterior surface of the metatarsals the connective tissue filling the gap begins to ossify, forming a bridge. The metatarsals do not fuse completely at the distal end and there is always a line of fusion between the third and fourth metatarsals (see fig. 8). As in *Tragulus*, there is a large foramen passing posteriorly through the bone. A closed gully has evidently also occurred independently in the genus *Pseudoceras*. A cervoid type of closed gully is present in this genus, which also has a pecoran type of compact, parallel-sided astragalus and complete distal metapodial keels. Webb (1983a) refers to *Pseudoceras* as a gelocid, but the relationships of this genus are under further study (Webb, personal commun.).

The primitive condition for ruminants is for metatarsals III and IV to be unfused. In

most fossil genera of Tragulidae the metatarsals are unfused, and the fused metatarsals of living tragulids are clearly an independently derived condition. Of the other traguloid families, the metatarsals are unfused also in the Hypertragulidae. In leptomerycids the metatarsals are fused, although the postcrania are primitive in other respects. In *Leptomeryx*, the gully forms a shallow, open groove, and the suture between metatarsals III and IV is not entirely obliterated. However, in metatarsals referred to the leptomerycid *Pseudoparablastomeryx* by Taylor and Webb (1976), the gully is closed. The association of the metatarsal with the cranial and dental material is not certain, but the metatarsal is primitive in other respects and there do not seem to be any other taxa with which it might more reasonably be associated. Although there is no developmental series available for this genus, the metatarsal is nearly identical to that of *Hyemoschus*. If this specimen is a leptomerycid, then the closed gully of *Pseudoparablastomeryx* is probably an independent closure from the condition in the cervoids, as is that of *Hyemoschus*.

Among primitive pecorans, postcranial remains are known in the genera *Gelocus*, *Prodremotherium*, and *Eumeryx*. Janis (1987) has suggested that *Gelocus* is the sister taxon to all other Pecora, and this genus is therefore of considerable interest. The specimen described by Kowalevsky (1876) includes a metatarsal, and this appears to have a shallow, open gully, although it is difficult to be certain of the condition as the distal end is broken. Other metatarsals from Ronzon in the collections at Le Puy (PAR 27-60), Paris (RZN 42), and Basel (Ro 41) all clearly show the open gully type of morphology, so that it seems reasonable to assume that the metatarsals are fused and that the gully is open in *Gelocus*. This would suggest that the primitive condition for ruminants is an open gully. However, the possibility should also be considered that the metatarsals have fused independently several times in higher ruminants and *Gelocus*, as has occurred in tragulids, and among other artiodactyl groups in the camelids, amphimerycids, xiphodontids, tayassuids, and entelodontids. *Prodremotherium* (Viret, 1961; Bouvraïn and Geraads, 1985) and *Eumeryx* (Matthew and Granger, 1924) both possess a cervid type of

gully with a short bridge, in contrast to *Gelocus*. The morphology of the preceding two genera may be regarded as a derived condition, linking them with cervids (see Janis, 1987, and further discussion later in this paper).

Interpretation of the gully would be facilitated if it were known whether metatarsals had fused independently in bovids and cervids. If so, both open and closed gullies would be derived conditions, with an unfused metatarsus representing the primitive condition. If bovids and cervids were derived from a common ancestor with a fused metatarsus, it would imply that a closed gully was derived from an open one (or vice versa) in evolution. Detailed examination of the ontogeny of fusion in the two groups might help to clarify the situation. Unfortunately, complete series of young individuals of bovid species with a pronounced gully were not available for us to examine. However, by combining specimens of three species, *Alcelaphus buselaphus* (the kongoni), *Antilope cervicapra* (the blackbuck), and *Aepyceros melampus* (the impala), in which the morphology of the adult gully is similar, we have been able to describe the process at least in part. In the youngest specimens available to us the distal ends of the diaphyses are just fusing distal to the nutrient foramen. There are no ridges along the sides of the groove on either the diaphysis or the epiphyses (which are not yet fused at this stage). In older specimens there is a distinct ridge on either side of the groove, and these ridges are continued on the epiphyses, even before they fuse. However, the edges of these raised areas do not project towards the midline as they do in cervids, and they appear later, after fusion of the distal ends of the diaphysis around the nutrient foramen (see fig. 8). This suggests that in bovids the raised edges along the gully are not remnants of the cervid type of shelf, but that they form independently, perhaps as attachment for a connective tissue covering for the blood vessels and nerve passing along the groove. However, it is difficult to judge how significant the differences in the relationship of the artery and nerve to the fusing metapodials are, and we do not consider it to be conclusive proof of either homology or nonhomology of fusion. The situation in bovids differs from the admittedly more limited diversity of

morphologies of the metatarsus in fossil and living giraffid species, where the metatarsals are somewhat laterally flattened, and the gully is shallow with low ridges. However, the giraffoid *Canthumeryx* has a deeper metatarsal gully, more reminiscent of tragelephine bovids, as seen in an unnumbered Nairobi Museum specimen from Moruorot.

Based on the evidence available at present, we can only state that an open gully appears to be the primitive condition for ruminants, since this is the condition in *Gelocus*. If this is true, then an open gully must have given rise to the closed cervid type. However, we know of no metatarsals among primitive ruminants which have an open gully, but have ridges which may give rise to a closed one. Neither is there fossil evidence of any intermediate type. No ridges form along the groove in *Gelocus*, and it is difficult to see how a *Gelocus*-like metatarsal would give rise to a cervidlike one. Further work will have to be done on the postcrania of primitive ruminants before this issue can be resolved. However, it is clear that a closed gully can give rise to an open one within a population, indicating that a mechanism does exist for this shift, and that this possibility must be considered in assessing relationships.

Presence of a closed cervid type gully appears to be a good derived character, although the possibility of independent acquisitions cannot be entirely ruled out. This type of gully is seen in all living and fossil cervids, *Palaeomeryx*, *Amphitragulus*, *Dremotherium*, *Moschus*, *Walangania*, *Eumeryx*, *Prodremotherium*, dromomerycids, antilocaprine, and *Hoplitomeryx*, and is present but variable in merycodontines and blastomerycines (see table 6). We will continue to regard the presence of an open gully as a retained primitive condition at this time, although the open gully may prove to be secondary in some groups. An open gully is present in all bovids and giraffoids, *Gelocus*, *Lepotomeryx*, *Bachitherium*, and *Propalaeoryx* (see table 6).

Condition of Digits I, II, and V

The primitive condition for ruminants is the presence of five complete digits in the forelimb and four complete digits (II–V) in the hind limb, a condition known only in

Hypertragulus and perhaps also in *Archaeomeryx* (Webb and Taylor, 1980). In primitive ruminants metatarsal I is already reduced and present as a proximal remnant which articulates with the posterior diarthrodial facet. The presence of this facet thus indicates that a metatarsal I rudiment is present. In more advanced ruminants, digits III and IV have fused to form a cannon bone and digits II and V are reduced so that only proximal remnants of the metatarsals and distal remnants of the phalanges remain.

This loss of the lateral digits is commonly referred to as the "loss of the side toes" (character 29c). Among living pecorans, the side toes are completely lost (with the exceptions of proximal remnants that fuse with the cannon bone) in the Bovidae, Antilocapridae, and Giraffidae, while proximal or distal remnants of the side toes are variously present among taxa in the Cervidae and Moschidae. In certain fossil cervids complete, though reduced, lateral digits were retained. As noted in the historical review section, this feature has been accorded taxonomic significance in ruminant phylogeny, but the reduction or loss of the side toes has occurred in parallel many times within the Artiodactyla (e.g., in the Camelidae, Tayassuidae, Entelodontidae, and Xiphodontidae). The common evolutionary pattern is for the hind limb to be more progressive than the forelimb in the development of this feature. For example, in dromomerycids and in the early merycodontines, such as *Paracosoryx*, the side toes have been lost in the hind limb, but complete reduced side toes or distal remnants are retained in the forelimb (Frick, 1937).

The configuration of the proximal remnants of the metatarsals can provide some information of taxonomic importance (character 30). The remnants are initially present but not fused to the cannon bone, and they fit into distinct notches on the proximal surface of the metatarsal. The presence of a notch on either the medial or lateral side of the cannon bone indicates the presence of an unfused proximal remnant II or V, respectively. These remnants fuse with the cannon bone independently, so that only one or the other may be present. After fusion, the remnant may form a distinct tubercle, as was pointed out by Heintz (1963, 1970) (see fig. 7).

The characteristics of digits II and V can provide some information of taxonomic value, but it must be recognized that the fusions can, and probably have, occurred independently. However, since a fused remnant presumably does not secondarily become free, it can be assumed that genera without fusion of metapodials II and V represent the primitive condition. The presence or absence of a distinct tubercle has been used by Heintz (1963, 1970) to distinguish *Eotragus* from *Dicrocerus*. Although a distinct tubercle for II characterizes *Eotragus*, the character is not consistent through the Bovidae; neither is the presence of a tubercle for V consistent for the Cervidae. The presence of a tubercle may be suggestive, but it is clearly not a reliable character. (See table 6.)

Posterior Tuberosity (character 31)

Another character used by Heintz (1963, 1970) to distinguish cervids from bovids is the presence of a posterior tuberosity, a raised eminence on the lateral side of the posterior surface of the metatarsal, visible when the bone is viewed from the proximal end, as well as when viewed in posterior aspect (fig. 7). This character is uniformly present in the cervids we have examined and is absent in bovids (except *Neotragus batesi*, Bate's antelope). It is uniformly absent in all giraffoids and antilocaprids, and absent in *Walangania* and *Propalaeoryx*. The character is somewhat problematical for two reasons. First, it is sometimes difficult to distinguish between no tuberosity and a slight one of the type that would be expected in the early evolution of this character. Additionally, in genera in which we would characterize the posterior tuberosity as "none" or "slight," there is also usually some individual variation. This appears to be the case in *Amphitragulus*, *Palaeomeryx*, and some dromomerycids. Second, the character appears to have arisen independently in dromomerycids, although interpretation is difficult because the character is both variable and only slightly developed in some genera. However, as the character is slight or absent in the early dromomerycids *Barbouromeryx* and *Sinclairiomeryx*, seems to be invariably absent in *Al-etomeryx*, but is most marked in the later

Tertiary cranioceratines, we conclude that it might have been developed independently in this group. In addition to living cervids, a well-developed posterior tuberosity is found in *Micromeryx*, *Moschus*, and *Parablastomeryx*, but not in other blastomerycines. (See table 6.) Although the presence of the tuberosity in *Neotragus* indicates that it can evolve independently, its development in this genus may be associated with secondary size reduction. In this genus both lateral and medial edges of the posterior surface are expanded, and this condition may have developed secondarily to provide additional area for insertion of the flexor muscles.

Posterior Cubonavicular Face (character 32)

Heintz (1963, 1970) described differences in the shape of the posterior cubonavicular facet which he found to be useful in distinguishing *Dicrocerus* from *Eotragus*. In *Dicrocerus* this facet is rectangular, long, and narrow, while in *Eotragus* it is diamond-shaped, short, and broad (see fig. 7). Although these differences are sufficient to distinguish between *Eotragus* and *Dicrocerus*, as Heintz indicated, they are not consistent throughout the Bovidae and Cervidae. However, the morphology of the anterior edge of the facet does provide a taxonomically useful character. In cervids, the anterior edge of the facet forms a distinct lip where it meets the small cuneiform facet, while in bovids no distinct lip is formed (see fig. 7). In addition to cervids, this "raised lip" is found in dromomerycids, moschids, *Amphitragulus*, *Dremotherium*, *Walangania*, *Palaeomeryx*, *Hoplitomeryx*, and antilocaprids. However, the raised lip appears to be a primitive pecoran character, since a more prominent type of raised lip is seen in the gelocids *Prodremotherium* and *Eumeryx* (see fig. 7), and possibly also in *Gelocus*. It is also present in material assigned to the advanced traguloid *Bachitherium* from Marseilles (St. Andre), France (UBCL 8900), as well as in limb material assignable to *Lophiomeryx* from the Phosphorites du Quercy (UCBL 8900). Although the condition in cervoids is distinctive among higher ruminants, it clearly represents a modified retention of a primitive condition. Bovid s are more derived in that

the cubonavicular facet is more flat, but among living bovids this condition is somewhat variable, and it is more cervidlike in certain genera (e.g., *Tragelaphus*). The Giraffoidea have a truly derived condition with respect to this character. In living giraffids the facet is extremely flat and elongated; we have also observed this character in every fossil giraffoid we have examined, including the primitive *Canthumeryx* (BMNH 30179, from Moruorot). A raised lip of the posterior cubonavicular facet is thus suggestive of cervoid status, but cannot be treated as a diagnostic character since it represents a modified retention of the primitive ruminant condition. (See table 6.)

FEATURES OF THE SOFT ANATOMY

All living ruminants are characterized by an enlarged, subdivided stomach, with a rumen forming the initial chamber (character 33). The primary enlargement of a rumen area appears to be shared with living camelids, but the subsequent development of the enlarged stomach appears to be independent (Langer, 1974). Living tragulids have a small rumen, a reticulum, and an abomasum (the equivalent of the true stomach in other mammals, serving as the site of protein degradation). Living pecorans have an enlarged rumen, and an additional chamber, the omasum, inserted between the reticulum and the abomasum. We follow Webb and Taylor (1980) in assuming a three-chambered stomach with a small rumen to be typical of the Tragulina and a four-chambered stomach with a larger rumen and an omasum to be typical of the Pecora.

The giraffe (*Giraffa camelopardalis*) has some features of stomach anatomy which differ from the condition in bovids and cervids (the okapi has not been investigated), notably the cranially positioned entrance of the esophagus to the rumen (Hofmann, 1973). Judging from the diagrams in Langer (1974), this appears to represent the primitive condition for the Artiodactyla. Further work is needed on this character, especially a more detailed examination of the relative position of the esophagus in the okapi and the Tragulidae. The condition in the giraffe may represent a secondarily derived state in associ-

TABLE 6
Distribution of Postcranial Characters in Ruminant Genera

	Complete distal metapodial keels	Fusion of metapodials	Posterior tuberosity	Posterior cubonavicular facet	Fusion of lateral metapodials
TRAGULINA					
<i>Hypertragulus</i>	No	Unfused	Absent	Raised, pointed	No
<i>Tragulus</i>	No	Unfused/fused w. closed gully	Absent	Raised, pointed	No
<i>Leptomeryx</i>	No	Fused w. open gully	Absent	Raised, pointed	Both
<i>Bachitherium</i>	No	Fused w. open gully	Absent	Raised, pointed	II
<i>Lophiomeryx</i>	No	Unfused	Absent	Raised, pointed	?Both
"GELOCIDAE"					
<i>Gelocus</i>	No	Fused w. open gully	Absent	Raised, pointed	No
<i>Notomeryx/Gobiomeryx</i>	?	?	?	?	?
<i>Prodremotherium</i>	No	Fused w. closed gully	Absent	Raised, pointed	II
<i>Eumeryx</i>	No	Fused w. closed gully	Absent	Raised, pointed	No
<i>Rutitherium</i>	?	?	?	?	?
GIRAFFOIDEA					
<i>Propalaeoryx</i>	Yes	Fused w. open gully	Absent	Raised w. lip	II
<i>Climacoceras</i>	Yes	Fused w. open gully	Absent	Elongated, flat	II
<i>Canthumeryx/Zarafa</i>	Yes	Fused w. open gully	Absent	Elongated, flat	II
Giraffids	Yes	Fused w. open gully	Absent	Elongated, flat	Both
BOVIDAE					
<i>Eotragus</i>	Yes	Fused w. open gully	Absent	Fairly flat,	Both
Other bovids	Yes	Fused w. open gully	Absent	no distinct lip	Both
MOSCHINA					
<i>Walangania</i>	Yes	Fused w. closed gully	Absent	Raised with lip	II
<i>Dremotherium</i>	Yes	Fused w. closed gully	Absent	Raised with lip	Both
<i>Blastomeryx</i>	Yes	Fused, closed or open gully	Absent	Raised with lip	Both
<i>Parablastomeryx</i>	Yes	Fused w. closed gully	Present	Raised with lip	Both
<i>Moschus</i>	Yes	Fused w. closed gully	Present	Raised with lip	Both
<i>Micromeryx</i>	Yes	Fused w. closed gully	Present	Raised with lip	Both
ANTILOCAPRIDAE					
<i>Paracosoryx</i>	Yes	Fused, open or closed gully	Absent	Raised with lip	II
Other merycodontines	Yes	Fused, open or closed gully	Absent	Raised with lip	Both
Antilocaprine	Yes	Fused w. closed gully	Absent	Raised with lip	Both
PALAEOMERYCIDAE					
<i>Prolibytherium</i>	Yes	?Fused w. open gully	?	?	?
<i>Amphitragulus</i>	Yes	Fused w. closed gully	Absent or small	Raised with lip	II
<i>Palaeomeryx</i>	Yes	Fused w. closed gully	Variably present	Raised with lip	Both
<i>Barbouromeryx</i>	Yes	Fused w. closed gully	Absent or small	Raised with lip	II
<i>Aletomeryx</i>	Yes	Fused w. closed gully	Absent	Raised with lip	II
Other dromomerycids	Yes	Fused w. closed gully	Variably present	Raised with lip	II or both
HOPLITOMERYCIDAE					
<i>Hoplitomeryx</i>	Yes	Fused w. closed gully	Present	Raised with lip	Both
<i>Amphimoschus</i>	?	?	?	?	?
CERVIDAE					
<i>Hydropotes</i>	Yes	Fused w. closed gully	Present	Raised with lip	Both
<i>Dicrocerus</i>	Yes	Fused w. closed gully	Present	Raised with lip	Both
Other cervids	Yes	Fused w. closed gully	Present	Raised with lip	Both

ation with the high, narrow thorax and the elongated neck. However, the possibility remains that a more ventral displacement of the esophageal entrance to the rumen is a derived feature within the Ruminantia, linking together the Bovidae and the Cervidae (the condition in *Antilocapra* is not known).

Cervids have been noted to have a number of features of soft anatomy which are specialized over the general pecoran condition. These are: the absence of a gall bladder (Flower, 1875); the possession of a placenta with few cotyledons (as opposed to many cotyledons as is typical of other pecorans) (Brooke, 1878); the absence of an ileocecal gland; and $2\frac{1}{2}$ (as opposed to $3\frac{1}{2}$) colic coils (Garrod, 1877) (character suite 34). These specialized features are shared by *Hydropotes* (Forbes, 1882; Garrod, 1877), clearly indicating that this genus belongs in the Cervidae.

DEFINING CHARACTERS OF LIVING PECORAN FAMILIES

As previously discussed, cranial appendages have obviously evolved independently within the higher ruminant families. It then follows that the horned ruminants cannot be assumed to have a single common ancestor, and other characters should be found to identify the sister taxa of the horned families among the hornless ruminants. In this section, we will review the characters that have been used to identify living and fossil pecoran families.

BOVIDAE

Bovids are undoubtedly the most successful ruminant family today, in terms of morphological and ecological diversity, and many genera possess the derived characters of hypsodont cheek teeth (character 12b) and elongated limbs with loss of the lateral digits (character 29d). Consequently, it tends to be assumed that bovids are "advanced" pecorans but, as previously discussed, such "advanced" features characterize many open habitat ungulates. Bovid genera can be united by their type of cranial appendages, or horns (character 7b). However, as far as we can determine, no other morphological feature uniquely characterizes the Bovidae. *Eotragus*, the earliest known bovid, was identified by the presence of postorbital horn cores. Ginsburg and Heintz (1968) identify *Eotra-*

gus from Artenay (Burdigalian of France) on the basis of dental remains, but assign it to the Bovidae primarily on the basis of the absence of cervoid characters (e.g., lack of a *Palaeomeryx* fold) (character 20) and on general appearance (molars somewhat higher-crowned and longer relative to the width than seen in the contemporary cervoid genus of similar size, *Amphitragulus*), rather than on any uniquely defined "bovid" autapomorphy.

Bovid limbs, too, show little in the way of uniquely characterizing specializations. Heintz (1963, 1970) describes a number of features that may be used to distinguish bovid from cervid limbs in a Pleistocene assemblage, but our examination of these character states in a range of living and fossil ruminants shows that, while many of the defining cervid characters represent an autapomorphic condition for the family, the bovid characters are mainly plesiomorphic characters of the Pecora. A possible derived feature of the bovids is the presence of a fused metatarsal with an open gully (character 28a). However, as previously discussed, this condition may represent the plesiomorphic condition for the Eupecora, and is also shared with the Giraffoidea.

The upper molars of relatively brachydont bovids (such as the first bovid genus *Eotragus*) can be distinguished from the giraffids by the presence of an entostyle, but this feature also characterizes brachydont cervoids. The auditory bulla of many bovid genera is distinctive, with the attachment of the styloid process toward the anterior edge, in contrast to the more posterior positioning in the cervids. However, many living bovid species (e.g., many species of the genus *Cephalophus*) lack any expansion of the auditory bulla, and so this character cannot be taken as diagnostic of the family.

In summary, it appears that no apomorphic characters, apart from the presence of horn cores, can be used to characterize the Bovidae, and on the basis of our presently available evidence, it is impossible to recognize a hornless bovid ancestor with any degree of certainty.

GIRAFFIDAE

The Giraffoidea was defined by Hamilton (1978a) to include all ruminants possessing

a bilobed lower canine (character 23). This comprises the Miocene East African genera *Climacoceras*, *Nyanzamerx*, and *Canthumerx*, probably also the genus *Injanatherium* from Iraq (Heintz et al., 1981), assigned to the family Climacoceridae, and the true giraffid genera, of which *Palaeotragus* is the earliest known and most primitive. Hamilton also included the Miocene European *Triceromeryx* in the Giraffoidea, but not in the Giraffidae, on the basis of p4 morphology (characters 24 and 25) alone, as the anterior dentition is unknown. However the use of premolar morphology to assign ruminants without question to the Giraffoidea has been refuted (Janis and Lister, 1985).

As previously discussed, living and fossil giraffids possess distinctive cranial appendages or ossicones (character 7a) but it seems unlikely that these are homologous with the cranial appendages of the giraffoids *Climacoceras* and *Nyanzamerx*. Other giraffoids, such as *Zarafa* and *Injanatherium*, genera which may both be synonymous with the genus *Canthumerx*, known only from dental remains (Hamilton, 1978a; Heintz et al., 1981), have cranial appendages which are peculiar in their dorsolateral orientation, but which present no evidence as to their mode of formation. Within the Giraffidae, the cranial appendages of the Sivatherinae may not be homologous with the ossicones of the other giraffids. In addition, all giraffoids possess the derived condition of a very flat and elongated posterior cubonaviclar facet on the proximal metatarsus (character 32b). All giraffoids possess an open type of metatarsal gully (character 28a).

In summary, the Giraffoidea can be characterized by the presence of a bilobed lower canine and the form of the proximal and distal metatarsus; the Giraffidae can be identified within this group by two features of their p4 morphology, although these are not unique features within the Pecora. The type of ossicone found in living giraffids is probably an autapomorphic character for the Giraffidae, with the possible exception of the Sivatherinae, but cranial appendages evidently arose more than once within the superfamily.

CERVIDAE

The Cervidae were diagnosed by Brooke (1878) as follows: two lacrimal orifices, on or

outside the orbital rim (character 9); lacrimal fossae (character 8); antorbital or ethmoidal vacuity, cutting off the lacrimal from articulation with the nasals; first molar brachydont; the parietosquamosal suture nearer the upper than lower border of the temporal fossa; placenta with few cotyledons (character 34). Flower (1875) noted the absence of a gall bladder (character 34), and Heintz (1963) noted the presence of a closed metatarsal gully (character 28b). Living cervids, with the exception of *Hydropotes*, are characterized by the presence of antlers (character 7d). Living cervids, including *Hydropotes*, also possess a lacrimal depression or fossa and an antorbital vacuity, although, as previously discussed, these characters are not unique to cervids or cervoids.

While these features, excluding the possession of antlers, typify living cervids (defined to include *Hydropotes* but to exclude *Moschus*), none of them is a unique defining character of the group that would clearly distinguish them from fossil "cervoids." The dromomerycids (Scott and Janis, 1987) and the antilocaprine (Leinders and Heintz, 1980) share the characteristics of the "cervoid" type double lacrimal orifices and the antorbital vacuity. The earliest antlered cervids, such as *Dicrocetus* and *Procervulus*, possess a protocone with a posterior bifurcation (character 19a) but this is also seen in *Amphimoschus* (Leinders, 1983). Living cervids possess a posterior tuberosity on the metatarsal (character 31) and a distinct raised lip on the posterior cubonaviclar facet (character 32d), and lack a posterior diarthrodial facet (the facet for the articulation of the remnant of metatarsal I, character 30c; see fig. 7). However, the first two features are also seen in a number of fossil cervoids, such as *Palaeomeryx* and the dromomerycids. The latter feature, along with a number of the cervid limb characters described by Heintz (1963, 1970), may be characteristic of Recent and Pleistocene antlered cervids, but have obviously evolved within the family, and these features do not necessarily characterize the limbs of Tertiary antlered cervids.

Most of the cervid characters can be used to unite a number of fossil genera with living cervids in a superfamily Cervoidea (see Scott and Janis, 1987). However, the presence of deciduous antlers is the only feature which can define a true cervid in the fossil record,

leaving the relative position of *Hydropotes* in some confusion with regard to fossil cervoids (see Leinders, 1983). At this level the presence of the lacrimal fossa may serve to unite it with antlered cervids, despite the parallel evolution of the lacrimal fossa within the other pecoran genera. As previously mentioned, *Hydropotes* is clearly allied with the Cervidae by features of its soft anatomy, but such features may also have characterized fossil cervoids above the level of *Moschus* or *Antilocapra*.

MOSCHIDAE

This family is represented today by a single genus, *Moschus* (musk deer). *Moschus* possesses a closed metatarsal gully (character 28b), a posterior tuberosity on the metatarsal (character 31), and a raised lip on the posterior cubonavicular facet (character 32d), but has only a single lacrimal orifice. It lacks any form of cranial appendage, possesses large sabrelike canines (character 11b), and retains the gall bladder. Leinders (1979) and Leinders and Heintz (1980) consider that the presence of a closed metatarsal gully indicates that *Moschus* should be placed in the Cervoidea, but that the single lacrimal orifice excludes it from the Cervidae.

Webb and Taylor (1980) expanded the Moschidae to include other small hornless genera with sabrelike canines. These are the North American blastomerycines (*Parablastomeryx*, *Blastomeryx*, *Problastomeryx*, *Pseudoblastomeryx*, *Longirostromeryx*, and *Machaeromeryx*) and the European genera *Amphitragulus* and *Dremotherium*. They cite the laterally enclosed, subcentral tympanohyal on the auditory bulla as the autapomorphous condition which unites the family (character 10). However, while this feature appears to be shared by *Moschus* and the blastomerycines and probably to a lesser extent by *Dremotherium*, the auditory bulla of *Amphitragulus* is more like a primitive cervoid, with a posteriorly positioned tympanohyal vagina with little enclosure (Webb, personal commun.). The sabrelike canines cannot be used to unite these genera into a single clade, for, as already discussed, this is a primitive cervoid feature, although it may be used to identify cervoids of moschid or higher status. Webb and Taylor (1980) mention a number of features of the basicranium

of *Moschus* that they consider make it on the one hand more advanced than *Gelocus* (such as a large supraorbital fissure and the loss of the promontory artery, part of character suite 6), and on the other hand more primitive than the horned ruminants (such as the retention of a subarcuate fossa on the endocranial side of the petrosal and the retention of a median branch of the carotid artery; that is, lacking the rest of character suite 6). However, as they base their conclusions on a comparison of *Moschus* with *Bos* and *Ovis*, further work needs to be done to elucidate whether those features are common to all of the Eupecora (sensu Webb and Taylor, 1980) or are merely autapomorphic of the Bovidae. We follow Leinders and Heintz (1980) in considering the Moschidae to belong to the superfamily Cervoidea.

ANTILOCAPRIDAE

The family Antilocapridae consists of two subfamilies, the Miocene Merycodontinae and the Miocene to Recent Antilocaprinae. As previously discussed, both possess supraorbital cranial appendages, but these appendages differ considerably in morphology, and may not be homologous. Antilocaprids traditionally have been allied with the Bovidae, especially by authors familiar with living species only, on the basis of the horn cores and the keratinous coverings (e.g., O'Gara and Matson, 1975), and the hypsodont cheek teeth and the loss of the side toes (e.g., Matthew, 1904; Pilgrim, 1941). But, as previously discussed, none of these features can serve as synapomorphies to unite the Antilocapridae with the Bovidae. O'Gara and Matson (1975) also link antilocaprids with bovids based on the presence of a gall bladder and the supposedly single lacrimal orifice. However, these characters are plesiomorphic for ruminants, and the lacrimal orifice (character 9) is in fact double in most specimens of *Antilocapra*. Leinders and Heintz (1980) use this character and the closed metatarsal gully (character 28b) typical of all antilocaprids to classify antilocaprids in the superfamily Cervoidea. We agree with this placement, but the phylogenetic position of the Antilocapridae within the Cervoidea is still problematical. No unique features can be found to define the Antilocapridae (other than the biogeographic feature of only occurring in

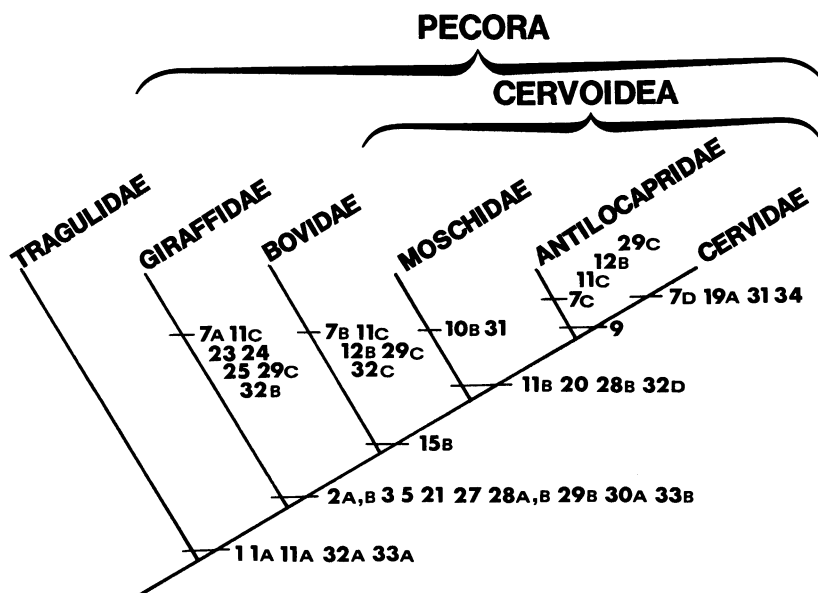


Fig. 9. Cladogram of living pecoran families. See table 1 for key to characters.

North America!). Similarly, no unique features can be found to link the merycodontines with the antilocaprids.

Fossil antilocaprids appear to have had a double lacrimal orifice, although this detail is often difficult to ascertain in fossil specimens, as the orbital rim is frequently broken, and the orbit itself usually filled with matrix. However, in the collections of the American Museum of Natural History we have observed probable double lacrimal orifices in the following specimens:

Antilocaprids: "*Plioceros*" *dehlini* (AMNH: AINS 793; Pros. 500.40), "*Plioceros*" *texanus* (F:AM 52089), and *Stockoceros onusrosagris* (F:AM 42250).

Merycodontines: *Paracosoryx wilsoni* (F:AM 31191), *Meryceros joraki* (F:AM 31163), and *Cosoryx furcatus* (F:AM 32902 and 51025).

The condition appears to be variable in merycodontines, as in the living genus *Antilocapra*, as only a single orifice is apparent in a specimen of *Paracosoryx wilsoni* (F:AM 32899-A). Both subfamilies have a closed metatarsal gully as the primitive condition, but this character state is variable in most merycodontine genera. Antilocaprids are somewhat more "advanced" than meryco-

dontines in the complete loss of the side toes in all genera, and in the larger body size of most genera, but these features can hardly be used as antilocaprine autapomorphies. We will return to a discussion of the phylogenetic position of the Antilocapridae in the light of other cervoid characters in a later section.

PHYLOGENETIC RELATIONSHIPS OF LIVING PECORAN FAMILIES

With regard to the distribution of character states among the living pecoran families and following our review of the differences in development of the cranial appendages, taking the position that these appendages have been evolved independently within each of the living families, we would construct a cladogram of the living pecoran families as follows (see fig. 9).

The Pecora can be united within the Ruminantia by the following features: a compact, parallel-sided astragalus (character 5); elongated, fused metapodials with an open metatarsal gully (character 28a) and complete distal metapodial keels (character 27); a four-chambered stomach with an omasum (character 33b); and a suite of derived molar characters such as a lingually situated protocone on P3 (character 14b), a large M3 metaconule

(character 16a), the reduction or absence of an internal cingulum on the upper molars (characters 13b, c), metastylids on the lower molars (character 21), and the postenterocristid usually complete (character 22b).

The Giraffidae can be characterized by the presence of a bilobed lower canine (character 23), a flat cubonavicular facet on the proximal metatarsus (character 32b), and ossicones which preform in cartilage (character 7a). Other pecoran families are united by the presence of an entostyle in the upper molars (in brachydont forms only), derived from the anterior face of the metaconule (character 15), and may also be united by the more ventral entrance of the esophagus to the rumen (see discussion in Characters section).

The Bovidae are characterized by the possession of horns with a nondeciduous keratin sheath (character 7b). No other morphological features can be found to uniquely define this family. Other pecoran families can be united into the Cervoidea by the possession of the following characters: a closed metatarsal gully (character 28b); a sabrelike upper canine in forms lacking cranial appendages (character 11b); a raised lip to the cubonavicular facet on the proximal metatarsus (character 32d); and the presence of a *Palaeomeryx* fold in brachydont members of the lineages (character 20). (This latter feature is assumed in the case of the Antilocapridae, as all known fossil taxa are highly hypsodont.)

The Moschidae are distinguished by the presence of a laterally enclosed, subcentral tympanohyal vagina (character 10), and have developed a posterior tuberosity on the metatarsus (character 31) in parallel with the Cervidae. The Cervidae and Antilocapridae can be united by the possession of a double lacrimal orifice on the orbital rim (character 9). Antilocaprids can be characterized only by the unique form of their cranial appendages, with a deciduous keratin sheath covering a bony horn core in the living species, *Antilocapra americana*. This bony horn core, while unbranched in *Antilocapra* (although the deciduous keratin sheath is forked in this species), had a propensity for branching in fossil taxa (character 7c). The Cervidae are characterized by the possession of a posterior tuberosity on the metatarsus (character 31),

the bifurcation of the posterior wing of the protocone in primitive forms (character 19a), and the absence of the gall bladder (along with other features of soft anatomy discussed previously, character 34). Cervids above the level of *Hydropotes* are characterized by the possession of antlers (character 7d).

Figure 9 summarizes this information in a cladogram of the living pecoran families.

A consideration of the distribution of character states among fossil pecorans does not alter this scheme of the interrelationships of the living families, but does result in the addition of information to the cladogram, supporting the use of these particular characters at the nodes, in some cases, and refuting the nodal position of certain characters in others. In particular, the suggestion that the posterior tuberosity of the metatarsal evolved in parallel within the Cervoidea is confirmed. The position of the Giraffidae is also in accordance the conclusion reached by Todd (1975) on the basis of chromosomal studies of the Ruminantia, who claimed that the Giraffidae represented the most primitive pecoran family in the absence of an X-autosome translocation fusion (seen also in the Tragulidae, but not in other pecorans). However, despite the concurrence of Todd's conclusion with our own, based on morphological characters, we reserve doubts about the validity of this chromosomal character as a true synapomorphy of all living pecorans above the level of the Giraffidae (see discussion in Scott and Janis, 1987).

DEFINING CHARACTERS OF FOSSIL FAMILIES

GELOCIDAE

Pecorans of the gelocid grade comprise the following Oligocene genera: *Gelocus* [Europe and possibly Africa (see Hamilton, 1973)]; *Notomeryx* [Asia (see Savage et al., ms)]; *Gobiomeryx* [Asia (see Sudre, 1984)]; *Prodremotherium* (Europe); *Eumeryx* (Asia); and *Rutitherium* [Europe (see Sudre, 1984)].

Many authors consider the Gelocidae to be the basal group of higher ruminants, although of traguloid status (e.g., Simpson, 1945; Viret, 1961; Romer, 1966). Webb and Taylor (1980) transferred this group to the Pecora on the basis of a number of advanced basi-

cranial features (character 6) and the possession of a compact, parallel-sided astragalus (character 5). They consider that the gelocids form the sister group to the other pecorans, and that they are united into a distinct clade by the presence of a narrow-waisted, backwardly situated protocone on P3 (character 14a). Janis (1987) has argued that this character cannot be used to unite the family, as it is also present in the traguloid genera *Lophiomeryx* and *Bachitherium*, and suggests that the gelocids are better considered a primitive grade of pecorans.

Gelocids are further characterized by the following features: the apparent absence of cranial appendages; moderately large, but not sabrelike canines (character 11a); brachyodont cheek teeth (character 12a); the presence of a small premolariform p1 separated from p2 by a small diastema (character 4b); lower premolars in which the metaconid is small, and does not extend backwards to form a posterolingual wall to the tooth (character 3; see fig. 6); lower molars which possess an anterior cingulum (character 2b) and an ectostylid (part of character suite 1a, see fig. 6), and in which the postentocristid is usually incomplete (character 22b); metastyles on the upper molars (character 16a) and the absence of a distinct entostyle; a small metaconule on M3 (character 18a); the presence of a lingual cingulum on the upper molars (character 13a); and fused, somewhat elongated metatarsals (character 28d), with the absence of complete distal keels. However, all of these features represent characters which are either primitive for the Pecora or primitive retentions of conditions seen in various traguloid genera, and none can be considered to uniquely characterize the "Gelocidae" (see Janis, 1987). *Gelocus* is apparently the most primitive genus, as it lacks metastylids in the lower molars that are characteristic of all other Pecora (character 21). *Prodremotherium* and *Eumeryx* possess the derived cervoid feature of a closed metatarsal gully (character 28b) and also possess an incipient entostyle (character 15a). *Eumeryx* and *Rutitherium* possess the derived feature of a *Palaeomeryx* fold (character 20). The condition of the metatarsals in *Rutitherium* is unknown. In our opinion, the Gelocidae as presently considered is a

polyphyletic group composed of taxa of various phylogenetic affinities within the Pecora.

PALAEOMERYCIDAE AND LAGOMERYCIDAE

The Palaeomerycidae were originally defined by Lydekker (1883) in his description of *Propalaeomeryx sivalensis*, taking the name of the family from *Palaeomeryx* Von Meyer, 1834. Roger (1904) established the genus *Lagomeryx* to include small species of "*Palaeomeryx*" with branched cranial appendages. Zittel (1925) and Colbert (1936) originally considered *Lagomeryx* to be a cervoid belonging to the subfamily Cervulinae (=Muntiacinae). Roman and Viret (1934) later suggested that the two genera were synonymous. Genera added to this family later in the 1900s included *Palaeomeryx*, *Blastomeryx*, *Dremotherium*, *Dicrocercus*, and *Micromeryx*. Teilhard de Chardin (1939) suggested the formation of a separate family to include *Lagomeryx* and *Procervulus*, and Pilgrim (1941) proposed the name Lagomerycidae as a family to include *Lagomeryx*, *Procervulus*, and *Climacoceras*. (The latter genus was previously assigned to the Cervidae by MacInness, 1936.) Both Teilhard de Chardin and Pilgrim considered the Lagomerycidae and the Palaeomerycidae to have giraffoid affinities. However, Stirton (1944) included the North American dromomerycids in the family Palaeomerycidae as the subfamily Dromomerycinae and added the Old World genera *Lagomeryx*, *Procervulus*, *Climacoceras*, *Amphitragulus*, and *Dremotherium* to the subfamily Palaeomerycinae. He considered the palaeomerycids to form the basal pecoran "cervoid" group from which the moschids, cervids, and giraffids were derived. On the other hand, Simpson (1945) placed the Palaeomerycinae as a subfamily of the Cervidae, including *Palaeomeryx*, *Amphitragulus*, *Dremotherium*, *Eumeryx*, and the North American blastomerycine genera; he considered the genera *Lagomeryx*, *Procervulus*, and *Climacoceras* to belong to the family Lagomerycidae within the Giraffoidea (see Hamilton, 1978b; Scott and Janis, 1987).

Whitworth (1958) supported Stirton's contention that *Palaeomeryx* and *Lagomeryx*

were synonymous, and considered the family Palaeomerycidae to be closely related to the Cervidae. Ginsburg and Heintz (1966) considered *Palaeomeryx* to be a separate genus from *Lagomeryx*, and restated the giraffoid affinities of *Palaeomeryx* on the basis of a giraffidlike ossicone found in association with other material of the genus. Crusafont-Pairó (1952) placed the North American Blastomerycinae in the Palaeomerycidae, and the Dromomerycidae in the Giraffoidea. Ginsburg and Heintz (1966) removed the genera *Walangania* and *Heterocemas* from the genus *Palaeomeryx*, and suggested that those Oligocene genera which lacked cranial appendages (*Dremotherium*, *Amphitragulus*, and the blastomerycids) should be placed in the family Dremotheriidae. Hamilton (1973) proposed that a superfamily Dremotherioidea should be erected to include the New World Blastomerycidae and the Old World Dremotheriidae, refuting the affinity of the Mongolian genus *Eumeryx* with the blastomerycids that was suggested by Simpson (1945). Viret (1961) assigned *Eumeryx* to the Gelocidae, and the lagomerycid genera *Procerulus* and *Heterocemas* to the Cervidae.

Hamilton (1973) assigned the Palaeomerycidae to the Giraffoidea. He agreed with two of Whitworth's (1958) assertions that the features uniting *Palaeomeryx* with giraffids ("unequal development of anterior and posterior external ribs on the upper molars" and "characteristically corrugated enamel of the teeth") could well be primitive pecoran features seen in early giraffoids and cervoids alike. However, Hamilton did not support Whitworth's third statement that "the possession of non-deciduous, velvet-covered antlers . . . was as likely to be the primitive cervoid condition as the giraffoid" (Whitworth, 1958: 19). Hamilton instead supported the assertion of Ginsburg and Heintz (1966) that the "ossicones" of *Palaeomeryx* were a true synapomorphy shared with the Giraffidae. Hamilton (1973) saw the Oligocene Dremotheriidae giving rise to three different lineages: the Old World Giraffoidea (including the Palaeomerycidae and presumably also the Lagomerycidae), Cervoidea, and a New World lineage of the Blastomerycidae and the Dromomerycidae (he did not con-

sider the position of the Bovidae in this scheme).

Hamilton (1978b) later pointed out that the Palaeomerycidae as defined previously had no unifying characters. Most "paleomerycids" have a *Palaeomeryx* fold, as the nomenclature suggests but, as previously discussed, this has long been considered a primitive pecoran character. He removed *Climacoceras* to the Giraffoidea on the basis of the bilobed lower canine (character 23), and pointed out that the large species of *Palaeomeryx* found in Africa was in fact synonymous with the giraffoid *Canthumeryx*. The other "paleomerycid" described from Africa by Whitworth (1958), *Palaeomeryx africanus*, was synonymized by Hamilton (1973) with *Walangania gracilis*, which he tentatively assigned to the Bovidae. Hamilton suggested that all other genera ascribed to the Palaeomerycidae be treated as Pecora incertae sedis. Subsequently, Webb and Taylor (1980) assigned the blastomerycines, plus *Amphitragulus* and *Dremotherium*, to the Moschidae. Neither Hamilton nor Webb and Taylor attempted to deal with the North American dromomerycids in these considerations. In our review of cervid interrelationships (Scott and Janis, 1987) we suggested that the following genera should remain incertae sedis until further information is available: *Palaeomeryx*, *Lagomeryx*, *Procerulus*, *Prolibytherium*, *Propalaeoryx*, and *Triceromeryx*.

Since the 1978 paper by Hamilton the families Lagomerycidae and Palaeomerycidae have been more or less abandoned by current workers in the field of ruminant taxonomy (e.g., Leinders, 1983). However, new fossil finds have thrown further light on the identity of the problematical genera *Palaeomeryx* and *Lagomeryx*. A complete skull of *Lagomeryx* from the middle Miocene of China (Chow and Shih, 1978) shows a number of features suggestive of true cervid affinities. The genus possessed nondeciduous antlers, consisting of a long, supraorbital pedicle supporting a whorl of palmated tines at the tip; a lacrimal fossa; large, muntjaklike canines; and lower molars possessing a *Palaeomeryx* fold. They consider the skull to be very similar overall to the living cervids *Elaphodus* (the tufted deer) and

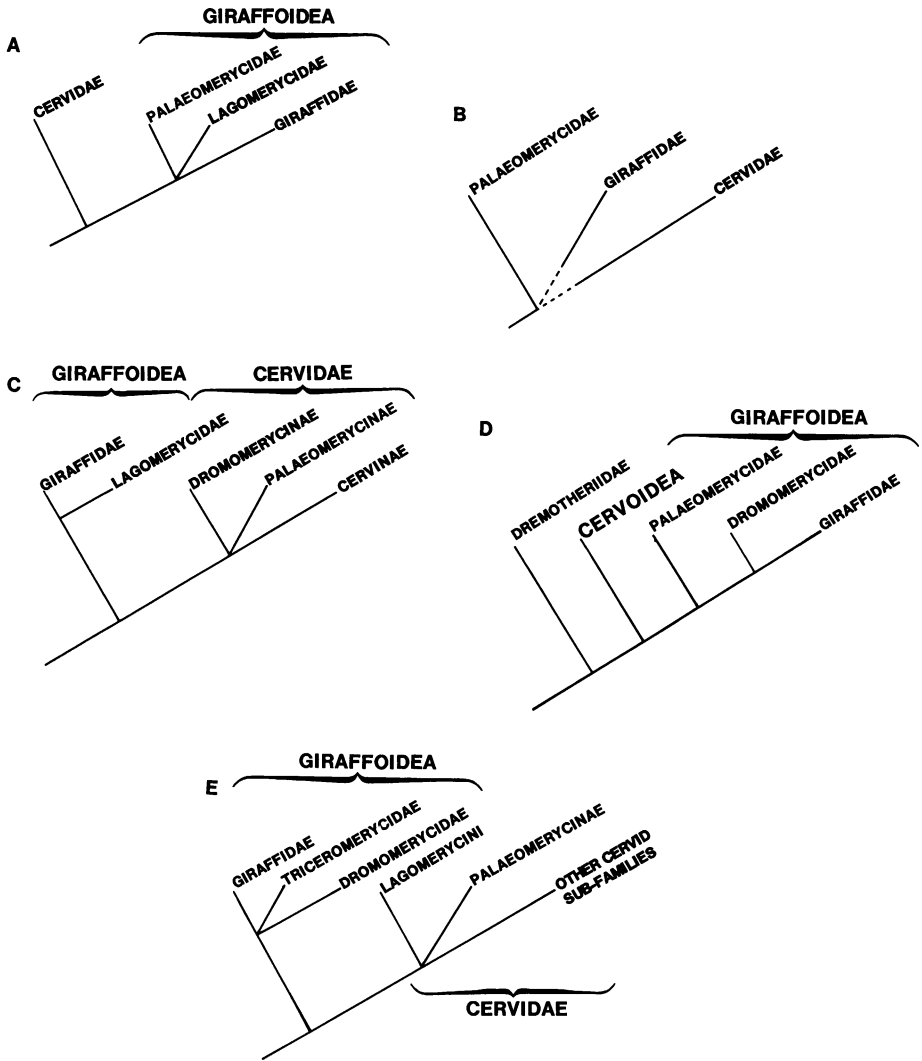
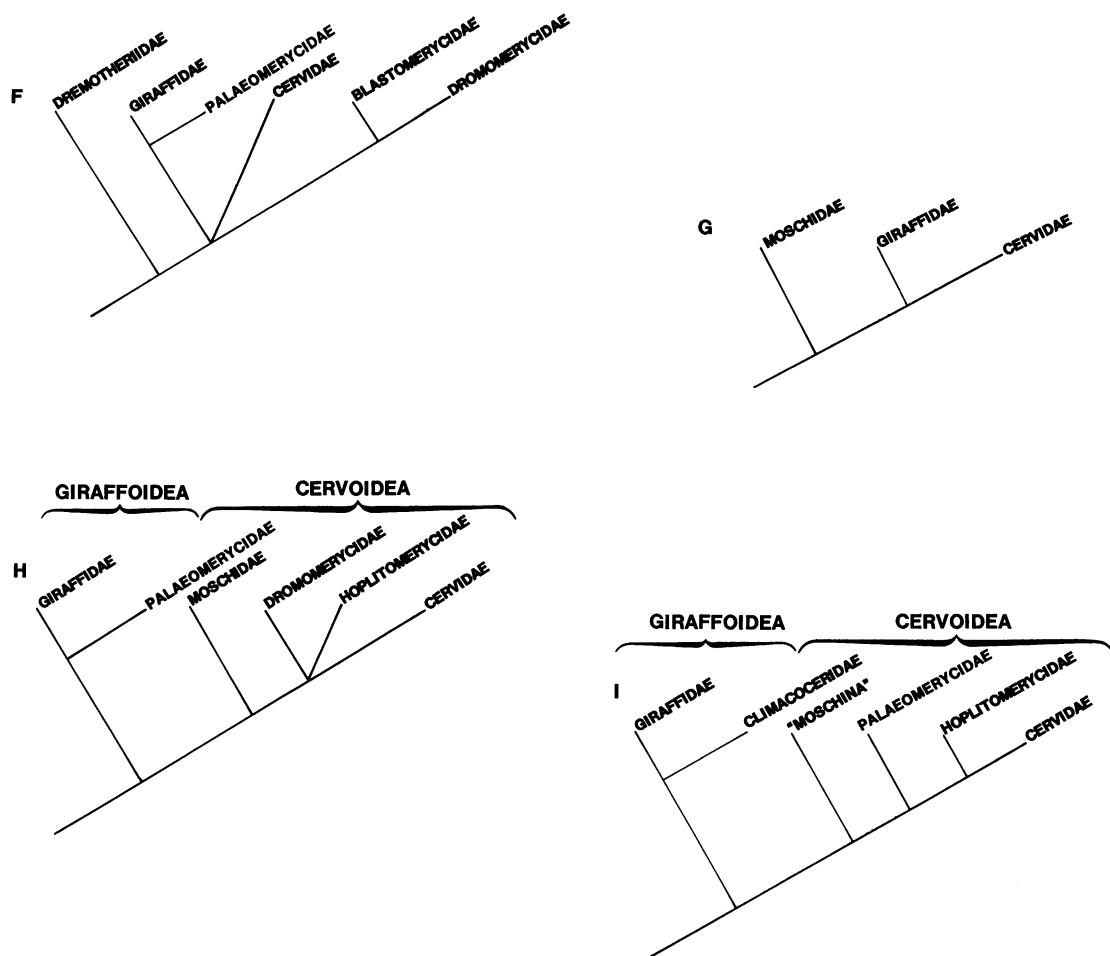


Fig. 10. History of ideas on phylogenetic position of fossil Eupecoran genera (sensu Webb and Taylor, 1980). (Position of Bovidae is excluded.) A. Composite diagram incorporating views of Teilhard de Chardin (1939) and Pilgrim (1941). "Lagomerycidae" includes the genera *Lagomeryx*, *Procervulus*, and *Climacoceras*. "Palaeomerycidae" includes the genera *Palaeomeryx*, *Blastomeryx*, *Dremotherium*, *Amphitragulus*, *Dicrocerus* (placed in Cervidae in all later schemes), and *Micromeryx*. B. View of Stirton (1944). "Palaeomerycidae" includes the divisions "Dromomerycini" (considered to be somewhat closer to the giraffids) and "Palaeomerycini" (considered to be somewhat closer to the cervids). "Dromomerycini" includes the dromomerycids and the blastomerycids. "Palaeomerycini" includes the genera *Palaeomeryx*, *Procervulus*, *Climacoceras*, *Dremotherium*, and *Amphitragulus*. C. Composite diagram incorporating the views of Simpson (1945) and Whitworth (1958). "Lagomerycidae" includes the genera *Lagomeryx*, *Procervulus*, and *Climacoceras*. "Palaeomerycinae" includes the taxa *Palaeomeryx*, *Amphitragulus*, *Dremotherium*, *Eumeryx* (considered to be a gelocid by other authors), *Walangania* (= *Palaeomeryx africanus*), and the blastomerycids. *Propalaeoryx* included in the Bovidae. D. Composite diagram incorporating the views of Ginsburg and Heintz (1966) and Crusafont (1952): "Dremotheriidae" includes the genera *Dremotherium* and *Amphitragulus*. "Palaeomerycinae" includes the blastomerycids. *Triceromeryx* is included in the Giraffidae. E. Composite diagram incorporating the views of Viret (1961) and Crusafont (1961): "Lagomerycinae" includes the genera *Lagomeryx*, *Procervulus*, and *Climacoceras*. "Palaeomerycinae" includes the Blastomerycini and the Palaeomerycini, the latter group containing the genera *Palaeomeryx*, *Amphitragulus*, and *Dremotherium*. The "other cervid subfamilies" include the



Muntiacinae, containing the extinct genera *Dicrocerus*, *Euprox*, *Heteroprox*, and *Stephanocemas*. F. View of Hamilton (1973). "Dremotheriidae" includes the genera *Dremotherium* and *Amphitragulus*. "Palaeomerycidae" includes the genera *Palaeomeryx*, *Zarafa*, *Climacoceras*, and *Propalaeoryx*. *Triceromeryx* and *Prolibytherium* are included in the Giraffidae. *Walangania* (= *Palaeomeryx africanus*) is included in the Bovidae. G. Composite diagram combining the views of Hamilton (1978b) and Webb and Taylor (1980). "Moschidae" includes the blastomerycids, the living genus *Moschus*, and the fossil genera *Amphitragulus* and *Dremotherium*. "Giraffidae" includes the fossil genera *Triceromeryx*, *Climacoceras*, and *Canthumeryx* (= *Zarafa*). *Walangania* is included in the Bovidae. Genera considered as incertae sedis are: *Palaeomeryx*, *Lagomeryx*, *Procervulus*, *Prolibytherium*, and *Propalaeoryx*. H. Current viewpoint, incorporating views of Leinders (1983), Qiu et al. (1985), and Chow and Shih (1978). "Palaeomerycidae" includes the genera *Palaeomeryx* and *Triceromeryx*. "Moschidae" is used sensu Webb and Taylor (1980). "Hoplitomerycidae" includes the genus *Hoplitomeryx* (Leinders, 1983). *Lagomeryx* and *Procervulus* are included in the Cervidae (subfamily Muntiacinae). *Walangania* is included in the Bovidae. *Prolibytherium* and *Propalaeoryx* remain as genera Pecora incertae sedis. I. View proposed in this paper. "Climacoceridae" includes the genera *Climacoceras*, *Nyanzameryx*, *Injanatherium*, and *Canthumeryx* (= *Zarafa*). *Propalaeoryx* is considered as the sister taxon to the Giraffoidea. "Moschina" is a paraphyletic assemblage, containing the monophyletic Moschidae (including the blastomerycids, *Moschus*, and the fossil genera *Dremotherium* and *Micromeryx*) and *Walangania* as the sister taxon to the Moschina plus Eupecora. "Palaeomerycidae" includes the dromomerycids and the fossil genera *Palaeomeryx*, *Amphitragulus*, and possibly also *Prolibytherium*. ("Palaeomeryx" also includes the isolated teeth from Gebel Zelten ascribed to *Zarafa*; Hamilton, 1973.) "Hoplitomerycidae" includes the genera *Hoplitomeryx* and *Amphimoschus*. *Lagomeryx* and *Procervulus* are included in the Cervidae. *Triceromeryx* remains as Cervoid incertae sedis.

Muntiacus (the muntjak), and consider *Lago-meryx* to belong in the Muntiacinae (=Cervulinae) within the Cervidae.

A complete skull and several complete skeletons of a small species of *Palaeomeryx* (*Palaeomeryx tricornis*) have recently been described from the Miocene of China (Qiu et al., 1985), confirming the assertion by Ginsburg and Heintz (1966) that this genus had giraffidlike ossicones. They agree with Ginsburg and Heintz in the placement of *Palaeomeryx* within the Giraffoidea, although noting that it lacked the giraffid autapomorphy of a bilobed lower canine. We will discuss our hypotheses of the phylogenetic affinities *Palaeomeryx* and other "palaeomerycid" genera in a later section and attempt to argue for the resurrection of the Palaeomerycidae, although on the basis of different characters than those in previous use.

DROMOMERYCIDAE

Dromomerycids were an endemic North American Miocene ruminant assemblage, characterized by supraorbital nondeciduous unbranched cranial appendages (character 7f), with the presence of a median occipital cranial appendage in the subfamily Cranioceratinae (Webb, 1983b). They were considered cervoids during the early part of this century (e.g., Matthew, 1926; Frick, 1937) but were classified by Stirton (1944) as a subfamily of the Palaeomerycidae, which he allied with the Giraffidae on the basis of the similarities of the cranial appendages. Since that time most authors have allied them with the giraffids (e.g., Crusafont-Pairó, 1952, 1961; Vi- ret, 1961; Hamilton, 1978a), although Romer (1966) classified them with the cervoids.

Since the concept of the family Palaeomerycidae was abandoned, following Hamilton (1973, 1978b), dromomerycids have tended to be referred to as a discrete family, the Dromomerycidae (e.g., Hamilton, 1978b; Webb and Taylor, 1980; Janis, 1982; Webb, 1983b; Leinders, 1983), but their status as a family has never been formally defined.

Dromomerycids have the derived cervid features of a closed metatarsal gully (character 28b), a double lacrimal orifice (character 9), and can clearly be considered cervoids (see Janis, 1982; Leinders, 1983; Scott and Janis, 1987). A cervidlike condition

of the double lacrimal orifice can be unquestionably observed in specimens of all three dromomerycid subdivisions (see Frick, 1937): in the Aletomerycini (e.g., *Aletomeryx* sp., F:AM 42883), the Dromomerycini [e.g., *Subdromomeryx scotti* (type), F:AM 33758], and in the Cranioceratini (e.g., *Cranioceras granti*, F:AM 31270). The giraffidlike features of their cranial appendages evidently represent an example of parallel evolution. Dromomerycids also possess cervoid features of the limbs including, in addition to the closed metatarsal gully, a somewhat raised lip to the cubonavicular facet (character 32d), and a posterior tuberosity to the metatarsus (character 31) in most genera (see later discussion). They possess the dental character of a sabrelike canine (character 11b) in the early genera (*Barbouromeryx* and *Aletomeryx*), plus a *Palaeomeryx* fold (character 20) in the more brachydont genera. They are excluded from the Cervidae by the lack of a naked, deciduous portion of the cranial appendages and the more ventral position of the parietosquamosal suture (Frick, 1937).

We would define dromomerycids as ruminants possessing general cervoid postcranial and dental features, including a double lacrimal orifice, an elongated occipital region, and supraorbital unbranched, nondeciduous cranial appendages. Unfortunately, as with the Antilocapridae, no unique autapomorphies are known that unequivocally unite these genera into a single clade, but they are unified by their biogeographic occurrence in the Miocene of North America. Their phylogenetic position in relation to the cervid lineages will be discussed further in a later section.

HOPLITOMERYCIDAE

Leinders (1983) has defined this family based on the finding of a new ruminant genus, *Hoplitomeryx matthewi* from the Late Miocene island fauna of Monte Gargano (Italy). The animal appears to have the cervoid features of a closed metatarsal gully (character 28b), a cervidlike double lacrimal orifice on the orbital rim (character 9), and a sabrelike upper canine (character 11b), but possesses five cranial appendages (two pairs of post-supraorbital appendages and a median nasal appendage) which resemble the nondecid-

uous, keratin-covered horn core otherwise found in the Bovidae. (The deep grooving of the horn cores of *Hoplitomeryx* is reminiscent of the condition of bovid horn cores with a permanent keratin sheath, rather than the spongy texture of the antilocaprid horn core.) Leinders considers the genus to be closely related to the Cervidae on the basis of these cervoidlike cranial and postcranial features, but to be excluded from the family by possession of apparent horn cores rather than antlers, and places it in a family of its own. He also considers that, on basicranial and dental grounds, the pecoran genus which most closely resembles *Hoplitomeryx* is the poorly known European genus *Amphimoschus*. Both possess a large, bicuspid third lobe on m3 in which the median valley between both cusps is open posteriorly (character 26b), which appears to be a unique feature among the Pecora (see fig. 6), and share a large, inflated, smooth-surfaced auditory bulla with a number of similarities in structural detail. Both genera lack a *Palaeomeryx* fold, but both have fairly high-crowned molars, so this probably represents a secondary loss from the primitive cervoid condition, and both have lost p1 and possess unmolarized premolars (in contrast to the condition observed in more advanced cervids and dromomerycids). *Amphimoschus*, unlike *Hoplitomeryx*, has a bifurcated protocone (character 19a), the retention of p2, and a strongly developed entostyle and ectostylid (Leinders, 1983).

Figure 10 summarizes the historical development of ideas about the systematic position of fossil Eupecoran taxa.

PROBLEMATIC RUMINANT GENERA AND FAMILIES

WALANGANIA

Walangania is a small ruminant known from partial remains from the lower Miocene of East Africa (Whitworth, 1958) and also possibly from South Africa (Hendey, 1978). The genus contains two species: *Walangania* (= *Palaeomeryx*) *africanus* and the smaller *Walangania gracilis*. *Walangania* apparently lacked cranial appendages, although a complete cranium is not known, and has generally been considered to be a bovid (e.g., Hamilton, 1973) largely on the basis of its somewhat hypsodont cheek teeth. However, Gen-

try (in Hendey, 1978) has expressed the view that while there may be no reason to debar *Walangania* from bovid ancestry (as it is a suitably hypsodont pecoran, predating the appearance of the first horned bovid in Africa), there is also no reason to assume it might not be a small moschid, and considers that it may be synonymous with *Amphitragulus* or *Dremotherium*.

Palaeomeryx africanus (Whitworth, 1958) was synonymized with *Walangania gracilis* (Whitworth, 1958) by Hamilton (1973). Despite Hamilton's classification, we prefer to regard *Walangania africanus* and *Walangania gracilis* as separate species for the time being, as they do possess different morphological characteristics (for example, the presence of a *Palaeomeryx* fold and an incipient entostyle in *Walangania africanus*.) Whitworth originally assigned the larger species to the genus *Palaeomeryx* because of the presence of a *Palaeomeryx* fold and the cervoid nature of the supposedly associated metatarsus (which possesses a closed metatarsal gully), whereas *Walangania gracilis* lacks a *Palaeomeryx* fold. Hamilton (1973) synonymized the two genera and placed them tentatively in the Bovidae, on the supposition that the *Palaeomeryx* fold is a primitive pecoran character. While we consider the *Palaeomeryx* fold to be a derived cervoid character, we do not consider this character to unite *Walangania* with *Palaeomeryx*, although we do consider this character to ally *Walangania* with the Cervoidea. Its absence in *Walangania gracilis* is probably related to the greater degree of hypsodonty in the smaller species.

The available material of *Walangania* presents an interesting assemblage of characters. Material of *Walangania africanus* from Rusinga includes an upper dentition in which M3 has a small metaconule and the upper molars generally lack an entostyle, although a small entostyle is apparent in BMNH 35251. The metastyle is not pronounced, resembling the condition in *Eumeryx*. Another specimen assigned to this species (BMNH 21364) has a P3 with a backwardly directed gelocidlike protocone resembling the condition in *Prodremotherium* (see fig. 11). The low molars have a moderate metastylid and small ectostylids and the postentocristid is incomplete (see fig. 12).

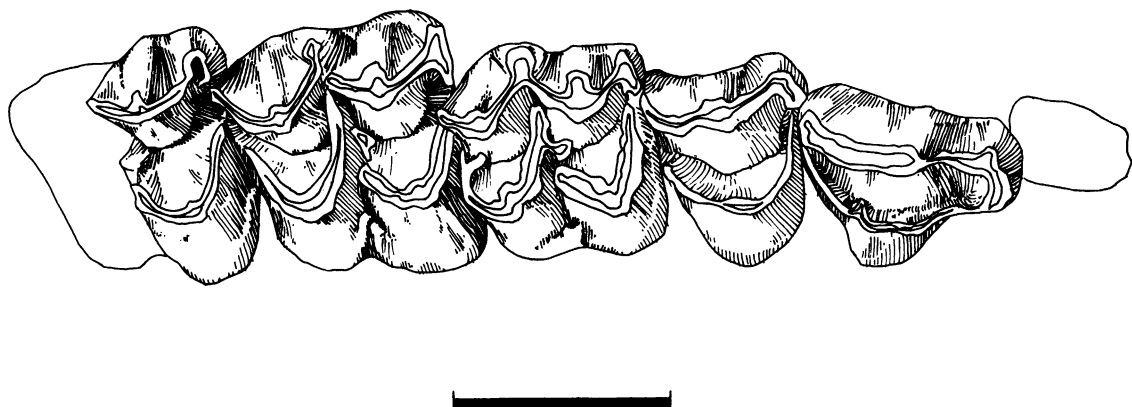


Fig. 11. *Prodremertherium elongatum*, right P3-M3, BMNH 1809, Phosphorites du Quercy (early Tertiary), France. Bar equals 10 mm.

Material of *Walangania gracilis* from Mfwangano includes upper molars (BMNH 21379) similar to those of *Walangania africanus*, but which have a slight lingual cingulum, as seen in gelocids. An immature lower jaw shows a possible alveolus for the deciduous p1. A proximal metatarsal assigned to *Walangania* shows a raised lip on the cubonavicular facet, but lacks a cervid type of posterior tuberosity. Metatarsal II is fused, but V is unfused, and a facet is present for the first metatarsal remnant. A distal metapodial fragment from Mfwangano in the Kenya National Museum, Nairobi, which is assigned to *Walangania gracilis*, shows the presence of complete distal keels.

Walangania africanus is also known from Songhor. An unassigned small distal metatarsal (BNNH Sgr. 232-1949) from this locality shows a closed metatarsal gully and complete distal keels. Whitworth (1958) assigned this metatarsal to *Walangania africanus*. However, it could belong to "*Gelocus*" *whitworthi*, a similar size animal of uncertain affinities in the same fauna. (*Gelocus whitworthi* is not known from dental remains at Mfwangano, so the small postcrania from that locality are more certainly assignable to *Walangania*.) *Walangania* may also be present in the Arrisdrift fauna from the early Miocene of South West Africa. Hendey (1978) describes this fauna, and comments on the similarities of the molars to *Walangania*, but follows Gentry (quoted as personal commun. in Hendey, 1978) in assigning this animal to the Bovidae because the lower molars are

more advanced than those of the East African *Walangania*. The Arrisdrift specimens have a smaller metastylid, weaker anterior ribs, and a complete postentocristid. However, there is also a small distal metapodial fragment in the collection at the South African Museum (PQ-AD-503) that has complete distal keels and appears to have a closed metapodial gully, but we were unable to ascertain with certainty whether this was a metacarpal or metatarsal.

On the basis of the dental evidence, *Walangania* appears to be similar to primitive cervoid genera such as *Eumeryx* despite the relative hypsodonty of the teeth. Similarities include the retention of a slight lingual cingulum (character 13b) in *Walangania gracilis*, the backwardly directed protocone on P3 (character 14a), the presence of a *Palaeomeryx* fold (character 20), and an incipient entostyle (character 15a) in some specimens of *Walangania africanus*, and the incomplete postentocristid (character 22a). However, the limbs suggest more advanced cervoid affinities; in addition to the closed metatarsal gully (character 28b) (seen also in *Prodremertherium* and *Eumeryx*), it also apparently had complete distal keels on the metapodials (character 27). We would assign *Walangania* to the Cervoidea on the basis of the presence of a *Palaeomeryx* fold (character 20), a closed metatarsal gully (character 28), and the raised lip on the posterior cubonavicular facet (character 32d). The presence of complete distal keels (character 27) make it a more derived cervoid than *Eumeryx*, but the re-

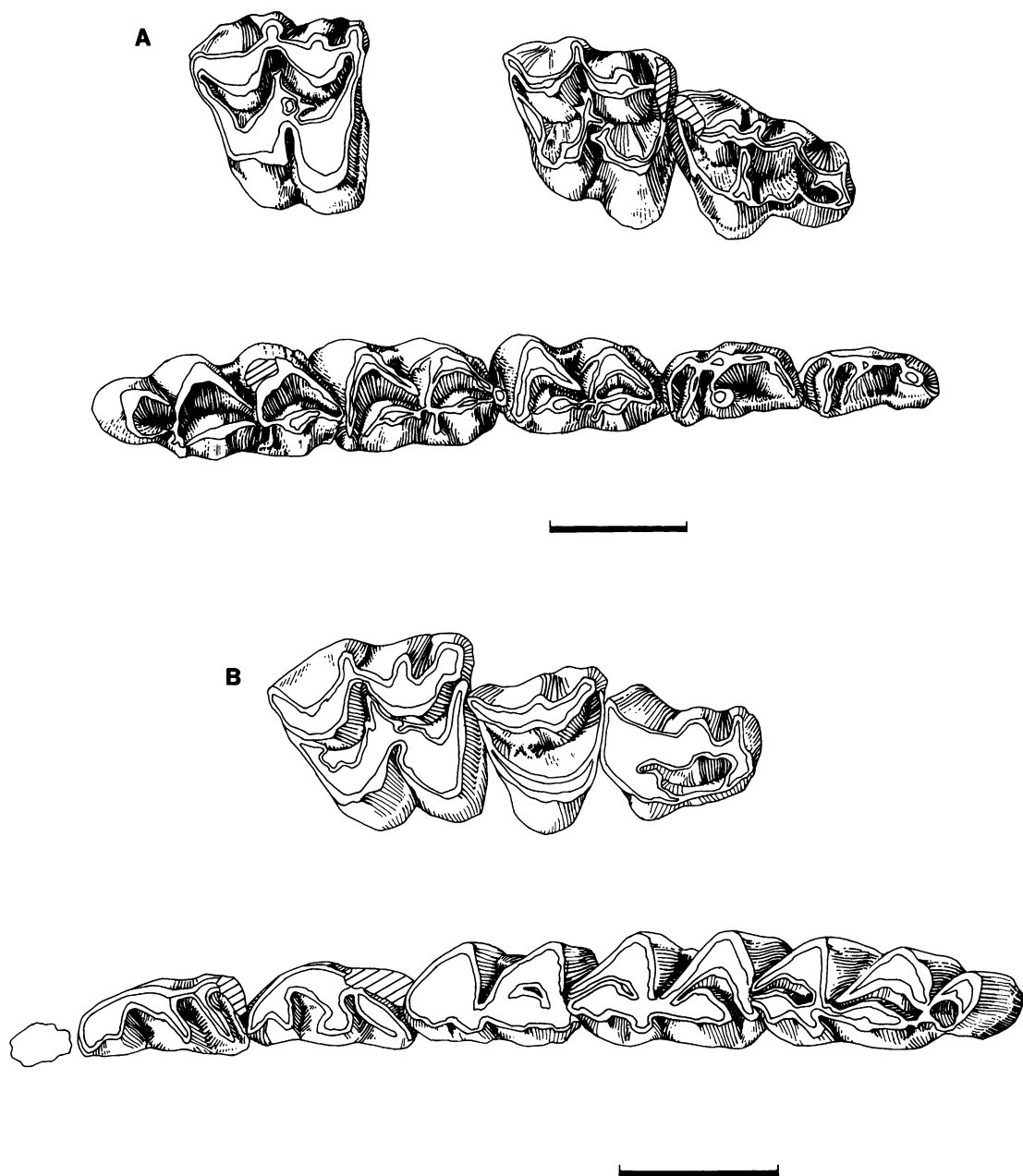


Fig. 12. A. *Walangania africanus*, left DP3-DP4 (reversed), BMNH 21362, right ?M2, BMNH 21363 and left p3-m3, BMNH 30137 (from cast), Songor (early Miocene), East Africa. B. *Propalaeoryx austroafricanus*, right P3-M1, BMNH 369 (cast of PQN 57) and right p2-m3, BMNH 369.59 (cast of PQN 51), Lagental (middle Miocene), Namibia. Bar = 10 mm.

tention of the aforementioned primitive pecoran dental characters relegates it to a more primitive position than other cervoids. There appears to be no evidence for the presence of a moschidlike upper canine in this genus.

"GELOCUS" WHITWORTHII

This taxon was described by Hamilton (1973), the type consisting of a mandible fragment containing a lightly worn m2 and m3. The type specimen and most of the other

material of this taxon are from Songhor, but teeth assigned to "*Gelocus*" *whitworthi* are also known from Maboko and Rusinga. The taxon is only known from remains of the lower molars.

"*Gelocus*" *whitworthi* differs from the tragulid *Dorcatherium* (also present at Songhor) in the absence of a *Dorcatherium* fold. The teeth are of a similar size to *Walangania*, but differ from his taxon in certain dental features. The metastylid in "*Gelocus*" *whitworthi* is closely conjoined to the metaconid, and is situated lingual to the posterior end of the metaconid, resulting in a median valley on the lower molars that is open lingually. In contrast, in *Walangania* the metastylid is situated lingual to the anterior end of the entoconid, resulting in a closed median valley. "*Gelocus*" *whitworthi* resembles *Gelocus communis* from Europe in the roundness of the metaconid, and in the forked posterior end of the entoconid, with the labial branch meeting the posterolingual end of the hypoconid and the lingual branch being produced posterolingually. In the m3 of "*Gelocus*" *whitworthi* there is a strong entostylid that runs posterolaterally to fuse with the hypoconulid, giving a unique appearance among Pecora to the posterior part of this tooth, and an accessory stylid is present in the labial end of the posterior valley.

These dental details, and others described by Hamilton (1973), warrant the distinction of "*Gelocus*" *whitworthi* from the small contemporaneous pecoran taxa, such as *Walangania* and *Propalaeoryx*. However, we would question the inclusion of this taxon with the genus *Gelocus*. As previously discussed, the type of *Gelocus communis*, and other specimens of this species from Le Puy (France), lack metastylids, and metastylids appear to be a good synapomorphy of pecorans above the level of *Gelocus* as evidenced by the European fossil material (see Janis, 1987). A few specimens of "*Gelocus*" *whitworthi* have a faint, but definite, *Palaeomeryx* fold. This is visible in the holotype (BMNH K.Sgr. 365-1949) and in the paratype (BMNH K.Sgr. 581-1949) from Songhor. We consider this taxon to have had affinities with the primitive pecoran taxa *Eumeryx* and *Rutitherium* on the basis of the derived cervoid character of a *Palaeomeryx*

fold (character 20). The similarities of the dentition of "*Gelocus*" *whitworthi* to *Gelocus communis* probably represent primitive pecoran features. However, we have not made a thorough study of this taxon, and present this taxonomic assignation as a possible hypothesis, awaiting the discovery of further material.

PROPALAEORYX

Propalaeoryx austroafricanus from the Namib Desert was described by Stromer (1926), and he originally assigned it to the Bovidae. However, Arambourg (1933) considered the dental characters to be more cervidlike. Whitworth (1958) described *Propalaeoryx nyanzae* from Rusinga (lower Miocene), allied this animal with Stromer's *Propalaeoryx austroafricanus*, and also concluded that the genus was more cervoid in nature, due to the strong metastylid and entostylid on the lower molars. He described a metatarsal ascribed to *Propalaeoryx* as possessing complete distal keels and as being bovidlike in the housing for the extensor tendon, with a cervidlike grooving on the posterior shaft, but having a bovidlike anterior shaft with an open metatarsal gully. Hamilton (1973) described *Propalaeoryx* from Rusinga as lacking a *Palaeomeryx* fold and possessing a metastyle and entostyle in the upper molars and a small p1 separated from p2 by a small diastema. He also concluded that the dentition bears a stronger resemblance to *Palaeomeryx* than to bovids, and placed it in the *Palaeomerycidae*. However, an entostyle is only apparent on one specimen of *Propalaeoryx* from Moruorot, consisting of a worn and badly damaged specimen (BMNH MT 67'51). This tooth was originally ascribed to "*Palaeomeryx*" (= *Walangania*) *africanus* by Whitworth (1958), and may have been misidentified by Hamilton. We have never observed an entostyle on any other specimens of *Propalaeoryx*, in the range of material available in British and African museum collections.

Additional characteristics of *Propalaeoryx* that we have noted include the presence of a bifurcated posterior crista of the metaconule (character 19b) (also depicted in Hamilton, 1973), a small metaconule on M3 (character 18a), a P3 with a posterior situated protocone

(character 14a) seen in the specimen of *P. austroafricanus* (BMNH 36928) from Langental, Namibia (see fig. 12), and the presence of a slightly raised lip on the cubonavicular facet (character 32d) (BMNH 36928, also from Namibia). A fragment of tusk like upper canine from Namibia (BMNH 36963) may also be assignable to *Propalaeoryx*. The bifurcated posterior wing of the metaconule is a character shared with the early giraffoids *Palaeotragus* and *Canthumeryx*, although this character, as previously mentioned, also appears in certain other pecoran genera as well as in early giraffoids.

Despite the assertion of the cervoidlike nature of the dentition in *Propalaeoryx*, including Gentry's (1978) comments that the shallow ramus of the mandible is more reminiscent of the cervid condition than of the bovid one, we see no reason to group *Propalaeoryx* with cervoids, as these characters represent the primitive pecoran condition seen, for example, in *Prodremotherium*. *Propalaeoryx* lacks any derived cervoid characters, such as a *Palaeomeryx* fold, and the presence of an open metatarsal gully and the lack of an entostyle make it a more primitive pecoran than *Prodremotherium*. However, the presence of complete distal metapodial keels (character 27) elevates this genus above the "gelocid" grade. Gentry (in Hendey, 1978) has suggested a possible affinity of *Propalaeoryx* with early giraffoids, based on the general similarity of the teeth with those of the larger genus *Climacoceras*, and also because its early presence in Africa makes its role as a giraffoid ancestor biogeographically plausible. The only possible synapomorphic feature that we can find to link *Propalaeoryx* with the Giraffoidea is the bifurcation of the posterior wing of the metaconule (character 19b). This is a pronounced feature of the early giraffid *Palaeotragus* but, as previously mentioned, is seen only occasionally in specimens of *Canthumeryx*, although it is present in the problematical teeth assigned to *Zarafa* from Gebel Zelten. Unfortunately, the anterior portion of the dentition of *Propalaeoryx* is not known, so it cannot as yet be determined whether this genus had a giraffoid type of bilobed lower canine (character 23) (though of course the absence of this character would not exclude it from the position of sister tax-

on to the Giraffoidea). The proximal surface of the metatarsus (character 32) is cervoidlike rather than giraffoidlike, but this merely represents the primitive pecoran condition, and again would not exclude *Propalaeoryx* from affinities with the Giraffoidea.

In the absence of any other available evidence, we would follow Gentry's suggestion for the time being in placing *Propalaeoryx* as the sister taxon to the Giraffoidea, but note that the synapomorphic character (19b) of the bifurcation of the posterior wing of the metaconule is a rather weak one.

AMPHITRAGULUS AND DREMOTHERIUM

Amphitragulus (Pomel, 1853) and *Dremotherium* (Geoffroy Saint-Hilaire, 1833) were small, apparently hornless ruminants that were common in the European middle Oligocene to early Miocene. They are known from dental remains and postcrania that have been assigned primarily on the basis of the size sorting. Sigogneau (1968) discusses the history of the genus *Dremotherium* and notes that while the original type first described by Pomel (1845–1846) consisted of a complete articulated skeleton, most of the material has been lost, and only the skull remains. Apparently the complete type of *Amphitragulus* has also been lost (M. Brunet, personal commun.). This had led to much confusion as to the identification of specimens of these genera; for example, several faunal sites in the BMNH have all the small ruminant limbs labeled "*Dremotherium*" and all the dental material labeled "*Amphitragulus*"! The two genera have usually been considered as a pair, and treated as sister taxa in various classifications. We consider the two genera to have some significant differences, resulting in a distinct separation between them in our proposed cervoid phylogeny.

With the exception of Pomel (1845–1846), who considered these genera to be tragulids, and Gervais (1859), who classified *Dremotherium* with the antelopes, *Dremotherium* and *Amphitragulus* have been considered to be cervoids of some sort. Geoffroy Saint-Hilaire (1833) and Richard (1946) considered *Dremotherium* to be a true cervoid, but closer to the tragulids than *Moschus*. Milne-Edwards (1864) related *Dremotherium* to *Mos-*

chus, while Rütimeyer (1881, 1883) placed it in the Cervidae in the subfamily Cervulinae. More recently, these genera have been lumped with a number of other early hornless ruminants in the Palaeomerycidae (e.g., Simpson, 1945; Stirton, 1944; Viret, 1961; Romer, 1966).

Sigogneau (1968) considered *Dremotherium* to be a true cervoid, resembling *Moschus* and *Hydropotes* (though retaining more primitive characters), and possibly closely related to the North American blastomerycids. She considered *Amphitragulus* to be possibly related to another cervoid lineage, and hints at certain similarities between *Amphitragulus* and *Palaeomeryx*. Webb and Taylor (1980) discuss a number of similarities between the basicranial regions of *Dremotherium*, *Moschus*, and *Blastomeryx*, and, linking *Amphitragulus* with *Dremotherium* primarily on the basis of the sabrelike canines, group these genera together in the Moschidae (which in their classification is considered as the sister group to the Eupecora, or horned ruminants).

There is little doubt that both *Amphitragulus* and *Dremotherium* are true cervoids. They both possess elongated, fused metapodials (character 28d) with complete distal keels (character 27) and a closed metatarsal gully (character 28b); a raised lip on the cubonavicular facet (character 32d); sabrelike upper canines (character 11b); an entostyle on the upper molars (character 15b); and a "Palaeomeryx" fold in the lower molars (character 20). Viret (1961) describes the differences between the two genera as follows: *Amphitragulus* has a short facial region, without lacrimal fossae or antorbital vacuities; short, thickset premolars and a relatively short diastema with p1 usually present; little elevation of the occipital region, and only slight projection of the supraorbital ledge; and normal length of cervical vertebrae. In contrast, *Dremotherium* has a longer facial area, with both lacrimal fossae and antorbital vacuities present; generally only three premolars, with a large diastema and more elongated premolars (see tables 3, 5); braincase more expanded, with a more elevated occipital area and a more strongly projecting supraorbital ledge; and elongated cervical vertebrae.

Sigogneau (1968) discusses these differences and also notes that the supraorbital

ledge is not only more strongly defined in *Dremotherium*, but projects laterally to form a convex supraorbital roof, bearing closer resemblance to the condition in true cervids. In addition, the supraorbital depressions on the skull roof are more narrow and covered by bone for a greater length of their traverse in *Amphitragulus* than in *Dremotherium*. Sigogneau provides measurements to show that the occipital region is considerably higher in *Dremotherium* than in *Amphitragulus*. She questions the supposed lack of the antorbital vacuity in *Amphitragulus*, as she points out that no cranium is well enough preserved to be absolutely certain of the condition. She also discusses some primitive, more tragulidlike features of *Amphitragulus*, including the relatively smaller orbits with the anterior border placed relatively further forward (i.e., at the level of the junction of the first and second molars, as opposed to at the level of the border between the second and third molars in *Dremotherium*), a *Hyemoschus*-like orbital extension of the palatine, and a contribution from the maxilla to the floor of the orbit. In contrast to *Dremotherium*, the orbitosphenoid does not attenuate toward the sphenopalatine orifice, and the infraorbital portion of the lacrimal extends less postero-ventrally. Sigogneau also considers *Dremotherium* to have a relatively larger basioccipital region than *Amphitragulus*. However, in her discussion of the amount of variation seen in the limited amount of cranial material known of the two genera, she considers that none of these differences could be considered as diagnostic for the separation of the two genera. She also points out that *Amphitragulus* has two lacrimal orifices (character 9), whereas there is only a single orifice in *Dremotherium*, but she does not comment on the potential significance of this character.

With regard to dental differences, Sigogneau adds to Viret's list by pointing out that the ectostylid and metastylid are less pronounced in *Amphitragulus* than in *Dremotherium*, the *Palaeomeryx* fold is less well-developed in *Amphitragulus*, and the lower premolars are less molarized, especially with regard to the development of the metaconid. In the upper molars, the entostyle is less well-developed in *Amphitragulus*, and the molars are more bunoselenodont in the development

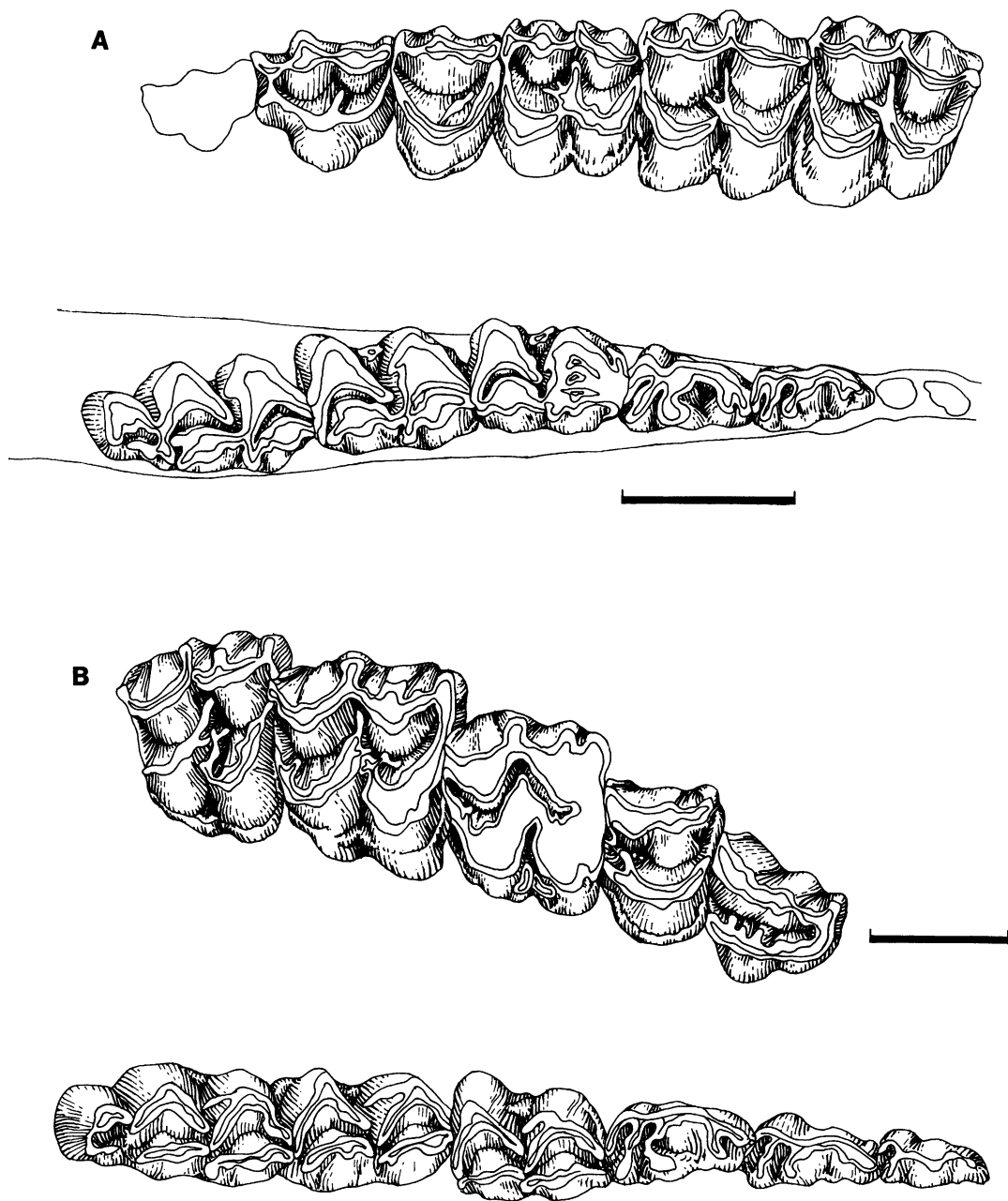


Fig. 13. A. *Amphitragulus* sp., left P3-M3, Ph 3107 and left p3-m3, Ph 4141. B. *Dremotherium feignouxii*, right P3-M3, Ph 52933 and left p2-m3, Ph 32488, Montaigu, Allier (early Miocene), France. Bar = 10 mm.

of the crescents. The paracone on P4 is less well developed in *Dremotherium*. *Amphitragulus* differs from *Dremotherium* in having a reduced metastyle, especially on M3 (character 16b), a reduced metacone on P4 (char-

acter 17b), and a double loph on the posterior lobe of m3 (character 26a) (see fig. 13).

To this list of dental differences, we would add the following: the molars of *Dremotherium* are more fully selenodont than those

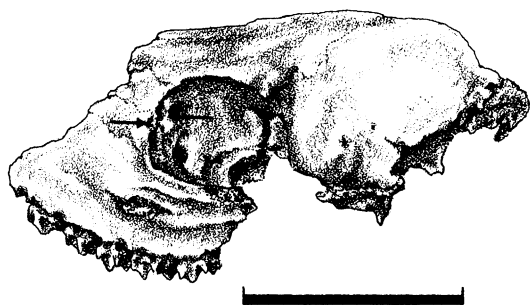


Fig. 14. *Amphitragulus* sp., Ph 3107. Bar = 5 cm.

of *Amphitragulus*, particularly with respect to the development of the postentocristid in the lower molars. The molars of *Amphitragulus* have a "chubby" appearance, and can be shown to be relatively broader than those of *Dremotherium*. In addition, the upper molars of *Dremotherium* retain the primitive pecoran condition of the reduced M3 metaconule (character 18a) and traces of an internal cingulum (character 13b), whereas in *Amphitragulus* the metaconule is equal in size to the protocone (character 18b) and there is little evidence of the internal cingulum (character 13c) (see fig. 13). (These differences were also noted by Sigogneau.)

Although there is no firm association of limb material with either of these two genera, we have examined many different faunal collections in museums where different size fossil species of the two genera are found together, and have found some invariant characters of the two genera on the basis of the size sorting. The metatarsals of *Dremotherium* have the tubercle for metatarsals II and V fused (characters 30a, b) and lack a posterior tuberosity. In contrast, the metatarsals of *Amphitragulus* have only V fused (character 30b), and have a variably present small cervidlike posterior tuberosity (character 31).

Amphitragulus is generally considered to be more primitive and more "tragulid-like" in its cranial and dental features than *Dremotherium* (e.g., Sigogneau, 1968). However, we consider the "advanced" characters of *Dremotherium* to be associated with a more folivorous dietary habit, as suggested by the more selenodont cheek teeth, the greater molarization of the premolars, and the longer

facial region and diastema. The elongated cervical vertebrae, similar to those of the modern bovid genera *Litocranius* and *Ammodorcas*, suggest that *Dremotherium* may have had a high browsing type of diet, as do these gazellines, which also resemble *Dremotherium* in the possession of a long basioccipital and a high occipital region (Janis, unpubl. data). The cranial and molar morphology and dental wear of *Amphitragulus* suggest a more tragulid or duikerlike mode of low-level browsing on more succulent material (Janis, 1979; unpubl. data). Thus the skull appears to be superficially more tragulidlike. However, it is clear that *Amphitragulus* has two definitive characters that make it a more derived type of cervoid than *Dremotherium*. These are possession of the posterior tuberosity on the metatarsal (character 31), and in particular the presence of two lacrimal orifices situated in the cervid position on the orbital rim (character 9) (see fig. 14). This specimen of *Amphitragulus* was figured in dorsal view by Sigogneau (1968), but she did not comment on the significance of the double lacrimal orifice. However, the significance of this feature in cervoid phylogeny was not widely recognized until the work of Leinders and Heintz (1980). We have also observed a double lacrimal orifice on a partial cranium of *Amphitragulus lemanensis* from St. Gerard-le-Puy, Allier, France in the collection of the Musée Gimet, Lyon (St. G. 600). We consider these differences between the two genera to ally *Amphitragulus* with the more advanced true cervids, whereas *Dremotherium* should be considered to be more closely allied to the moschids (see Webb and Taylor, 1980). The exact systematic position of these genera within the phylogeny of the Cervoidea will be discussed in more detail in a later section.

MOSCHIDAE

Webb and Taylor (1980) linked the living genus *Moschus* with the fossil genera *Amphitragulus*, *Dremotherium*, *Blastomeryx*, and the other blastomerycine genera in the family Moschidae on the basis of sabrelike upper canines (character 11b) and a laterally enclosed subcentral tympanohyal on the auditory bulla (character 10). We have argued in

this paper and elsewhere (Scott and Janis, 1987) for the inclusion of the Moschidae with the Cervidae in opposition to Webb and Taylor (1980), who place the Moschidae as the sister group to the horned ruminants. However, the question of whether moschids represent a clade or a grade within the cervoid phylogeny remains to be answered, and will be discussed here.

As previously stated, *Amphitragulus* possesses some derived cervoid characters absent in *Dremotherium*, and should not be grouped with the other moschid genera. In their discussion of basicranial anatomy, Webb and Taylor (1980) discussed only the condition in *Dremotherium*, and included *Amphitragulus* because of the presence of the moschidlike upper canines. However, as previously discussed, such canines appear to be a derived character of certain higher cervoids, but their presence may well serve to unite a clade of cervoids that are more derived than *Eumeryx* and *Walangania*.

We would define moschids as cervoids with a closed metatarsal gully (character 28b), a *Palaeomeryx* fold (character 20) primitively present in brachyodont members of the lineage, a raised lip on the cubonavicular facet, upper dentition with an entostyle, a pronounced metastyle, and a P3 with a linguall directed protocone, but with a single lacrimal orifice and lacking any form of cranial appendages. The fossil genera retain the gelocid condition of a small metaconule on M3 (character 18a). However, all moschids are derived in the fusion of metatarsal V (character 30b).

Webb and Taylor's (1980) comparison of the ear regions of *Moschus* and the blastomerycids presents a convincing case for strong similarities, although the situation in *Dremotherium* is not as pronounced. Examination of the type of *Dremotherium* in the Paris museum shows that the tympanohyal is placed more posteriorly on the bulla, with a lesser degree of lateral enclosure than is seen in *Moschus* or *Blastomeryx* (character 10a). However, the distribution of the posterior tuberosity (character 31) among the moschid genera is problematical. As previously discussed, this appears to be a fixed trait in true cervids, present in other cervoids such as *Palaeomeryx* and *Hoplitomeryx*, but it may have

arisen in parallel within the dromomerycids. A posterior tuberosity is present in *Moschus* and *Parablastomeryx*, but absent in *Dremotherium* and *Blastomeryx*. *Parablastomeryx* also differs from *Blastomeryx* in the following characters: a large premolar row, lower molars with a pronounced *Palaeomeryx* fold (absent in *Blastomeryx* but present in *Problastomeryx*), more prominent entostyle in the upper molars, entostylid and metastylid in the lower molars, a reduced metastyle in the upper molars (character 16b), an attenuated protocone on p4 (character 17b) (features 16b and 17b resemble the normal pecoran condition in *Blastomeryx*), posterior lobe of m3 with a double loph that is closed posteriorly (character 26a) (the molar is compressed with a single loph in *Blastomeryx*), and a P3 with a somewhat posteriorly directed protocone (character 14a) (lingually directed in *Blastomeryx*).

Some of these differences between *Parablastomeryx* and *Blastomeryx* were noted by Frick (1937), who also commented on the shorter diastema of *Parablastomeryx* and the more lightly proportioned limbs. Frick grouped the genera *Longirostromeryx*, *Blastomeryx*, and *Machaeromeryx* in the subfamily Longirostromerycinae, and the genera *Parablastomeryx*, *Pseudoblastomeryx*, *Problastomeryx*, and *Pseudoparablastomeryx* in the Parablastomerycinae. *Pseudoparablastomeryx* was referred to the Leptomerycidae by Taylor and Webb (1976). We believe that a thorough review of the interrelationships of the "blastomerycids" and of the distribution of basicranial characters throughout the "moschids" and the other higher Pecora is essential before the phylogenetic reality of the "Moschidae" can be evaluated. However, at the present time we consider the scheme of Webb and Taylor (1980), based on ear region characters (character 10), to be a working hypothesis (but excluding the genus *Amphitragulus*), and consider the posterior tuberosity in *Moschus* and *Parablastomeryx* to have evolved in parallel with the condition in the other cervoids (though it should be probably considered a synapomorphy linking these two genera within the Moschidae).

Further genera which may be included within the Moschidae are the European *Micromeryx* and *Hispanomeryx*. The interre-

lationships of *Micromeryx* with the blastomerycids was first suggested by Frick (1937), and reiterated by Leinders (1983). *Micromeryx* possesses a closed metatarsal gully and a *Palaeomeryx* fold, so it is undoubtedly a cervoid. It lacks cranial appendages, possesses a sabrelike upper canine, and has a distinct posterior tuberosity on the metatarsus. Metatarsal V is fused, as in other moschid genera. To the best of our knowledge, the condition of the lacrimal orifice is unknown, and the ear region has not been studied. We tentatively place it in the Moschidae on the assumption of a single lacrimal orifice, and would group it with *Moschus* and *Parablastomeryx* on the basis of the posterior tuberosity.

Hispanomeryx duriensis was recently discovered in the Vallesian of Spain (Morales et al., 1981). Morales et al. place this taxon in the Moschidae (sensu Webb and Taylor, 1980), and comment that it may also bear a relationship to *Walangania*, which they suggest should also be classified with the Moschidae. We have not had the opportunity to examine the original material of *Hispanomeryx*. However, to judge from the illustrations in Morales et al. (1981), the lower molars resemble the condition in *Parablastomeryx* in the possession of an m3 with a double posterior lobe closed posteriorly (character 26b) and a vertical groove on the posterolingual region of p4 (character 25), but resemble the situation in the more hypsodont *Moschus* in the absence of a *Palaeomeryx* fold and the reduction in the size of the metastyles. The upper molars resemble *Moschus* in the absence of an entostyle and in the presence of a large metastylid. Morales et al. (1981) describe the metatarsus as possessing a closed metatarsal gully and a posterior tuberosity, and having metatarsal II (but not metatarsal V) fused with the proximal surface of the metatarsus. Their illustration of the proximal metatarsal surface appears to resemble the generalized cervoid condition, with a raised lip for the posterior cubonavicular facet.

We would agree with Morales et al. (1981) in assigning *Hispanomeryx* to the Moschidae, despite the fact that no upper canine is known from this taxon, and consider the genus to be closer to *Moschus* and *Parablastomeryx* (on the basis of the posterior tu-

berosity of the metatarsus) than to *Dremotherium* or the other blastomerycids. However, since we did not see the original material, we would not presume to comment further on the affinities of this taxon within the Moschidae.

PALAEOMERYX AND THE PALAEOMERYCIDAE

Palaeomeryx has traditionally been placed within its own family, the Palaeomerycidae, and the family has been variously considered cervoid (Viret, 1961; Simpson, 1945) or giraffoid (e.g., Stirton, 1944). Although the composition of the Palaeomerycidae has varied, the family has traditionally included a number of problematical genera, as discussed in a previous section.

A recent definitive statement on the systematic position of *Palaeomeryx* was that by Ginsburg and Heintz (1966). They found what appears to be a dermal ossicone, similar to a giraffid dermal ossicone, associated with a specimen of *Palaeomeryx kaupi*, and consider this to be strong evidence of giraffoid association. They also point out a number of other characteristics of *Palaeomeryx* that seem to be more giraffid than cervoid, such as the lack of bifurcation of the protocone, the absence of an antorbital vacuity, the possession of a ridge on the proximal metacarpus, the absence of a diarthrodial facet on the proximal metacarpals, and the equal length of the metacarpals and metatarsals. Leinders (1983) points out that these characters are all primitive pecoran characters, also seen in most early cervids (as defined by the presence of antlers). Other giraffid characters possessed by *Palaeomeryx* from Sansan (Helvetian), such as the morphology of p4, the form of the distal articulation of the humerus, the grooved surface on the anterior side of the distal part of the radius, and the groove on the posterior surface of the metapodials, are said by Leinders (1983) to be absent from the earlier specimen of *Palaeomeryx* from Artenay, and so must have been derived within the evolution of this genus, in parallel with the condition in giraffids.

While the form of the associated ossicones is similar to the condition in giraffids (character 7a), this need not be indicative of a close

relationship, as previously discussed. Leinders (1983) discusses the cervoid condition of the closed metatarsal gully in *Palaeomeryx*, which he included in the Cervioidea. He points out that even if a complete cranium of the animal were known, the absence of a double lacrimal orifice would not exclude the genus from the Cervioidea, as it could represent a moschid level of cervoid evolution. Leinders suggests that *Palaeomeryx* and *Triceromeryx* may be related to the North American dromomerycids, and may have reinvaded Eurasia from North America in the early Miocene along with the equid *Anchitherium*.

Whitworth (1958) commented on a feature in the upper molars of *Palaeomeryx* that he considered to be cervidlike, rather than giraffid. That is, the position of the metacone, which in *Palaeomeryx* resembles the cervoid condition, being placed parallel to the labial edge of the fold (in contrast to the giraffid condition, where the metacone is placed more obliquely). However, this feature is probably a derived giraffid feature, as the position of the metaconid in *Canthumeryx* resembles that in *Palaeomeryx* and the other cervoids (and indeed is the condition in primitive pecorans), so the character is probably not significant for assessing the phylogenetic relationships of *Palaeomeryx*.

Recent discoveries from the Miocene of China of a complete skull and several complete skeletons of *Palaeomeryx tricornis* (Qiu et al., 1985) have thrown new light on the anatomy of this genus. They describe the specimens as having sexually dimorphic cranial appendages, consisting in the (presumed) males of a pair of supraorbital giraffidlike "ossicones," which were triangular at the base and sloped posteriorly, with a bulbous or pointed tip, a rough and cancellous surface (suggestive of a giraffidlike skin covering), and a suture demarking the base of the appendages from the skull in one specimen. In addition, these animals possessed a dromomerycid-like single, unbranched occipital appendage with a smooth surface, the distal part of the appendage forming a laterally compressed, bulblike structure. Sexual dimorphism was also shown in the possession of upper canines, which were large and sabrelike in the males, and small and peglike in the females.

The skull had both a lacrimal fossa (character 8) and an antorbital vacuity. There was apparently only one lacrimal orifice, but this was only discernible on a single specimen in which the anterior orbital rim was damaged. The lower canine, while not fully preserved, apparently did not exhibit the giraffoid type of bilobed condition (character 23). P4 had a weak metacone (character 17b), and the molars exhibited weak metastyles (character 16b) and a bifurcated posterior wing of the metaconule (character 19b). Weak entostyles (character 15a) were variably present. Both P4 and the upper molars retained traces of an internal cingulum (character 13b). p1 was present in some specimens, separated from p2 by a small diastema (character 4b). The lower molars show the presence of a strong *Palaeomeryx* fold (character 20), and the ectostylids and metastylids were also strong. The posterior lobe of m3 was double and closed posteriorly (character 26a), described by the authors as "horseshoe shaped." The lower premolars were little molarized. p4 had a small metaconid and a posterolingual groove (character 25). The neck of the animal was not elongated. The metapodials were completely fused, with slender, complete metacarpals II and V. The metatarsal gully was closed, with the hind limb longer than the forelimb.

Qiu et al. (1985) remain convinced that *Palaeomeryx* was a giraffoid, or at least represents the sister group to the other giraffoids, as it apparently lacked the giraffoid synapomorphy of a bilobed lower canine, although they note that it shared many plesiomorphic features with cervids. They also point out that Ginsburg and Heintz (1966) were incorrect in stating that there was no antorbital vacuity in this genus (although they also note that an antorbital vacuity is indeed found within the Giraffidae, and is probably a plesiomorphic condition for the Pecora, or one evolved a number of times in parallel, as we concluded in an earlier section).

Qiu et al. (1985) consider that the morphology of the p4 of *Triceromeryx* justifies its inclusion in the Giraffidae (after Hamilton, 1978a), and note that the supraorbital cranial appendage in this genus is comparable to the situation in *Palaeomeryx tricornis*. However, it has been demonstrated recently

that this type of p4 morphology cannot be used as a diagnostic giraffid autapomorphy (Janis and Lister, 1985). They also comment that the dolicocephaly of the skull, the central position of the orbit, the relatively small degree of flexion of the face on the basicranium, and the long basicranial region all resemble the condition seen in the giraffoids *Zarafa* and *Giraffokeryx*. However, this type of skull morphology is also apparent in many dromomerycid genera. They note that the apparently single lacrimal orifice is a plesiomorphic character for the Pecora, not necessarily suggestive of giraffoid affinities, although it would exclude *Palaeomeryx* from the Cervoidae above the level of the Moschidae (see Leinders, 1983). However, we would question their assertion that this is the true condition in *Palaeomeryx*. As previously discussed, the condition of the lacrimal orifice is variable among the antilocaprids (see also Scott and Janis, 1987), even though most specimens *do* possess a double lacrimal orifice, and so a single specimen of a taxon that exhibits the plesiomorphic condition cannot be taken as representative of the taxon as a whole. (In contrast, if a single specimen shows a *derived* character condition, this is a much more convincing situation, although of course the possibility of parallel evolution cannot be ruled out, as shown by the occurrence of a double lacrimal orifice in some of the bovid tribes). We have discovered, in our examination of fossil material in the Frick collections, AMNH, where many complete skulls exist for dromomerycid and antilocaprid species, that a single specimen with a damaged orbital rim is a poor basis for the determination of this character in a taxon or in a pecoran lineage. The condition of the lacrimal orifices is only clearly discernible in a few individuals in the Frick collections. Interestingly enough, their drawings of *Palaeomeryx tricornis* (Qiu et al., p. 175) suggests a double lacrimal orifice.

Qiu et al. (1985) note that the lacrimal fossa and sabrelake upper canine present in *Palaeomeryx* are generally considered to be cervoid characters, but that the polarity of these characters is unknown to them. However, previous discussions in this paper have pointed out that a sabrelake upper canine is a derived feature of cervoids at the level of

the Moschidae. The lacrimal fossa is a less useful character, but we note that it is also characteristic of primitive dromomerycids. Qiu et al. are very impressed by the similarities of the cheek teeth of *Palaeomeryx tricornis* with those of *Zarafa*, as described by Hamilton (1973). We agree with them, but as noted in our previous discussions in this paper, we feel that there is no reason to associate these isolated molars with the type of *Zarafa*. The feature of the bifurcated posterior wing of the metaconule is seen in many dromomerycids as well as in early giraffids. This seems to us a convincing case for assigning the Gebel Zelten "*Zarafa*" teeth to an unknown African species of *Palaeomeryx*.

Qiu et al. (1985) also comment on the cervoidlike nature of the closed metatarsal gully in *Palaeomeryx*, but note that this condition could be independently derived with the Ruminantia. They cite as evidence (from Frick, 1937) the presence of a closed metatarsal gully in the Antilocapridae, but the presence of an open gully in some merycodontines. However, as previously discussed, our studies of the Antilocapridae clearly show that the polarity of this character within the Merycodontinae is from a closed gully to a secondarily open one (although we concede that this type of closed metatarsal gully may have evolved more than once within the Ruminantia, as evidenced by the condition in *Pseudoceras*). Finally, they are obviously impressed by the fact that it can at last be conclusively shown that *Palaeomeryx* did indeed possess giraffidlike ossicones, as originally hypothesized by Ginsburg and Heintz (1966) on the basis of an isolated "ossicone" found at Artenay. However, previous discussions in this paper have clearly shown that the cranial appendages in the giraffoids *Climacoceras* and *Nyanzameryx* cannot be homologous with true giraffid ossicones. If cranial appendages have evolved independently within the Giraffoidea, as defined by Hamilton (1973) on the basis of the possession of a bilobed lower canine, then the cranial appendages of *Palaeomeryx* cannot be homologous with giraffid ossicones, despite their superficially similar appearance, since the lack of a bilobed lower canine excludes *Palaeomeryx* from the Giraffoidea.

Our analysis of *Palaeomeryx* is as follows:

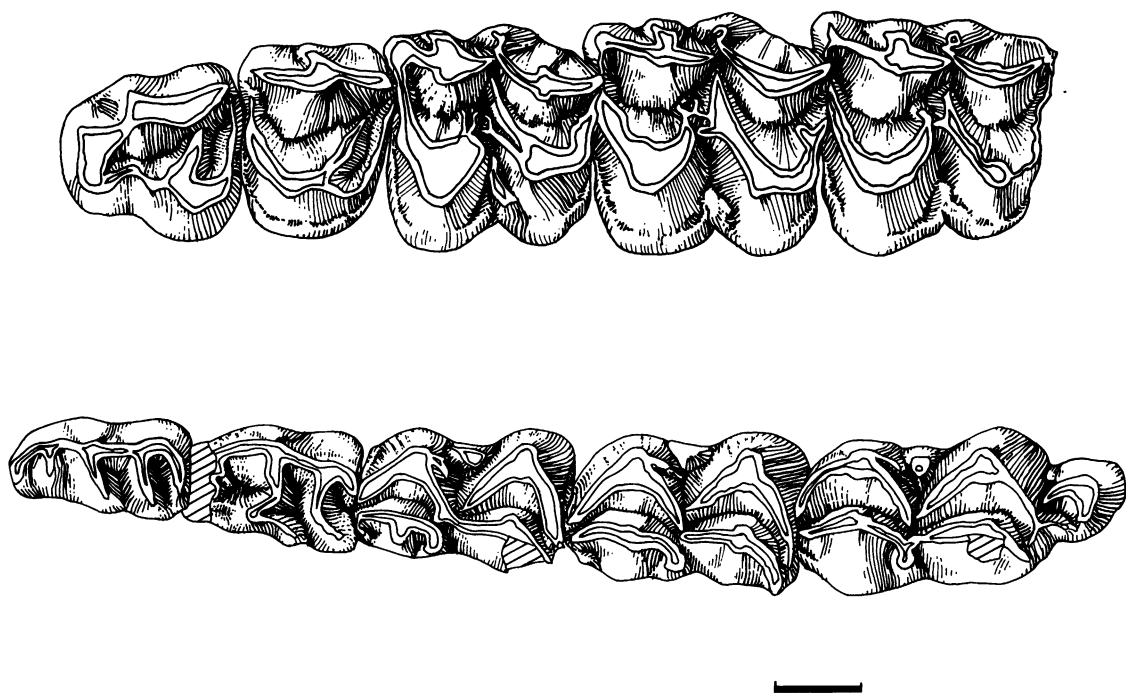


Fig. 15. *Palaeomeryx bojani*, left P3-M3, BMNH 29623 and right p3-m3, BMNH 21868, Sansan (middle Miocene), France. Bar = 10 mm.

the genus possesses a number of characters which suggest that it is a more derived pecoran than the level of the Giraffoidea. The presence of an entostyle (character 15) raises the genus to the level of the cervoid/bovid dichotomy, and the character of a closed metatarsal gully (character 28b) is a synapomorphy linking *Prodremotherium* with the cervoids. The raised lip of the cubonavicular facet (character 32d) is a plesiomorphic feature for the Pecora, and while the morphology of the proximal metatarsus of *Palaeomeryx* is generally cervoid in appearance, this feature cannot be used to exclude the genus from the position of sister taxon to the Giraffoidea. *Palaeomeryx* also possesses a number of characters which are undoubtedly of a derived cervoid condition. These include: a *Palaeomeryx* fold (character 20); a sabrelike upper canine (character 11b, also noted in a specimen attributed to *Palaeomeryx magnum* in the collections of the Musée Gimet in Lyon, France, from the la Grive St. Alban collections of the Middle Miocene of France, LaG. 15280); and a posterior tuberosity on the metatarsus (character 31). This last char-

acter suggests a level of cervoid evolution above the level of the Antilocapridae.

Sigogneau (1968) hinted at a relationship between *Palaeomeryx* and *Amphitragulus* in describing a number of dental synapomorphies; these were: a weak metastyle in the upper molars, especially on M3 (character 16b), an attenuated metacone on P4 (character 17b), and a posterior lobe of m3 which had a double loph with a closed posterior valley (character 26a). We would add to this list the posterolingual groove on p4 (character 25), a feature which is also characteristic of giraffoids (Hamilton, 1978a). These dental characteristics are also seen in the blastomerycid *Parablastomeryx*, but this genus has a moschid type of auditory bulla (character 10) (Webb and Taylor, 1980), and an undoubtedly single lacrimal orifice. However, what is interesting about this suite of cranial and dental characters is that—along with the derived cervoid character of a closed metatarsal gully (character 28b), a variably present posterior tuberosity (character 31), sabrelike upper canines in the males (character 11b), and the presence of a double lacrimal orifice

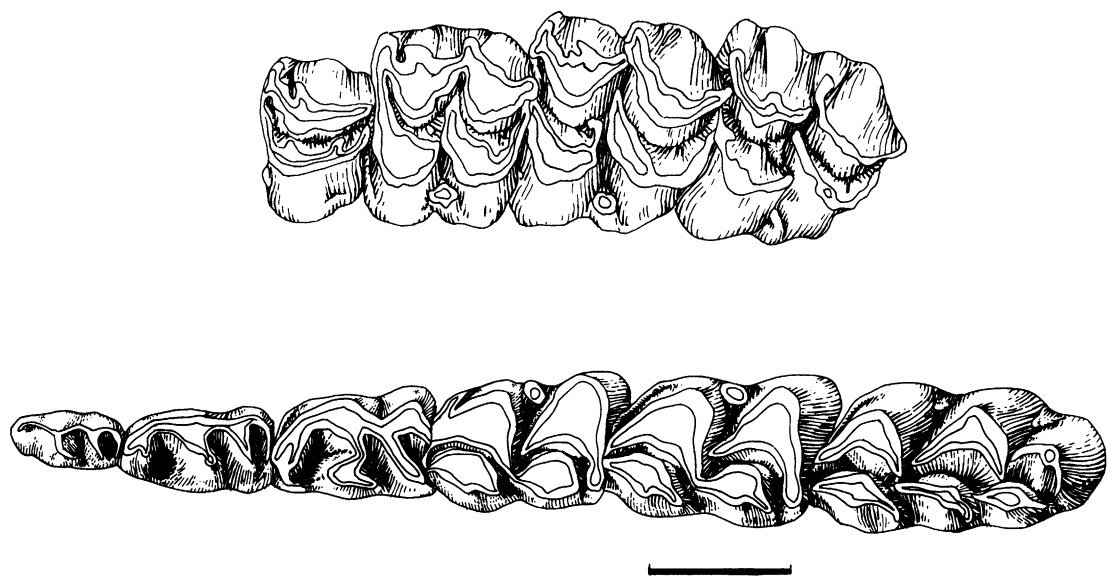


Fig. 16. *Subdromomeryx wilsoni*, left P4–M3, F:AM 52933 and right p2–m3, F:AM 32488, Olcott formation (middle Miocene), North America. Bar = 10 mm.

(character 9) (at least in *Amphitragulus*, the situation in *Palaeomeryx* being as yet undetermined in our opinion)—they are all shared with the North American dromomerycids. (See figs. 15 and 16 for dentition of *Palaeomeryx* and *Subdromomeryx*.) Features shared by *Palaeomeryx* and early dromomerycid genera include the bifurcation of the posterior wing of the metaconule (character 19b) and the presence of a lacrimal fossa (character 8) although, as previously discussed, neither of these features is unique to these genera (although their occurrence in combination may well be unique). The limbs of *Palaeomeryx* are somewhat more derived than in *Amphitragulus* and the dromomerycids, as the tubercle for metatarsal V is fused with the proximal surface of the metatarsal (character 30b) (although we do not know the condition in the Chinese species of *Palaeomeryx*.)

Aletomeryx is the only dromomerycid that does not possess this derived suite of dental characters, and additionally lacks a posterior tuberosity on the metatarsus. It is a problematical genus in many respects. It is dentally advanced for a dromomerycid in its possession of small entostyles, its lack of a *Palaeomeryx* fold, and its lack of metastylids (except for a small metastylid on m3). However, these

progressive characters may merely be linked with the level of hypsodonty, as their teeth resemble the more simplified teeth of hypsodont bovids and antilocaprids. The complete lack of a posterior tuberosity is also problematical, but as limb proportions of their genus suggest a preference for a more open habitat than that seen in any other dromomerycid, or in most living cervid genera (Scott, unpubl. data; see also Janis, 1982), the absence of a posterior tuberosity could be correlated with ecological considerations. (Among the Bovidae, a slight posterior eminence is seen in the woodland-dwelling tribes Tragelaphini and Cephalophini, but is absent in the more open-habitat lineages.) In light of the absence of good synapomorphic characters uniting either the Antilocaprinae or the Dromomerycidae, and their similarity in the position of cranial appendages, we have considered the possibility that *Aletomeryx* may represent an early offshoot of the Antilocaprinae. However, pursuit of this idea awaits more detailed studies of ruminant basicranial regions. The genus *Rakomeryx* is also problematical because, despite the variable presence of a posterior tuberosity and the derived features of the lower dentition, it has a prominent metastyle and a large metacone on P4.

These problematical genera notwithstanding—

ing, we suggest that this suite of characters constitutes a basis for reestablishment of the family Palaeomerycidae, to include *Palaeomeryx*, *Amphitragulus*, and the dromomerycids. Further material of *Palaeomeryx* and study of basicranial similarities between *Amphitragulus* and the dromomerycids would be needed to confirm this hypothesis, as would confirmation of our hypothesis that the condition of the lacrimal orifices in *Palaeomeryx* may actually have been double. *Prolibytherium* may also be included in this ruminant clade (see discussion in following section). The dental material of *Triceromeryx* depicted by Crusafont-Pairó (1952) does not demonstrate any of these derived dental characters, with the exception of the posteroventral groove on p4 used by Hamilton (1978a) to unite this genus with the Giraffidae, although the presence of a *Palaeomeryx* fold implies cervoid affinities. We would leave the genus as cervoid incertae sedis, rather than include it with the Palaeomerycidae. As previously mentioned, the isolated molars from Gebel Zelten ascribed to *Zarafa* by Hamilton (1973) bear dental similarities to *Palaeomeryx* and may possibly represent an African palaeomerycid.

Certain members of the Palaeomerycidae are also characterized by the evolution of supraorbital, unbranched, nondeciduous cranial appendages. These may well have been homologous between *Palaeomeryx* and the dromomerycids. The isolated appendage described by Ginsburg and Heintz (1966), and the line of suture between the appendage and the skull described by Qiu et al. (1985) in one of the Chinese specimens of *Palaeomeryx tricornis*, suggest that the appendages were formed initially from a dermal structure fusing with skull, as in giraffids. However, in other respects (especially in the possession of an occipital appendage) the appendages are at least superficially similar to those possessed by the North American dromomerycids, although it has been suggested that these appendages represent frontal outgrowths (Bubenik, 1982). The additional dental synapomorphies shared by *Palaeomeryx* and the dromomerycids suggest that this genus shares a closer common ancestor with the North American forms than does *Amphitragulus*, and that the type of cranial appendages (in-

cluding the development of an occipital appendage) may have been shared by this common ancestor. We are impressed by the similarity of *Palaeomeryx tricornis* with the earliest known dromomerycid *Barbouromaryx trigonocorneus*, both superficially in general morphology (especially of the cranial appendages), but also in the details of the skull and dentition discussed in this section. Finally, the limbs of *Palaeomeryx* are somewhat more derived than in *Amphitragulus* and the dromomerycids, as the tubercle for metatarsal V (character 30b) is fused with the proximal surface of the metapodial.

ZARAFa AND PROLIBYTHERIUM

Zarafa zeltini and *Prolibytherium magneiri* were pecoran taxa known only from the Gebel Zelten, in the lower Miocene of Libya. *Zarafa* was about the size of a fallow deer (*Dama dama*) and *Prolibytherium* was about the size of a roe deer (*Capreolus capreolus*) (Hamilton, 1973). Both possessed lacrimal fossae (character 8), which Hamilton (1973) considered to be a primitive pecoran feature, and *Zarafa* also appears to have possessed an antorbital vacuity. Both were characterized by unusual forms of cranial appendages: *Zarafa* had supraorbital appendages with a dorsolateral orientation (the basal part of the ossicone alone is preserved), and *Prolibytherium* had flattened, horizontal winglike cranial appendages divided into anterior and posterior lobes in a butterflylike pattern. The grooves on the surface of the cranial appendages of *Prolibytherium* suggest a vascularized, skin-covered structure (see Hamilton, 1973; Churcher, 1978). *Zarafa* has been variously assigned to the "Palaeomerycidae" (Hamilton, 1973), or to the Giraffoidea (Hamilton, 1978a, 1978b; Churcher, 1978). Churcher described *Zarafa* as a "palaeotragine," while Hamilton (1978a) synonymized the genus with *Canthumeryx*. Heintz et al. (1981) described the skull of an upper Miocene giraffoid from Iraq (*Injanatherium hazimi*) which appears to be very similar to *Canthumeryx*, and may represent part of a radiation of Miocene giraffoids with these peculiar types of cranial appendages. Hamilton (quoted personal commun. in Patterson, 1981), later suggested that *Zarafa/Canthumeryx* might also

be synonymous with the genus *Progiraffa*, described from India by Pilgrim (1911). *Prolibytherium* was originally referred to the Giraffidae, subfamily Sivatheriinae, on the basis of its palmated cranial appendages (Hamilton, 1973; Churcher, 1978), but was later reassigned to "*Pecora insertae sedis*" (Hamilton, 1978a, 1978b). The anterior dentition is unknown in both taxa.

As previously noted, there is a problem with the dental material from Gebel Zelten referred to *Zarafa* by Hamilton (1973). These teeth are too large to belong to the same taxon as the type specimen of *Zarafa* (a skull with fragmentary dental remains), and their preservation appears to be of a different type. These teeth resemble those of *Canthumeryx* in the possession of a bifurcated metaconule (character 19b), but this dental feature is also seen in *Palaeomeryx* (Qiu et al., 1985). In addition, these teeth possess an entostyle derived from the anterior surface of the metaconule (character 15) which, as previously noted, is a character seen primarily in *Pecora* of a higher level than the Giraffoidea. We have never observed an entostyle in any specimens of *Canthumeryx*, and an entostyle is not observable in the type of *Zarafa*, where the lingual portion of M3 is preserved. Hamilton (1973) also assigned postcranial material from Gebel Zelten to *Zarafa* on the basis of size sorting and general "palaeotragine-like" similarities, in which the metatarsal gully was open. We concede that Hamilton may be correct in synonymizing *Zarafa* with *Canthumeryx*, but see no compelling reason for it. We regard the disassociated teeth ascribed to *Zarafa* as problematical, and possibly belonging to a palaeomerycid taxon (*sensu* our definition in this paper).

In contrast, *Prolibytherium* presents a more complex problem. The teeth associated with the type in the BMNH are all heavily worn, and it is impossible to tell if a *Palaeomeryx* fold (character 20) was present in the unworn condition. Later material assigned to this genus in l'Institut de Palaeontologie, Paris, includes a lightly worn lower dentition which lacks a *Palaeomeryx* fold. However, as noted by Hamilton (1973), *Prolibytherium* is a fairly hypsodont taxon (about as hypsodont as the dromomerycid *Cranioceras*, in which the *Palaeomeryx* fold has already been lost). The upper molars of *Prolibytherium* show the typ-

ical "palaeomerycid" features of an entostyle (character 15), a small metastyle (character 16b), and an attenuated metacone on P4 (character 17b) (seen in BMNH 21901). The lower molars show a condition that could possibly represent an incipient double loph on m3 (character 26a) (BMNH 21899), noted by Hamilton (1973) as a "weak ectostylid in addition to the hypoconulid." The teeth of *Prolibytherium* also show the primitive features of a small M3 metaconule (character 18a), and a somewhat posteriorly situated protocone on P2 (P3 is missing from the dentition) (character 14a). p4 shows the primitive pecoran condition of a small metaconid, but has a vertical groove on the posterolingual region (character 25). As previously noted, this could be suggestive of either giraffoid or palaeomerycid affinities.

Hamilton (1973) described both *Zarafa* and *Prolibytherium* as having a double lacrimal orifice (character 9), although this assertion was refuted by Leinders (1983). Reexamination of the material shows that the type of *Zarafa* (BMNH 26670) appears on first inspection to have had a double orifice, but the dorsal "orifice" is clearly a postmortem break in the anterodorsal orbital wall, and in any case is situated too far dorsally above the more ventral orifice to resemble the cervoid condition. (Additional breaks of similar appearance are also apparent in the upper dorsal orbital rim.) The condition in *Prolibytherium* is more convincing. In one preserved skull fragment (BMNH 26679) the orbit is broken in a critical position midway along the anterior rim. However, there is a definite dorsal orifice visible on the preserved portion of the rim, and just ventral to this is a bony spur highly reminiscent of the spur seen between the two lacrimal orifices in cervids. However, the orbital rim is completely broken off just ventral to this spur, so it is impossible to ascertain if a more ventral orifice was actually present. (None of the other skull fragments preserve any anterior portion of the orbital rim.) However, what *is* preserved of the morphology of the orbital rim does appear very cervoidlike, and we are prepared to believe that a cervoidlike double lacrimal orifice was indeed present.

Hamilton (1973) described the brain of *Prolibytherium*, and decided that it was closely comparable to the brain of *Dremotherium*,

but also stated that these similarities may simply reflect primitive pecoran features. He also noted that the petrosal was more similar to that of the living cervid *Capreolus* than to present-day giraffids, but the polarity of these characters has not as yet been ascertained. Hamilton (1973) also assigned certain disassociated postcranial elements, which were similar to those of *Capreolus* in certain respects, to *Prolibytherium* because he believed certain features of its skull were cervidlike. These postcranial elements included an astragalus and calcaneum that bore similarities to those of *Palaeomeryx*, and a metatarsal with an open gully, which is not typical of either *Palaeomeryx* or *Capreolus* (or any other cervid). However, he describes the gully in this metatarsal as being very restricted in the region just proximal to the condyles. It may thus represent an immature specimen in which the distal bridge over the gully was not yet fully formed. We have not had the opportunity to examine this specimen and thus cannot comment further on its probable affinities. In any event, there seems to be little reason to firmly associate this postcranial material with *Prolibytherium*.

We would suggest, on the basis of the dental morphology and the probable cervoidlike condition of a double lacrimal orifice, with the additional assumption that the metatarsal with an open gully was misinterpreted, or wrongly assigned to this genus, that *Prolibytherium* may have been a palaeomerycid of some sort. Obviously, additional material would be necessary before we could be confident of this assignation.

ANTILOCAPRIDAE

Both merycodontines and antilocaprids share the derived characters of a closed metatarsal gully (character 28b) (variably open in merycodontines) and a double lacrimal orifice (character 9) (variably single in both subfamilies). Both subfamilies share the features of nondeciduous supraorbital cranial appendages that appear to be formed from outgrowths of the frontal bone, rather than by fusion of a separate dermal ossicone. However, as previously discussed, there is no firm evidence for the homology of these cranial appendages between the two subfamilies.

The cervoid feature of large upper canines

is never seen in known specimens of antilocaprids. While such canines are secondarily lost in antlered cervids, they tend to be retained as a primitive feature in early antlered cervids (such as *Dicrocerus*, persisting today in *Muntiacus* and *Elaphodus*) and in dromomerycids (i.e., *Barbouromeryx*, *Aletomeryx*, and *Sinclairiomeryx*), although they are somewhat reduced in these genera. Antilocaprids also lack any evidence of a *Palaeomeryx* fold, although as the earliest known antilocaprids are highly hypsodont, the absence of this character may not be significant. The entostyle and ectostylids are generally lacking in antilocaprids, but a small entostyle and ectostylid are present in some species of the earliest merycodontine genus *Paracosoryx* (e.g., *Paracosoryx minor* AMNH ESP 622-4745). Antilocaprids lack metastylids in the lower molars, but the reduction and loss of the metastylids is another progressive feature associated with increasing hypsodonty in ruminants, e.g., within the Bovidae and in *Aletomeryx* within the dromomerycids. (However, small metastylids may be seen in the unerupted molars of *Antilocapra americana*.) Both merycodontines and antilocaprids possess an antorbital vacuity.

In their limb characters, all antilocaprids share the characters of the raised lip of the cubonavicular facet (character 32d), but uniformly lack the posterior tuberosity on the metapodials that characterizes most higher cervoid lineages, that is completely absent only in the genera *Blastomeryx*, *Dremotherium*, and *Aletomeryx*. The form of the cubonavicular facet is not a uniquely cervoid feature, but the antilocaprid form bears a greater resemblance to the condition retained in the cervoids than that seen in the earliest bovids.

Antilocaprids are problematical because they possess no unique defining characters as a group; no unique characters can typify either the merycodontines or the antilocaprids. However, both subfamilies share a similar mixture of primitive and derived cervoid characters. A major problem is the question of whether the double lacrimal orifice in antilocaprids is homologous with that of other cervoids. The double orifice in antilocaprids is not completely cervidlike in nature (in contrast with the condition in dromomerycids, *Amphitragulus*, and *Hoplitomeryx*), as the

dorsal orifice may be placed inside the orbital rim, and the presence of a double orifice is variable (see Scott and Janis, 1987). However, the double orifice of *Antilocapra* bears a greater resemblance to the cervid condition than to the condition of the double lacrimal orifice occasionally found in bovine or tragelaphine bovids (see Leinders and Heintz, 1980, and discussion in Characters section). Leinders and Heintz (1980) consider *Antilocapra* to be definitely a cervoid and consider this trait to be a synapomorphy linking antilocaprids and cervids; on the basis of currently available evidence we would agree with their conclusions.

Assuming the double lacrimal orifice to be a true synapomorphy linking antilocaprids with cervids, we would consider the antilocaprids to have branched off the cervoid lineage above the level of the moschines, but below the level of the "Palaeomerycidae," because of the lack of even a variably present posterior tuberosity. (In addition, antilocaprids lack any of the derived dental characters of the Palaeomerycidae.) This would assume the original possession and subsequent loss of sabrelike canines in the antilocaprids (which, of course, has occurred numerous times within other cervoid lineages, linked with the evolution of cranial appendages), and would also assume the parallel evolution of the posterior tuberosity in *Moschus* and *Parablastomeryx* with the condition in higher cervoids. Regardless of the phylogenetic position of the Antilocapridae, if the "Moschidae" (sensu Webb and Taylor, 1980) are to be considered as a monophyletic group, this hypothesis would also entail the parallel evolution of the posterior tuberosity within this family independent of the cervid condition. We consider the phylogenetic position and the cladistic reality of the Antilocapridae to remain unresolved, and hope that the suggestions in this paper will stimulate other workers to further research on this topic.

OLIGOCENE AND EARLY MIOCENE "BOVIDS"

A variety of small, hypsodont taxa known primarily or exclusively from dental remains have been ascribed to the Bovidae. Trofimov (1958) claims the taxon *Palaeohypsodontus*

asiaticus as the earliest known bovid, from the middle Oligocene of Mongolia. The specimen consists of the two lower molars (m2 and m3), which are moderately hypsodont, and are about the size of the teeth of the living tragulid genus *Hyemoschus*. The teeth clearly belong to a pecoran ruminant, as they possess metastylids (character 21), but are simplified in their morphology, lacking an anterior cingulum and ectostylids, and show no trace of a *Palaeomeryx* fold. Trofimov (1958) considers these teeth to belong to a bovid because of the crown height, and the absence of a *Palaeomeryx* fold and other accessory styles that usually characterize cervoid molars. However, as previously discussed, such features are also lost in the teeth of mesodont or hypsodont cervoids (for example, the progressive loss of these features is documented in the three tribes of dromomerycids). The absence of such dental features is certainly not diagnostic of bovids, as such dental morphology is also typical of antilocaprids (to give but one example). Indeed, some American palaeontologists have claimed *Palaeohypsodontus* as the earliest merycodontine antilocaprid (Earl Manning, personal commun.). Other problematic early "bovids" include *Gobiocerus mongolicus* from the lower Miocene of Mongolia (Sokolov, 1952), *Hypsodontus miocenicus* (Sokolov, 1949), and *Kubanotragus sokolovi* (Gabunia, 1973), both known from Belometcheskaia (middle Miocene of the north Caucasus). *Hypsodontus* may also be present in the Miocene of Yugoslavia (Pavlovic and Thenius, 1959). Thomas (1984) discusses these taxa, concluding that *Gobiocerus* and *Hypsodontus* may be synonymous, and that the differences in size between the fragmentary portions of cranial appendages at Belometcheskaia, attributed to *Hypsodontus* (small) and *Kubanotragus* (large), may be due to sexual dimorphism rather than to the presence of two different taxa.

All these dental remains do undoubtedly resemble those of present-day neotragine ("dwarf") antelope in size and morphology, but there is nothing specific that allies them with bovids, and they may equally well represent small cervoids of some sort (moschoids or antilocaprids). Neither are the fragmentary remains of cranial appendages at Belometcheskaia unequivocally bovid in na-

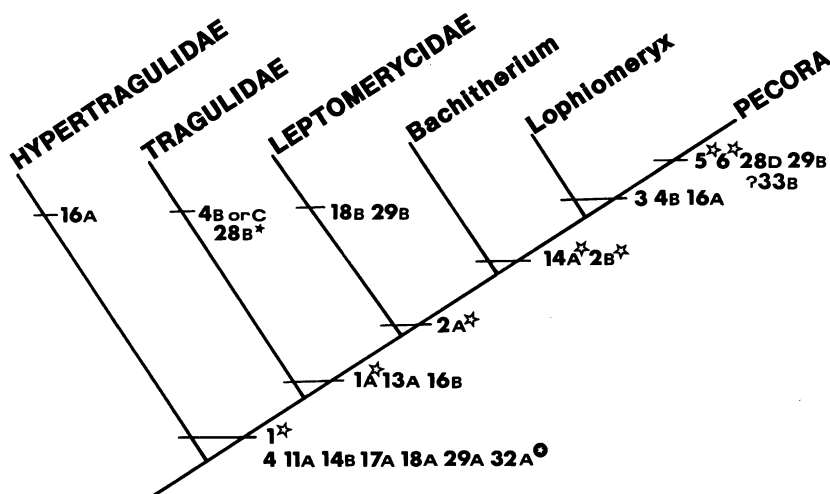


Fig. 17. Position of the Pecora within the Ruminantia. See table 1 for key to characters.

● = primitive characters for the Ruminantia (not necessarily unique).

☆ = unique characters for clade.

★ = character derived in parallel with condition in pecorans.

ture. It is our opinion that these "bovid" taxa should be classified as Pecora incertae sedis until more material is known. To classify them as bovids is misleading in terms of drawing conclusions about the time and place of the origin of the Bovidae.

CONCLUSIONS

The presence of derived cervoid characters, such as the closed metatarsal gully (character 28b) and the *Palaeomeryx* fold (character 20) within the primitive Pecora assigned to the "Gelocidae," leads us to the conclusion that the higher Pecora did not have a single common ancestry from within the "Gelocidae," but must have been derived independently from within the diversity of primitive pecoran taxa. If this is indeed the case, then certain conclusions must be drawn about the probable parallel evolution of certain character states that are shared by more advanced ruminants. We previously discussed the fact that cranial appendages (character 7) and complete distal metapodial keels (character 27) are likely to have evolved in parallel among the higher pecorans. Further characters that apparently evolved in parallel are the presence of a larger metaconule on M3 (character 18b) and a lingually directed pro-

tocone on P3 (character 14b). Evidence for the parallel evolution of these character states can be gained by noting the conflict of these characters with those held synapomorphous of higher pecoran lineages. Both primitive dental features are retained in the genera *Walangania* and *Propalaeoryx*, animals which have complete distal metapodial keels. A posteriorly directed protocone on P3 is retained to a lesser extent in both *Dremotherium* and *Eotragus*, and many antlerless cervoids retain an M3 with a small metaconule.

Given the assumptions that the aforementioned characters have been acquired in parallel by higher pecoran lineages, we have arrived at the following conclusions about the origins of the pecoran superfamilies. Figure 17 depicts the position of the Pecora within the Ruminantia, and figure 18 presents a cladogram of the families within the Pecora. The origin of the Cervoidea (including the Cervidae, Moschidae, Antilocapridae, and "Palaeomerycidae," as we have redefined it) is the most readily apparent. The genera *Eumeryx*, *Rutitherium*, and "*Gelocus*" *whitworthi* possess the derived cervoid character of a *Palaeomeryx* fold (character 20), and *Eumeryx* (at least) possesses the derived characters of an incipient entostyle (character 15a) and a closed metatarsal gully (character 28b).

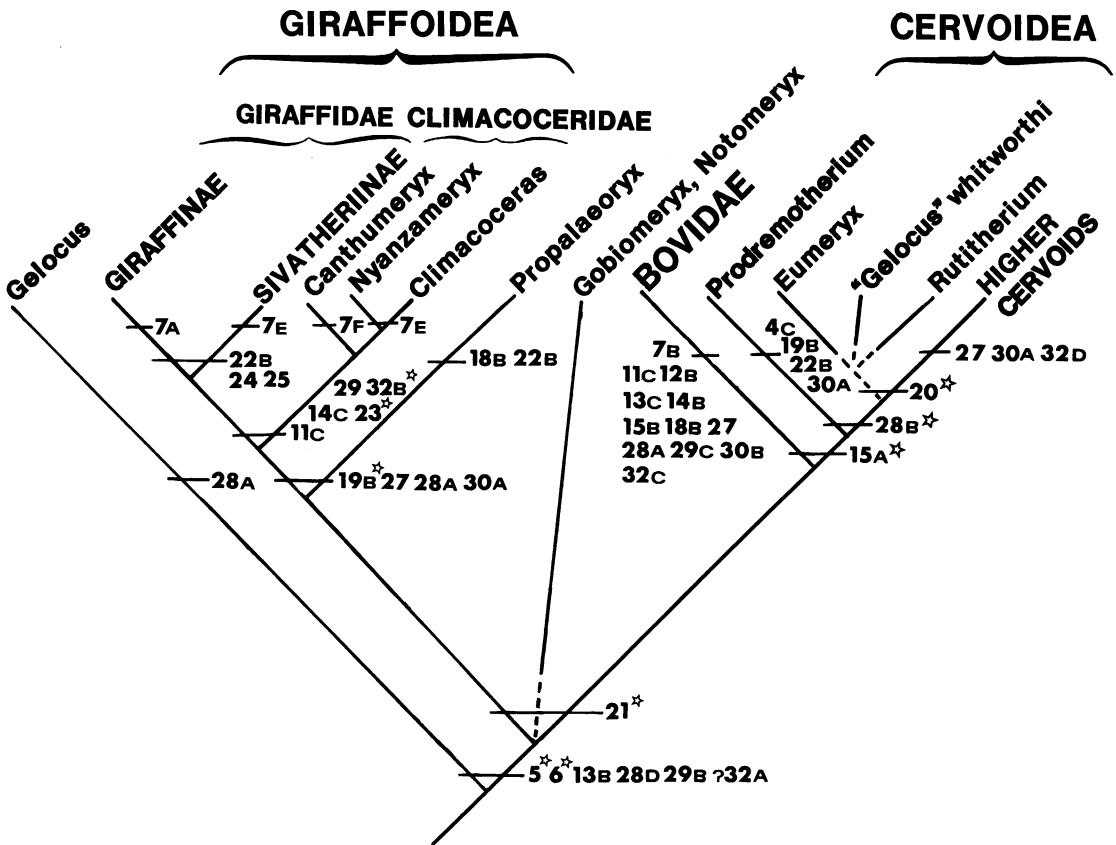


Fig. 18. Interrelationship of pecoran families. See table 1 for key to characters.

We would thus include our definition of the Cervoidea (in the cladistic sense) to include such genera.

The origins of the Giraffoidea and the Bovidae are less clear. If we consider that the presence of an entostyle derived from the anterior face of the metaconule (character 15) to be a true synapomorphy linking the Bovidae with the Cervoidea, it follows that the Giraffoidea remain as the most primitive of the pecoran superfamilies. Bovids and cervoids may also be united by the soft anatomy feature of a more ventrally positioned entrance of the esophagus to the rumen (see discussion in Characters section). With the exception of the postorbital horn cores (character 7b), no apomorphic feature can be found to unite the Bovidae. The absence of a closed metatarsal gully (character 28b) suggests that their divergence from the post-giraffoid pecoran lineage was below the level of *Prodeumeryx*. However, given the fact that

we have clearly shown in this paper that an open metatarsal gully can be secondarily derived from a closed one, there remains a possibility that bovids may share a more recent common ancestor than *Prodeumeryx* with cervoids.

The Giraffoidea are defined by two distinct apomorphies: the presence of a bilobed lower canine (character 23) (Hamilton, 1978a) and the possession of a posterior cubonavicular facet on the proximal metatarsus that is elongated and flat (character 32b). An entostyle derived from the anterior face of the metaconule is rarely a feature of giraffoids, which suggests a branching off from the pecoran lineage below the level of the Bovidae or *Prodeumeryx*. However, giraffoids possess metastylids in the lower molars (character 21), which suggests a more derived pecoran ancestry than *Gelocus*. The only known taxa which fall in this appropriate pecoran grade for giraffoid ancestry are the poorly known

Asian genera *Notomeryx* and *Gobiomeryx*. The condition of the metatarsal gully in these genera is not known, although the type of open gully seen in giraffoids (character 28a) might, as previously mentioned, represent the plesiomorphic condition for the Pecora. The African genus *Propalaeoryx* may possibly represent the sister taxon to the Giraffoidea, as originally suggested by Gentry (in Hendey, 1978). Like the giraffoids, *Propalaeoryx* lacks an entostyle and possesses an open metatarsal gully, but these are both plesiomorphic features. *Propalaeoryx* does not possess the giraffoid autapomorphy of the flat and elongated cubonavicular facet on the posterior metatarsus. To the best of our knowledge, the anterior dentition is not known, so it is impossible to ascertain the condition of the lower canine.

The only possible synapomorphy between *Propalaeoryx* and the Giraffoidea is the presence of a bifurcated posterior wing of the metaconule (character 19b). However, this is not a truly unique feature, as it is also seen in many palaeomerycids, and in a few cervids. Neither can a strong biogeographical case be made for uniting *Propalaeoryx* with the Giraffoidea. If Hamilton (quoted in Patterson, 1981) is correct in synonymizing *Progiraffa* with *Canthumeryx*, then the Giraffoidea may well have had an Asian origin, rather than an African one, as commonly supposed. Clearly, more fossil material of both Asian and African "gelocids" would prove invaluable in determining giraffoid relationships. For the moment, we would consider that a common ancestor for the Bovidae and the Cervioidea would lie among the primitive pecorans at just below the level of *Prodremotherium*, while the ancestry of the Giraffoidea is more distant, among more primitive pecorans which possess metastylids but which lack any evidence of an entostyle. We consider that *Propalaeoryx* may well represent the sister taxon to the Giraffoidea, but on the basis of the presently available evidence it is impossible to make a strong case for this hypothesis.

Within the Cervioidea, which we would define as pecorans possessing (primitively at least) a *Palaeomeryx* fold (character 20) as the defining autapomorphic character, we perceive the interrelationships as follows (see

fig. 19 for summary). *Eumeryx* (and *Rutitherium*) are clearly the most primitive cervoids, possessing a closed metatarsal gully (character 28b) and a *Palaeomeryx* fold (character 20); but lacking complete distal metapodial keels and possessing a primitive pecoran type of dentition. *Walangania* is clearly a cervoid based on the presence of a *Palaeomeryx* fold in *Walangania africanus*, and is more derived than *Eumeryx* in the possession of complete distal keels (character 27) (Whitworth, 1958). However, the primitive nature of the dentition, with the variable presence of a lingual cingulum in the upper molars (character 13b), the small metaconule on M3 (character 18a), the somewhat posteriorly situated and directed protocone on P3 (character 14a), and the apparent lack of a sabrelike upper canine, relegates *Walangania* to the most primitive branching off point in the cervoid phylogeny after *Eumeryx*. Like *Eumeryx*, *Walangania* lacks the fusion of metatarsal V.

We consider the Moschidae to be the next group to branch off the cervoid lineage. They are more advanced than *Walangania* in the following characters: a lingually situated and directed protocone (character 14b), a prominent entostyle in the more brachyodont genera (character 15b) (such as *Dremotherium* and *Parablastomeryx*), and the possession of a large, sabrelike upper canine (character 11b). The genus *Dremotherium* and the blastomerycines retain the primitive feature, also seen in *Walangania*, of a small metaconule on M3 (character 18a), but are more dentally advanced than more primitive cervoids in possessing a complete postentocristid in the lower molars (character 22b) (in all but some individuals of the early genus *Problastomeryx*). Moschids are more primitive than higher cervoids in the possession of a single lacrimal orifice.

We follow Webb and Taylor (1980) in uniting the moschid genera by the presence of a laterally enclosed, subcentral tympanohyal vagina on the auditory bulla (character 10), but note that the problem with this classification scheme is that it necessitates the parallel evolution of the posterior tuberosity of the metatarsus (character 31) in *Moschus*, *Parablastomeryx*, *Micromeryx*, and *Hispantomeryx* with the condition in higher cer-

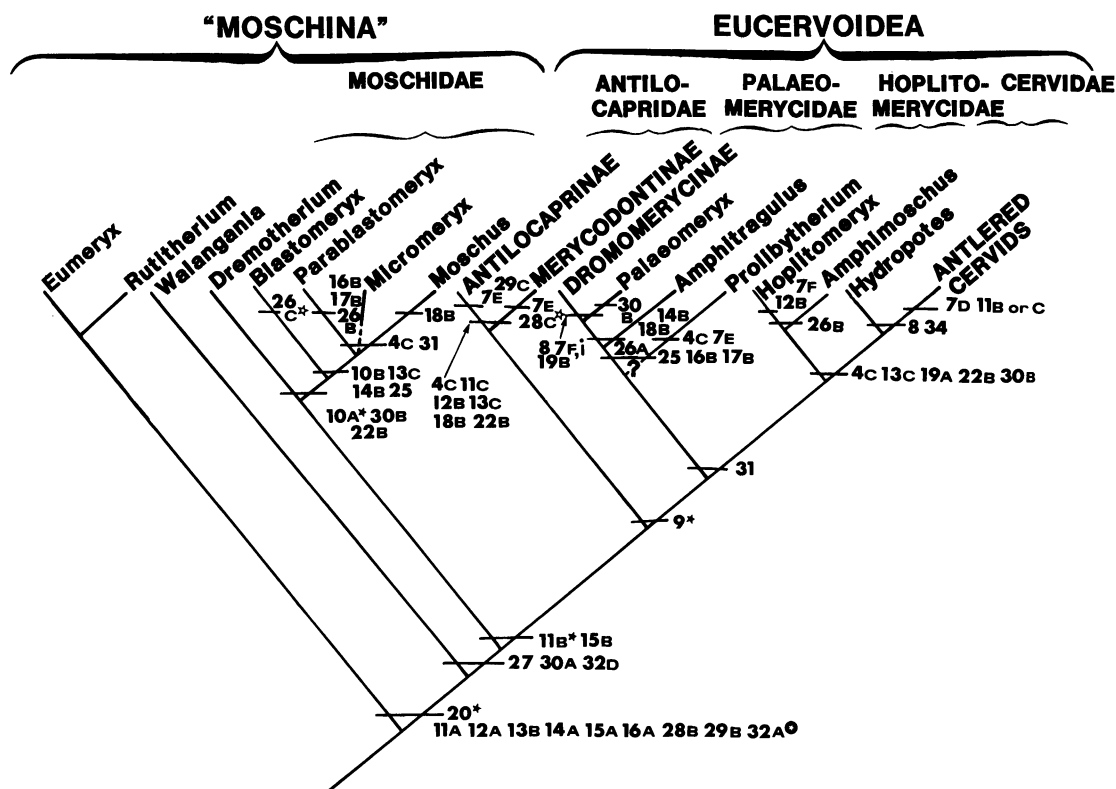


Fig. 19. Interrelationships within the superfamily Cervoidea. See table 1 for key to characters.

voids. All but the latter genus share the derived feature of the fusion of metatarsal V (character 30b).

The position of the Antilocapridae, as the next group to branch off the cervoid lineage, reflects our assumptions that the double lacrimal orifice (character 9) is a synapomorphy linking them with higher cervoids, and also that the posterior tuberosity (character 31) has evolved more than once within the Cervoidea. However, we note that no unique feature can be found to unite the Antilocapridae and, with the exception of the form of the cranial appendages, no unique feature can distinguish the Antilocaprinae from the Merycodontinae. It is not clear whether the cranial appendages of the two subfamilies are homologous although both contain genera with branched appendages and they may share a common developmental origin as an outgrowth of the frontal bone.

The next family to branch off the cervoid lineage consists of our tentatively redefined family Palaeomerycidae, including the gen-

era *Palaeomeryx* and *Amphitragulus*, possibly also the genus *Prolibytherium*, and the Dromomerycidae (which we would now relegate to subfamily status as the Dromomerycinae). As previously discussed, we are here making the assumption that more complete cranial material of *Palaeomeryx* will reveal the presence of a double lacrimal orifice (character 9). Palaeomerycids can otherwise be united by: the variable presence of a posterior tuberosity (character 31); the absence of fusion of metatarsal V in primitive members of each lineage; the retention of p1 (character 4b) in the primitive members of each lineage; a sabrelike upper canine (character 11b) in at least the early members of each lineage; and a dentition in which the meta-style is reduced (character 16b), the metacone is attenuated in P4 (character 17b), there is a posterolingual groove on p4 (character 25), and the posterior lobe on m3 possesses a double loph that is closed posteriorly (character 26a). We note that none of these features is unique in defining the family, but that this

suite of characters does characterize members of the three lineages (with the exception of the genus *Aletomeryx*, as mentioned previously, for which we make the assumption that these have been secondarily lost). It is not clear to us, on the basis of currently available evidence, whether the posterior tuberosity evolved independently within the Dromomerycinae, or was a primitive character, lost in some early taxa that were more open-habitat in their ecology (Scott, unpubl. data). However, on the assumption that some form of posterior tuberosity characterizes the primitive members of all lineages within the Palaeomerycidae, and the presence of a double lacrimal orifice in all taxa in which the orbital region is clearly observable, this character combination leads to the more derived position of the Palaeomerycidae in the cervoid phylogeny than the Antilocapridae. (Despite the fact that the posterior tuberosity has obviously arisen more than once within the Cervoidae, as evidenced by the presence of this character in the Moschidae, we consider this placement of the Palaeomerycidae to be the most parsimonious, as it only entails the parallel evolution of this character state twice.)

Within the Palaeomerycidae, we note that the genus *Palaeomeryx* can be united with the dromomerycids (or at least with some of the earlier genera) by the presence of a bifurcation of the posterior wing of the metacnule (character 19b), although we note that this character is also seen in *Propalaeoryx* and in some early giraffoids (*Canthumeryx* and *Palaeotragus*). If *Palaeomeryx* and the dromomerycids really do share a more recent common ancestry than *Amphitragulus*, then it might be reasonable to assume that the form of cranial appendages in both (supraorbital appendages that appear to have been formed in a giraffidlike fashion from fusion of a dermal ossicone with the skull, and the additional presence of a single median occipital ossicone) was inherited from a common ancestor. However, we would note, while endorsing this hypothesis, that a similar morphology of the cranial appendages is seen in the genus *Triceromeryx*, which lacks many of the palaeomerycid derived dental characters. We would prefer to leave *Triceromeryx* as "cervoid insertae sedis" for the time being. However, we note that another prob-

lematical genus, *Prolibytherium*, which like *Triceromeryx* has also been linked to the giraffoids in past classificatory schemes, may actually be a better candidate for palaeomerycid affinities on the grounds of dental morphology, although the very peculiar cranial appendages can probably not be homologized with those of *Palaeomeryx* and the dromomerycids. We also note that the isolated molars at Gebel Zelten ascribed to *Zarafa* by Hamilton (1973) cannot belong to the skull of *Zarafa* from this locality, and may belong to some unknown African species of *Palaeomeryx*.

Cervoids higher than the palaeomerycids can be characterized by the invariable presence of the posterior tuberosity (character 31), combined with the fusion of metatarsal V (character 30b); by the complete absence of p1 (character 4c); and possibly also by the primitive presence of a bifurcated protocone (character 19a). The bifurcated protocone is present in *Dicrocerus* and some living cervids (although not in *Hydropotes*), and while it is absent in *Hoplitomeryx*, it is present in *Amphimoschus*, which on other criteria appears to be the closest related genus to *Hoplitomeryx* (see Leinders, 1983). It may have been primitively present in *Hoplitomeryx*, and lost with the other cervoid features of the dentition that are usually lost in cervoids with the evolution of increasing hypsodonty, such as the entostyle, the ectostylids, and the *Palaeomeryx* fold. (The first two of these features are present in the more brachyodont *Amphimoschus*, but have been lost in *Hoplitomeryx*.) We follow Leinders (1983) in assigning *Hoplitomeryx* to its own family, the Hoplitomerycidae, and tentatively place *Amphimoschus* in the same family, despite the apparent lack of cranial appendages, on the basis of similarities of the cranium and the possession of a double loph on the posterior lobe of m3 that is open posteriorly (character 26b) (see Leinders, 1983).

Finally, we would group *Hydropotes*, the living antlerless cervid, with antlered cervids on the basis of possession of the lacrimal fossa (character 8), as well as the common features of soft anatomy (character suite 34). The lacrimal fossa is found throughout antlered cervids, and while it does occur in parallel among other isolated pecoran genera (as

previously discussed), at this level of cervoid evolution it may be considered a valid character state, especially as a lacrimal fossa is absent in *Hoplitomeryx* (Leinders, 1983). (The condition of the lacrimal fossa in *Amphimoschus* is unknown.) We would agree with Chow and Shih (1978) in assigning *Lagomeryx* and other related "lagomerycid" genera to the subfamily Muntiacinae within the Cervidae.

On the assumption that the double lacrimal orifice (character 9) has evolved only once within the Cervoidea, we would group the Antilocapridae, Palaeomerycidae, Hoplitomerycidae, and Cervidae in the higher cervoid assemblage Eucervoidea. The term "Moschina," originally used by Webb and Taylor (1980), could then be used as a paraphyletic grouping of other cervoids (as defined by the presence of a *Palaeomeryx* fold,

character 20). Our final conclusions in figures 18 and 19 represent our tentative summary of the interrelationships within the pecoran genera that we consider to be the most parsimonious, based on the presently available evidence from living animals and the existing fossil record. It is our hope that these proposed phylogenies, with or without the discovery of additional fossil evidence, will stimulate other workers in ruminant taxonomy to support or refute our hypotheses, as we consider the evolution of the higher ruminant grade, with the capacity of its members for enormous physiological and ecological flexibility in the evolution of cursorially adapted animals capable of dealing with vegetation of high cellulose content, to be one of the more interesting areas of mammalian evolution.

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