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Cranial and postcranial morphological data in ruminant phylogenetics

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Abstract

While the identity and validity of the extant families of ruminants are undoubted, there are significant problems with the determination of the interrelationships among the families, notably within the families of the Pecora, or horned ruminants. The morphological features used to construct ruminant phylogeny have been a source of controversy: many features used over the past century have been shown to be highly homoplastic and related to functional similarities. Ruminants evolved in the context of the later Cenozoic climatic changes, and many lineages adopted functional morphological adaptations related to feeding on more abrasive diets (resulting in the parallel evolution of a greater extent of loph development in the molars and, in some lineages, hypsodonty) and locomotion in open habitats (resulting in the parallel evolution of fused metapodials and reduction and/or loss of lateral digits). The fact that the molecular phylogeny shows a very different pattern from the currently accepted morphological one is of particular cause for concern, especially as molecular data are of no use for understanding the relationships of extinct lineages. Here we review the morphological data used in ruminant phylogenetics, and show even many of the less obviously functional features (e.g., number and position of the lacrimal orifices) are subject to homoplasy and variation, especially when fossil taxa are included. In addition, many morphological features treated as independent traits in phylogenetics are correlated (e.g., cranial morphology associated with hypsodonty). Some potentially reliable features are identified, but these do not help to sort out relationships within the Pecora. We advocate for the investigation into better morphological features, possibly derived from basicranial and ear region characters (although these features are not without their own issues of homoplasy), and for caution in character consideration in performing phylogenetic analyses.

Key words: Ruminants, systematics, phylogenetics, morphology, Pecora, traguline, bovid, cervoid, giraffoids, moschid.

1. Introduction

This paper provides a review of the morphological characters that have been used to unite clades (usually families) within the Ruminantia. A persistent problem with ruminant systematics is that, although the different families can usually be defined by discrete synapomorphies (and the compositions of the extant families are borne out by the molecular data), with the exception of the unity of the extant Pecora, and the monophyly of the extant families, there is much confusion and debate as to the relationships among the different families, extinct and extant. Part of the problem is that the characters that have been used to group lineages of ruminants are subject to much homoplasy: this paper will discuss these characters and their utility in ruminant systematics.

1.1 History of ideas about ruminant systematics

Fig. 1 shows the scientific consensus in the mid twentieth century (e.g., Pilgrim 1941; Simpson 1945; Romer 1966). Ruminants have long been united by a suite of characters: fused navicular and cuboid bones in the tarsus, loss of the upper incisors, and an incisiform lower canine. Pecorans were united by their stomach anatomy (presence of an omasum) and physiology (rumination with cud-chewing), plus the possession of fused metapodials. The hornless musk deer (*Moschus* spp.: Moschidae) were usually considered to be the sister taxon to the horned ruminants. The Giraffidae and Cervidae were united in the Cervoidea, mainly by the retention of brachyodont molars. The Bovidae and Antilocapridae (when not included within the Bovidae) were united by hypsodont cheek teeth, a greater reduction and/or loss of the side toes than seen in cervids, and the retention

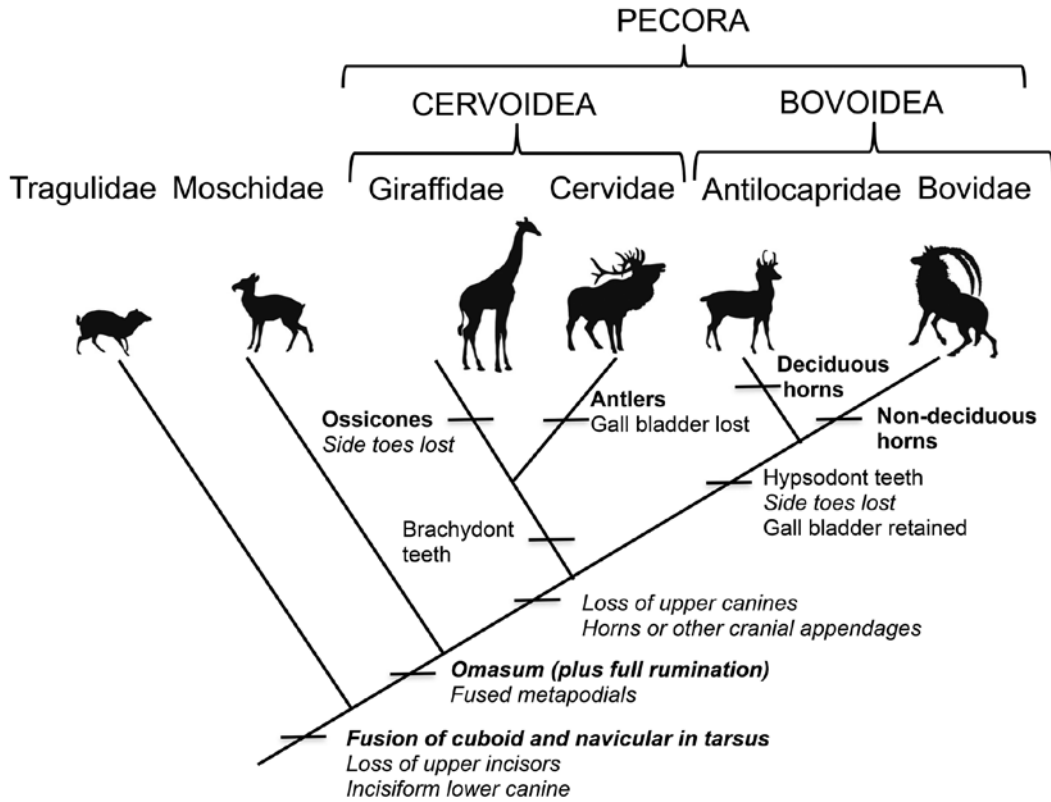


Figure 1: Historical overview of ruminant phylogeny ~1940. Key to characters: bold Roman = derived character, apomorphic; bold italics = derived character, synapomorphic; plain Roman = plesiomorphic character; plain italics = convergent character.

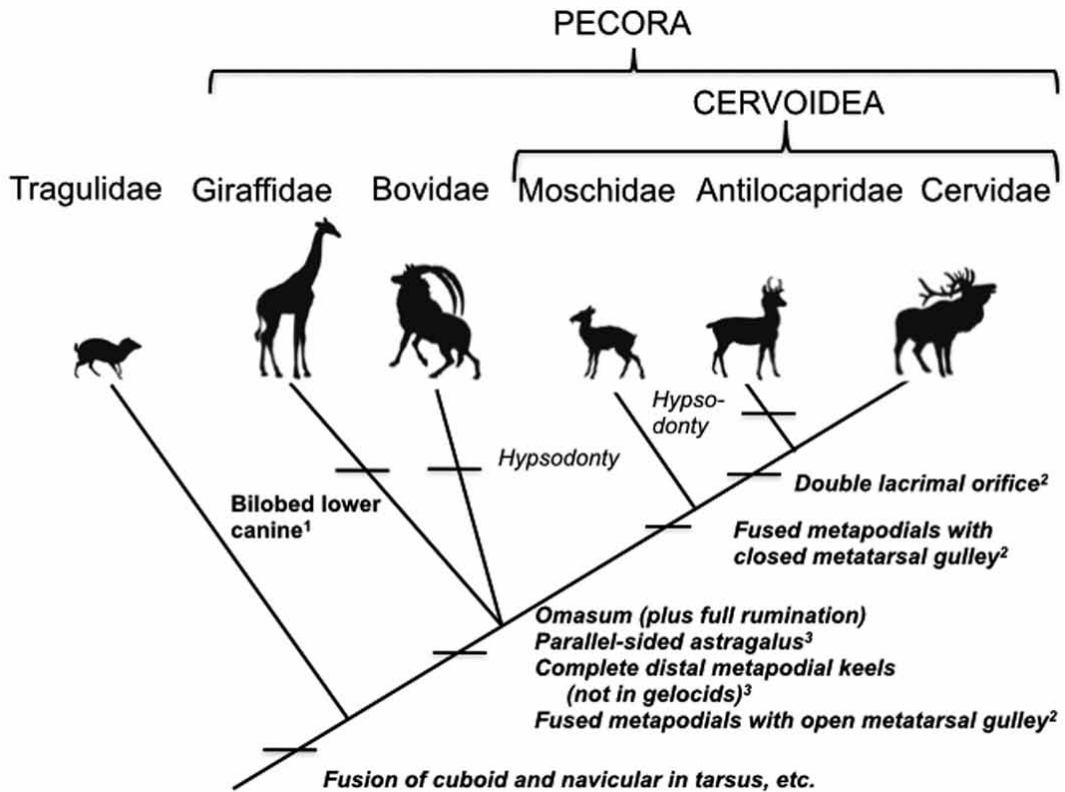


Figure 2: Historical overview of ruminant phylogeny ~1980. Key to characters: bold Roman = derived character, apomorphic; bold italics = derived character, synapomorphic; plain Roman = plesiomorphic character; plain italics = convergent character. 1 = from Hamilton 1978; 2 = from Leinders & Heintz 1980; 3 = from Webb & Taylor 1980.

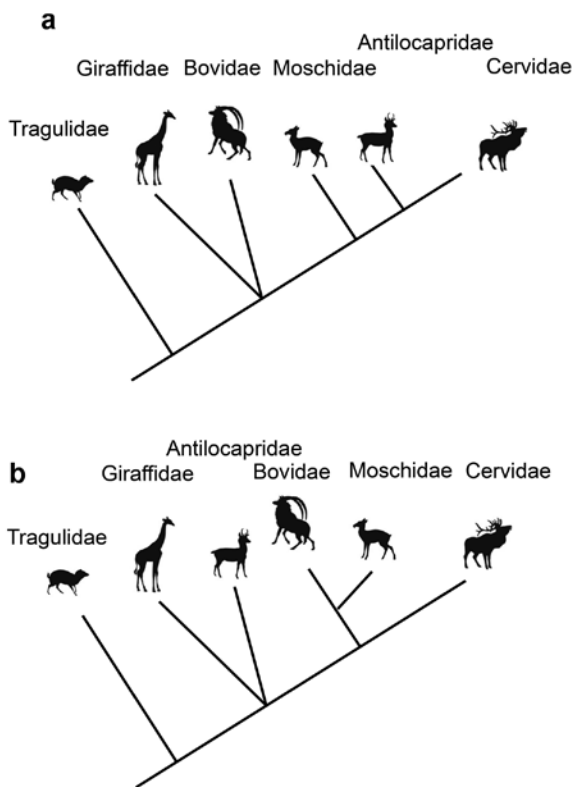


Figure 3: Ruminant phylogeny 2014. (a) morphological, (b) molecular.

of a gall bladder. With the exception of the omasum, which as a soft anatomy character is of no use for the placement of extinct taxa, none of these characters are viable synapomorphies; cranial appendages are not homologous in development among the pecoran families; brachydonty and presence of a gall bladder are primitive characters; hypsodonty, metapodial fusion, and reduction or loss of the lateral digits have occurred within other ungulate lineages (most notably in the Camelidae, within the order Artiodactyla), and are functionally associated with changing diets and locomotion associated with Cenozoic climate change (see later discussion).

Fig. 2 shows a consensus in ruminant phylogenetics in the late twentieth century. Roger Hamilton (1973) showed that a bilobed lower canine united a number of extinct African pecorans with the Giraffidae into a new version of the Giraffoidea. Joseph Leinders (Leinders 1979; Leinders & Heintz 1980) identified a number of characters that united many pecoran families into a new version of the Cervoidea: moschids were united with antilocaprids plus cervids by the presence of closed metatarsal gully, and antilocaprids and cervids were united by the presence of a double lacrimal orifice on the orbital rim. David Webb (Webb & Taylor 1980) showed that pecorans, including the extinct “gelocids” could be united by the possession of a compact, parallel-sided astragalus. Webb & Taylor (1980) also described ear region characters that could be used to unite various extinct hornless pecorans with the extant *Moschus*

into the Moschidae, but still considered that this was the sister taxon to the horned pecorans (contra Leinders). They also showed that the early occurring *Archaeomeryx*, despite retaining many primitive features of the locomotor system, possessed cranial features that placed it above the level of the extant Tragulidae, and they placed it as a basal member of the family Leptomerycidae.

The phylogenetic hypothesis in Fig. 2 was the framework for the phylogeny of Janis & Scott (1987). The original impetus for this work was the desire to determine the systematic position of the Miocene North American dromomerycids (now usually united with the European palaeomerycids into the Palaeomerycidae), but it turned into a much more extensive study with an attempt to place many extinct taxa, especially hornless forms. They extensively discussed the characters used for classification, and also suggested that the Giraffoidea might be the sister taxon to a united Bovidae plus Cervoidea.

The “gelocids” were shown to be a paraphyletic (or polyphyletic) assemblage of basal pecorans rather than a distinct family (Janis 1987; Janis & Scott 1987), and a number of them were placed into Leinders’ original concept of the Cervoidea. The European data collected for this study also led to a separate paper on the systematics of hornless ruminants, where the distinct identity of the taxa *Lophiomeryx* (and some related forms) and *Bachitherium* were noted, taxa that had previously been placed in the either within other traguline families or the “Gelocidae” (Janis 1987). Janis (1987) made the tentative suggestion that these taxa should be assigned their own families, and was somewhat dismayed to later discover that this proposal was being taken as gospel. The Lophiomerycidae is probably a viable family, but *Bachitherium* is probably best left as a plesion.

Fig. 3 shows a current view of ruminant phylogenetics. The morphological phylogeny of Janis & Scott (1987) has held up fairly well, but the molecular phylogenetics of the past decade (e.g., Hassanin & Douzery 2003; Price et al. 2005; Hassanin et al. 2012) have proposed a very different pattern of interrelationships among the pecoran families. About the only concordance with the morphological phylogeny is the monophyly of the Pecora. A potentially serious issue here is limited taxon sampling of some families (e.g., Giraffidae, Antilocapridae) due to extinctions, and possibly over-sampling of some families due to recent adaptive radiations (e.g., Bovidae), which may affect the topology of the phylogeny. The placement of the Moschidae as the sister taxon to the Bovidae is at complete variance with its former alliance with the Cervidae, but some morphological evidence from the basicranial region has been proposed to link these two families (Sánchez et al. 2010). None of the traditional morphological characters support the molecular phylogenetic pattern of the Antilocapridae and Giraffidae being basal to the other families.

1.2 Ruminant character homoplasy and Cenozoic climatic events

Many of the features characterizing different ruminant lineages (e.g., hypsodonty, loss or reduction of lateral digits) are functional ones that are best viewed against the backdrop of changing environmental conditions leading to changes in feeding and locomotion (see Fig. 4).

The earliest ruminants appeared around 42 million years ago in the late middle Eocene. This was a time of relative cooling and drying, following the Eocene Climatic Optimum, and the earliest ruminants were more derived than the basal “dichobunid” artiodactyls: all ruminants had teeth that were more selenodont than those of the than bunodont dichobunids, and they also all possessed limbs that showed a degree of elongation with morphology indicative of some restriction of motion to the parasagittal plane, both indicating adaptations to a more open forested habitat with a more folivorous diet. However, these early ruminants were still of small body size, with

teeth that were brachydont and bunoselenodont (indicative of a fairly non-fibrous folivorous/frugivorous diet), and limb proportions indicative of a closed habitat lifestyle (e.g., forelimbs shorter than hind limbs). Modern-day tragulids represent this type of ecomorphology and dietary/habitat preference today, although this was not true for the many of the extinct taxa (Claus & Rössner 2014).

A further diversification of traguline lineages, with the appearance of the Hypertragulidae, Leptomerycidae, and Tragulidae, as well as the “gelocid” pecorans, coincided with further cooling in late Eocene/early Oligocene times. These animals now showed adaptations for a more folivorous diet (longer faces, more selenodont cheek teeth with incipient hypsodonty in some forms), and for a habitat of more open woodland or scrub (longer legs, especially forelimbs; more restriction of limb motion to parasagittal plane, with reduction of lateral digits, tendency for fusion of metatarsals, etc.).

Finally, the radiation of the horned pecoran lineages coincided with the emergence of more open

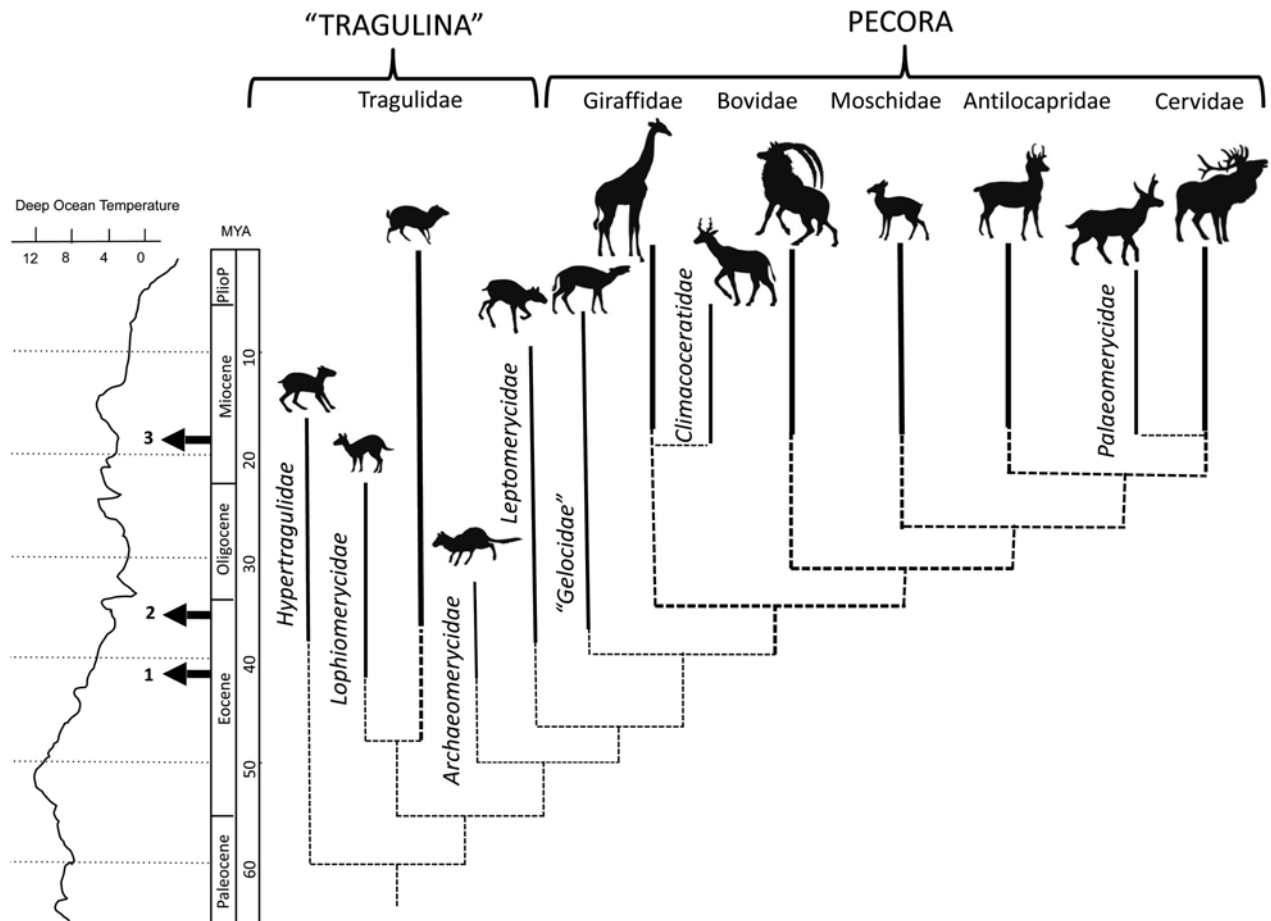


Figure 4: Ruminant phylogeny (according to Janis & Scott, 1987, & Métais and Vislobokova 2007) against the backdrop of climatic change. Roman type and thicker lines = extant families; italics and thinner lines = extinct families (not all shown). Dotted lines show phylogenetic relationships only, and do not indicate ghost lineages. Palaeotemperature curve from Zachos et al. 2001. **1**, Initial radiation of tragulines in the cooling phase of the late middle Eocene. **2**, Further radiation of tragulines, and appearance of gelocids, in the cool-temperate late Eocene/early Oligocene. **3**, Origin and diversification of pecorans with increasing temperatures and spread of more open habitats in the late early Miocene. Note that composition of the Moschidae shown here follows Sánchez et al. (2010) in including only the genera *Micromeryx*, *Hispanomeryx*, and *Moschus* (but also note that the radiation of the North American blastomerycids also began at a similar time, ending in the late Miocene). The North American taxa *Pseudoceras* and *Floridameryx* are considered as “gelocids” here.

habitats (including grasslands) in the early Miocene, and non-pecoran ruminants (with the exception of the Tragulidae) declined in diversity and abundance; all non-tragulid families were extinct by the end of the epoch. Most pecoran lineages showed (or underwent during the course of the Miocene) an increase in body size, with multiple lineages showing postcranial changes indicative of open habitat preference (longer limbs even more restricted to the parasagittal plane, fusion of metacarpals, development of complete distal metapodial keels, almost complete loss of lateral digits in some lineages), and many lineages showed adaptations for including grass in their diets (increasing hypsodonty). The evolution of cranial appendages at this point in time, apparently independently in different lineages, may be related to changing social structure correlating with habitat change (Janis 1982).

An understanding of changing ruminant palaeobiology, in correlation with changing global climate and environmental conditions, enables us to understand why so many morphological characters evolved in parallel in different lineages, and hopefully to take the probably homoplastic nature of these characters into account in phylogenetic analysis.

2. Morphological characters used in ruminant phylogenetics

2.1 Characters uniting the Ruminantia, and uniting clades below the level of the Pecora.

Fig. 5a shows the phylogeny of the Tragulina (the paraphyletic assemblage of non-pecoran ruminants) used in this discussion, based on the hand-drawn cladogram in Métais & Vislobokova (2007). New data on cranial and postcranial material make their placement of the Lophiomerycidae a more parsimonious one than in the reconstructed phylogeny of Janis (1987). Many other reconstructions exist (e.g., the computer generated one by Métais & Vislobokova 2007, shown in Fig. 5b): indeed, perhaps the only stable node in this part of the ruminant phylogeny is the one uniting the Hypertragulidae and Praetragulidae into the Hypertraguloidea (although this grouping is mainly on the basis of primitive characters), and the Hypertraguloidea is usually placed as the sister group to the other ruminants. Almost no phylogenetic tree presents a monophyletic Tragulina as the sister taxon to the Pecora (but see discussion in Webb & Taylor 1980). The phylogenetic hypothesis presented in Fig. 5a will serve its purpose in a discussion of various morphological characters that have been used to define the Ruminantia and the interrelationships between the (mainly extinct) families of Tragulina.

Ruminants are traditionally united by a suite of three features: a fusion of the cuboid and navicular in the tarsus, the loss of the upper incisors, and an inci-

siform lower canine (see Fig. 6a-c). Of these features, the only one to show no variation within the clade is the fused cubonavicular, although fused cubonavicular bones have been observed in the Eocene-Oligocene Eurasian artiodactyls *Amphimeryx* and *Pseudamphimeryx*. Amphimerycids are usually excluded from the Ruminantia on the basis of their distinctive dentition (see discussion in Erfurt & Métais 2009), and may be related to the “tylopod” family Xiphodontidae (see discussion in Webb & Taylor 1980). However, the convergent occurrence of this particular “diagnostic” character of the Ruminantia lessens confidence somewhat in its reliability, although it is not inconceivable that the amphimerycids represent the sister taxon to the Ruminantia that independently evolved longer legs and more selenodont cheek teeth.

The dental characters used to unite the Ruminantia are much more problematical than the cubonavicular bone. Reduction and/or loss of the upper incisors is seen in many other artiodactyls, including extant Camelidae (where the third incisor is retained). Complete loss of the upper incisors is also seen in the members of the Protoceratidae, an exclusively North American group that has been allied with Camelidae in the Tylopoda, but on basicranial grounds may be more closely related to the Ruminantia (see Joeckel & Stavas 1996; Norris 2000). However, protoceratids lack the fused cubonavicular. Within the Ruminantia small upper incisors are retained in *Archaeomeryx*, and the condition is unknown in the Lophiomerycidae. The retention of the upper incisors (or the unknown condition of this character) is likely one of the reasons that the Archaeomerycidae and Lophiomerycidae occupy a basal position in the computer-generated phylogeny of Métais & Vislobokova (2007: fig. 5b).

Given the frequency of incisor reduction and loss in mammals, this may be a character that has been lost several times independently within the Ruminantia, and perhaps should not be accorded much weight in reconstructing a phylogeny. The incisiform lower canine is another useful, but rather dubious, ruminant synapomorphy. It is also present in protoceratids, and the condition is not fully present in the Praetragulidae.

2.2 Characters uniting the Ruminantia above the level of the Hypertraguloidea

A major character uniting this clade is the fusion of the magnum and trapezoid bones in the carpus. This seems to be a good diagnostic character, not seen in other artiodactyls. For example, while camelids parallel ruminants in many postcranial features (e.g., fusion of metapodials, reduction of the fibula to a malleolar bone, etc.), they retain an unfused magnum and trapezoid (see Fig. 6d).

Other potential synapomorphies at this level include the loss of the trapezium in the carpus, the loss of the first metatarsal, the fusion of the tibia and

fibula (but these bones remained unfused in many fossil tragulids, Gertrud Rössner, pers. comm.), the loss of the first upper premolar, and the presence of a mesostyle in the upper molars. The presence of a mesostyle in the upper molars is probably not a reliable character, as this feature is also seen in the unworn teeth of the Praetragulidae (Métais & Vislobokova 2007). With regard to the other characters, there are numerous problems and conflicts; all of these characters represent losses, and are likely to have occurred in parallel. The first upper premolar has been lost many times independently in mammals, not least among the Praetragulidae. The postcranial characters are related to adaptations for greater “cursoriality”, with the motion of the limbs restricted to a more parasagittal plane (this, of course, is also true of the fusion of the magnum and trapezoid). The loss of the trapezium and the loss of the first metacarpal essentially represent the same morphological character (see discussion below).

The trapezium is retained in the Archaeomerycidae, which is likely another contributory factor to the assessment of a basal position of this family in the computer generated phylogenetic tree of Métais & Vislobokova (2007; see Fig. 5B). The trapezium is the carpal bone that articulates with first metacarpal, so loss of the first metacarpal (common among more cursorially-adapted mammals, including camelids and other artiodactyls) will result in the loss of the trapezium: thus these features should not be treated as independent characters in phylogenetic analysis. The loss of the first metacarpal is in general true of all ruminants above the level of the Hypertraguloidea, although a small rudiment is retained in *Archaeomeryx* (see discussion in Webb & Taylor 1980). The fusion of the tibia and fibula is also a condition seen in many other artiodactyls; these bones are unfused in the Archaeomerycidae and Lophiomerycidae, and the condition among both modern and fossil tragulids is variable (Métais & Vislobokova 2007; Rössner & Heissig 2013).

2.3 Characters uniting the Ruminantia above the level of the Tragulidae

Webb & Taylor (1980) were among the first to recognize that, despite the primitive nature of its postcranial skeleton, the late Eocene *Archaeomeryx* evidenced synapomorphies with ruminants above the level of the Tragulidae. Webb & Taylor (1980) placed *Archaeomeryx* within the Leptomerycidae, based on ear region characters. More recently *Archaeomeryx* has been placed in its own family, the Archaeomerycidae, including other Asian genera: *Indomeryx*, *Miomeryx*, *Notomeryx*, and *Xinjiangmeryx* (see discussion in Métais & Vislobokova 2007). A more extensive study of basicranial characters may eventually resolve this issue.

The synapomorphies at this level that have no conflicts within the phylogeny include the restriction

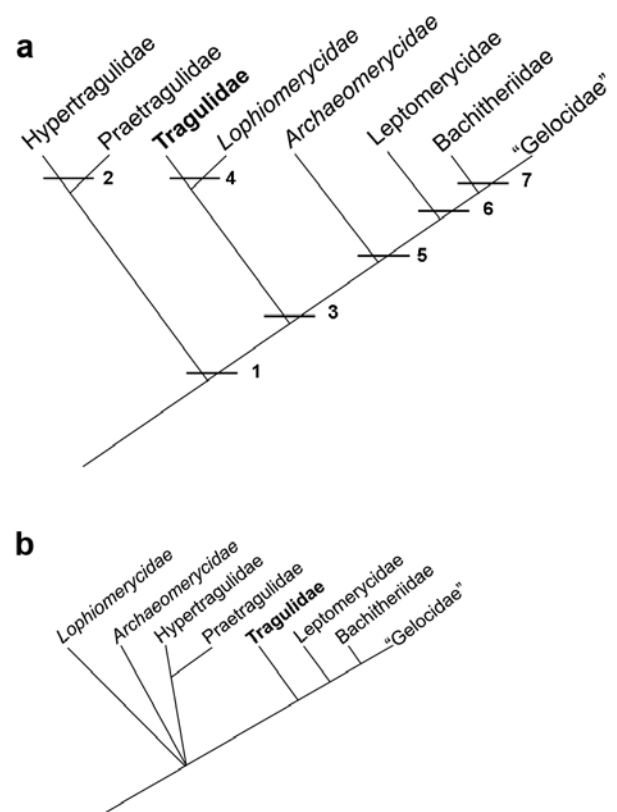


Figure 5: Phylogeny of the Tragulina. **(a)** Adapted from the hand drawn phylogenetic tree of Métais & Vislobokova 2007. **(b)** Adapted from the computer generated phylogenetic tree of Métais & Vislobokova 2007. Key: bold Roman = extant family; plain Roman = extinct family; italics = extinct families with highly labile positioning on varying cladograms. Key to characters: **1**, Fused cubonavicular in tarsus; loss of upper canines; incisiform lower canines. **2**, Orbital part of lacrimal enlarged. **3**, Fused magnum and trapezoid in carpus; trapezium in carpus lost; first metacarpal lost; upper first premolar lost; mesostyle in upper molars. **4**, Malleolar articulation on the calcaneum simple and concave. **5**, Complete postorbital bar formed mainly from the frontal bone; mastoid restricted to occipital region; longer and more tapered odontoid process of axis, with hint of dorsal crest; malleolar articulation on calcaneum with large proximal convexity and small distal concavity; premolar row shortened and premolars more complex; more complete lophs on molars. **6**, Odontoid process of axis semi spout-like; proximal fibula splint-like and fused to tibia, distal fibula reduced to malleolar bone; fusion of third and fourth metatarsals, reduction of metatarsals two and five to proximal rudiments; some reduction of metacarpals two and five. **7**, Postglenoid foramen enclosed.

of the mastoid exposure to the occipital region, the postorbital bar formed from the frontal bone, the shape of the odontoid process of the axis (which in *Archaeomeryx* is intermediate between that of the less derived tragulines and the condition in *Leptomeryx* and *Gelocus*, see Webb & Taylor 1980), and the shape of the malleolar articulation on the calcaneum. The latter character, in a different form (simple concave shape) is a convincing character uniting the Tragulidae and the Lophiomerycidae (see Métais & Vislobokova 2007). (In contrast, the shape of the malleolar facet in the Hypertragulidae is large and convex.) It is not clear which, if any, of these morphologies is the primitive condition for the Ruminantia.

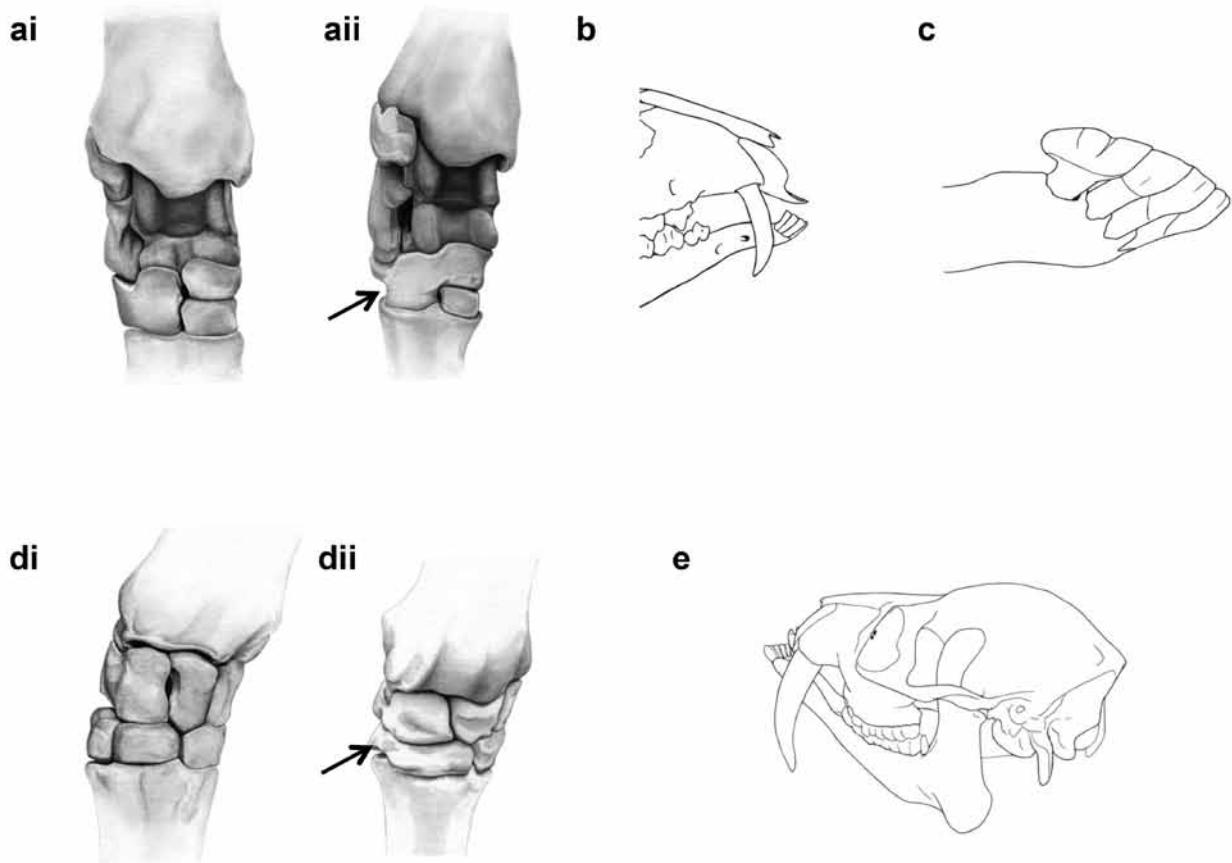


Figure 6: (ai) Tarsus (right) of a llama, showing condition of unfused cuboid and navicular bones (based on an unnumbered mounted specimen of *Llama glama* in the Brown University teaching collection). (a ii) Tarsus (right) of a moose, showing condition of fused cuboid and navicular (see arrow) (based on an unnumbered mounted specimen of a *Alces alces* in the Brown University teaching collection). (b) Loss of upper incisors (based on *Tragulus meminna* MCZ 6035); (also shows laterally flared traguline upper canine). (c) Incisiform lower canine (based on *Giraffa camelopardalis* MCZ 14564); (also shows bilobed lower canine of Giraffoidea). (di) Carpus (left) of a llama showing lack of fusion between trapezoid and magnum (same as Ai). (dii) Carpus (left) of a white-tailed deer, showing fusion between trapezoid and magnum (see arrow) (based on an mounted unnumbered specimen of *Odocoileus virginianus* in the Brown University teaching collection). (e) Sabre-like upper canine in cervoid males (based on Skulls Unlimited cast of *Hydropotes inermis*). MCZ = Museum of Comparative Zoology, Harvard University.

The issue of the postorbital bar is a more complex. There is incomplete closure in the Hypertraguloidea and the Lophiomerycidae; in the Tragulidae there is a complete bar formed primarily from the jugal; in *Archaeomeryx* the condition resembles that of *Gelocus* and other pecorans in having a bar formed mainly from the frontal bone, although in *Leptomeryx* and *Bachitherium* there is a greater contribution from the jugal than in other taxa (see Fig. 7a). A postorbital bar also evolved independently among the Hypertragulidae in the North American genus *Hypisodus*. This animal was clearly adapted to the more arid habitats of late middle Eocene to late Oligocene of North America than were seen in Eurasia at that time, and shows convergence to later pecorans in its hypsodont molars, and elongated, partially fused metatarsals with reduction of the lateral digits.

The dental features (see Fig. 8) are subject to much parallelism, as they are related to a diet of more fibrous food (i.e., a folivorous diet as in extant pecorans, as opposed to a folivorous/frugivorous diet in

extant tragulids), and vary within families as well as among them (some of these are paralleled within the Hypertraguloidea, as well as within the Camelidae) (see discussion in Janis & Scott 1987).

2.4 Characters uniting the Ruminantia above the level of the Archaeomerycidae

The semi spout-like odontoid process, transitional between the short, peg-like condition of other tragulines and the fully spout-like condition of pecorans, is likely a good synapomorphy at this level. Note, however, that the condition in *Bachitherium* is not yet published, and if Webb & Taylor (1980) are correct in notion of a sister relationship of the Archaeomerycidae and the Leptomerycidae, the utility of this character is weakened.

The postcranial characters at this node have less utility, as they are all related to adaptations towards a more cursorial lifestyle (see previous discussion), and show evidence of parallelism. These same characters are seen in the Camelidae, and are approa-

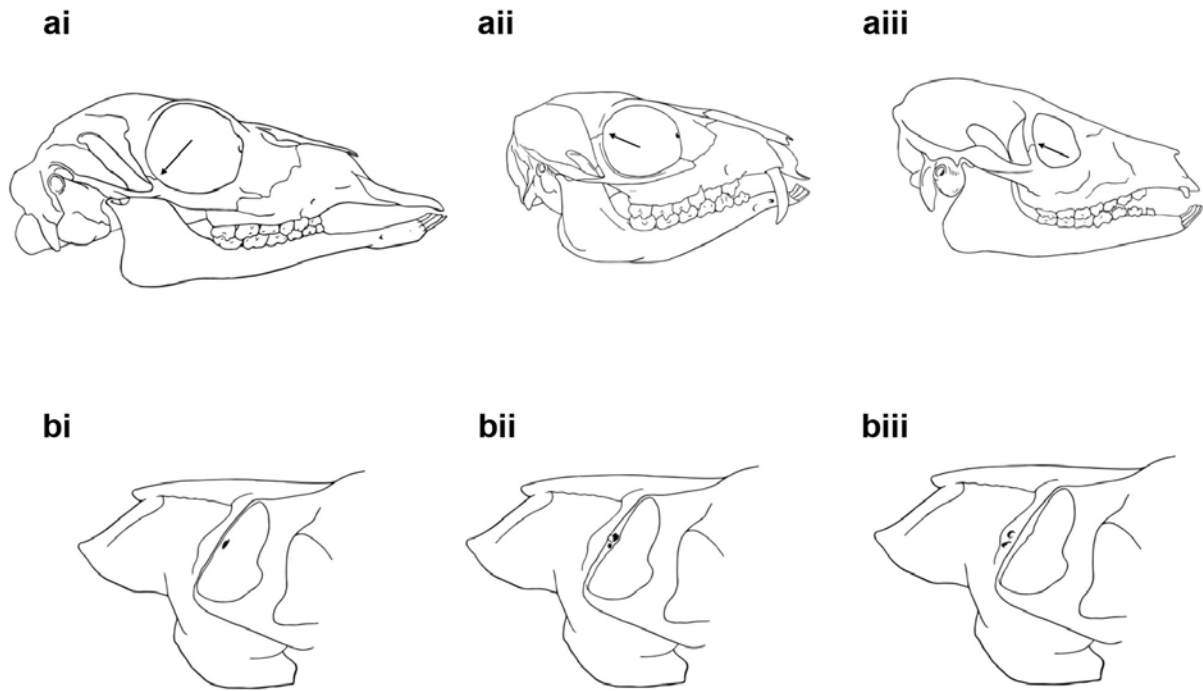


Figure 7: (a) Skulls (not to scale) showing condition of postorbital bar in different ruminants (arrow indicates the suture between the frontal and the jugal). (ai) Formed primarily from the frontal in the bovid *Litocranius walleri* (MCZ 8199). (aii) Formed primarily from the jugal in the tragulid *Tragulus meminna* (MCZ 6035). (aiii) Intermediate condition in the extinct traguline *Leptomeryx evansi* (modified from Frick 1937). (b) Skulls (not to scale) showing condition of the lacrimal orifice(s): (bi) Single orifice within orbit in bovid. (bii) Double orifice on orbital rim in a cervid. (biii) Double orifice outside of the orbit in a tragelaphine bovid. MCZ = Museum of Comparative Zoology, Harvard University.

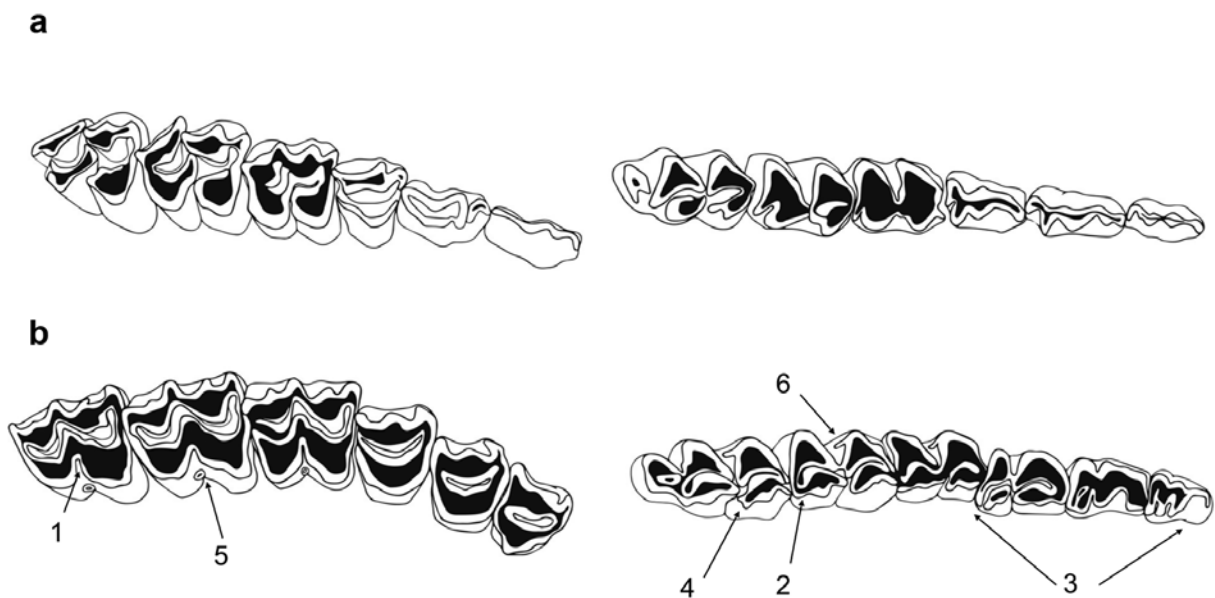


Figure 8: Dental features (cheek teeth) of ruminants. (a) Upper and lower left dentition of a tragulid (based on *Tragulus napu*, MCZ 38648). (b) Upper and lower left dentition of a pecoran (based on unnumbered specimen of a deer, probably *Odocoileus virginianus*, in the Brown University teaching collections, with some modifications to show palaeomerycid features). Key to characters: 1, Joined up selenes at earlier stages of wear in upper teeth (e.g., linked protocone and metaconule). 2, Lophs more complete in lower teeth (e.g., postentocristid). 3, Premolars more molarized, less sectorial. 4, Metastylid. 5, Entosyle. 6, *Palaeomeryx* fold. MCZ = Museum of Comparative Zoology, Harvard University.

ched by the derived hypertragulid *Hypisodus*. Within the Tragulidae, *Hyemoschus* has a distinct malleolar bone while *Tragulus* does not (Webb & Taylor 1980). Métais & Vislobokova (2007) use the character of a more elongated snout with the nasals projecting anteriorly between the premaxillae as a synapomorphy for this node: however, this character is also subject to parallelism, and is also used by them to link the Tragulidae and Lophiomerycidae.

2.5 Characters uniting the Bachitheriidae with the Pecora

Bachitherium (the only genus in the family Bachitheriidae) has had a checkered systematic history, being alternatively placed in the Hypertragulidae, Leptomerycidae, or Gelocidae (see discussion in Janis 1987). Its combination of derived features place it close to the origin of the Pecora. However, *Bachitherium* is excluded from the Pecora by the possession of a non parallel-sided astragalus. Métais & Vislobokova (2007) unite *Bachitherium* and *Gelocus* (plus other Pecora) by the presence of an enclosed postglenoid foramen.

2.6 Characters uniting the Pecora

Webb & Taylor (1980) recognized the importance of the character of the compact, parallel-sided astragalus that is shared by *Gelocus* (and other “gelocids”) and the extant pecoran ruminants (Fig. 9a). We follow them in placing *Gelocus* within the Pecora, rather than with the tragulines (as is the preferred classification among Europeans, as followed by Métais & Vislobokova, 2007). Mennecart & Métais (2014) place *Gelocus* in a more basal position in the ruminant phylogeny than *Bachitherium*, but they do not include this character of the astragalus in their analysis. There is no support for a monophyletic Gelocidae (Janis 1987; Métais & Vislobokova 2007; Webb 2008), and various “gelocids” more derived than *Gelocus* itself share various derived features with different pecoran families: for example, *Prodremotherium* shares with cervoids the character of a closed metatarsal gully (see discussion below). Extant pecorans are united by the soft anatomy character of the presence of an omasum within the chambered stomach.

While the parallel-sided astragalus, which functionally relates to the further restriction of the mobility of the foot to the parasagittal plane, appears to be a good synapomorphy, problems remain with this character. A pecoran-type of astragalus is seen in the North American middle Miocene taxon *Pseudoparablastomeryx*. As its name suggests, this taxon was originally considered to be a blastomerycid pecoran, but Taylor & Webb (1980) placed it with the leptomerycids based on dental characters (primarily the small upper canine and the presence of a tusk-like first lower incisor). They considered the pecoran-

like postcranial features of *Pseudoparablastomeryx*, which also include fusion of the metacarpals, fusion of the metatarsals with a closed gully, and complete distal metapodial keels, to have been evolved convergently with the pecoran condition in relation to adaptations to more open habitats in the middle Miocene (other North American leptomerycids did not survive the early Miocene). Examination of the basicranial regions of this taxon should clarify its taxonomic position.

More troubling is the possession of an asymmetric (although still relatively compact) astragalus in the undoubted pecoran *Hoplitomeryx* (see Mazza 2013) (Fig. 9a_{iii}), which indicates that this can be reversed. However, reports of a similarly asymmetric astragalus in the bovid *Myotragus* are not supported (Meike Köhler, pers. comm.). Note that both of these taxa are from island faunas.

Extant pecorans all show the features of “greater cursoriality” in their limbs of complete distal metapodial keels (Fig. 9b, which lock the metapodials in place on the phalanges), and fused metacarpals. However, if the various primitive ruminants more derived than *Gelocus*, but loosely termed “gelocids” (represented on Fig. 10 only by *Prodremotherium*, but up to a dozen have been named) are indeed scattered in a polyphyletic fashion through the pecoran phylogeny (as shown in Janis & Scott 1987), then these features must have arisen in parallel in the pecoran families (but note that Mennecart & Métais [2014] show “gelocid” taxa such as *Prodremotherium* to be stem pecorans, with complete metapodial keels being one of the characters uniting the more derived pecorans). Complete distal metapodial keels and fused metacarpals are seen in the Miocene North American “gelocids” *Pseudoceras* and *Floridameryx* (Webb 2008), but their systematic relationship to other pecorans is obscure. Note also that complete distal metapodial keels have been evolved in other cursorial ungulates: they are present in equids, and also in the extinct South American proterotherid litopterns (Cifelli & Dias 1989). Fused metacarpals are also seen in the Camelidae. In any event, it is clear that fused metacarpals and/or complete distal metapodial keels have evolved convergently outside of the Ruminantia, likely evolved convergently within the Ruminantia, and are functionally related to the evolution of cursorial adaptations: thus they are poor characters to use to unite the Pecora, or to unite clades within the Pecora.

Webb & Taylor (1980) also suggested that a shallow subarcuate fossa and loss of the stapedia artery are pecoran synapomorphies. Loss of the stapedia artery is generally inferred in extinct forms from the lack of promontorial sulci: but O’Leary (2010, characters 20-21) reported the presence of transpromontorial grooves in *Bos*, *Giraffa*, *Moschus* and *Antilocapra* in spite of the lack of a stapedia artery; and Wilkie (1936) reported that the tympanic nerve leaves such impressions in *Bos*, casting doubt on

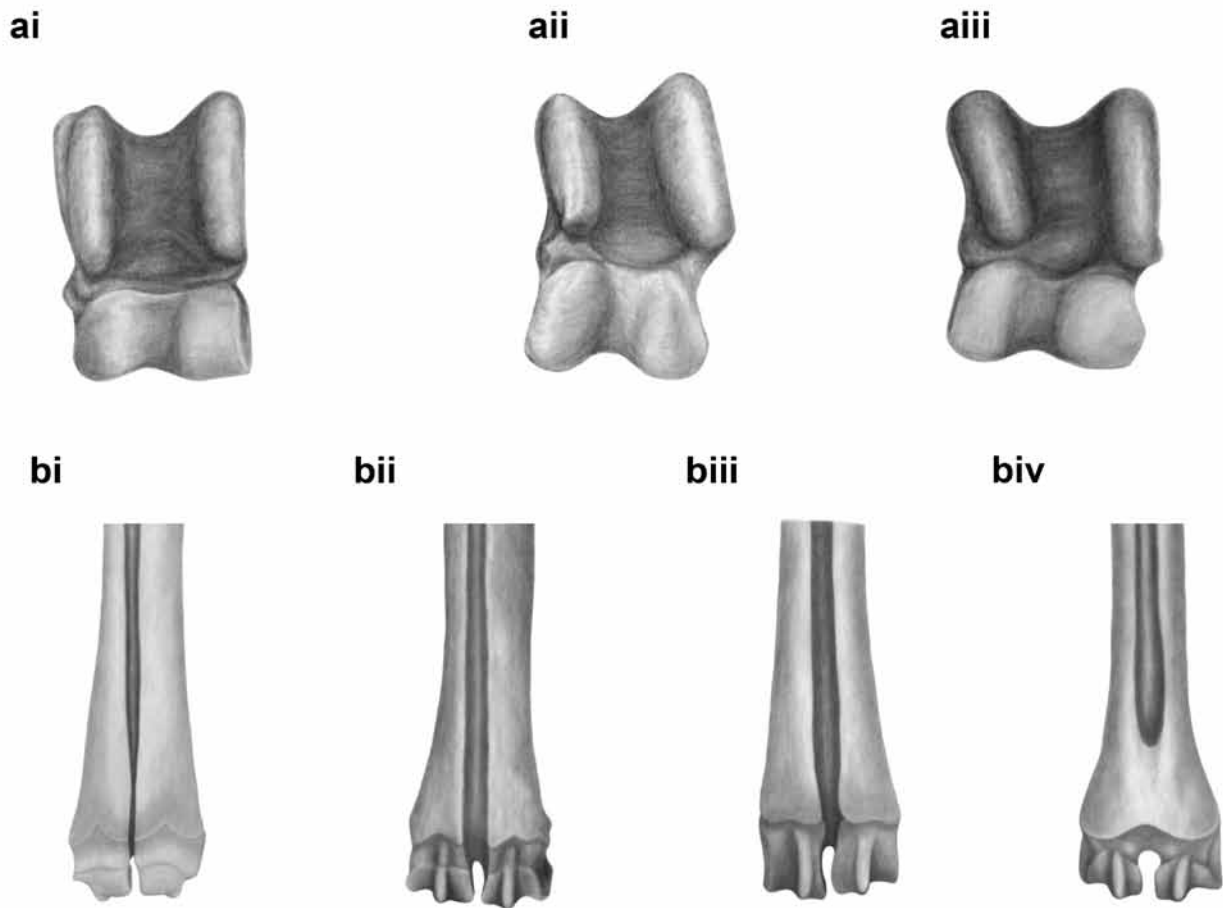


Figure 9: Postcranial features of ruminants (bones not to scale). **(a)** Morphology of the astragalus (all right side). **(ai)** Compact, parallel sided astragalus of a pecoran (*Pudu puda* MCZ 5180). **(aii)** Longer, asymmetric astragalus of a traguline (*Hyemoschus aquaticus*, MCZ 23179). **(aiii)** Asymmetric astragalus in the extinct pecoran *Hoplitomeryx* (modified from Mazza 2013). **(b)** Morphology of the metatarsals. **(bi)** Traguline (*Hyemoschus aquaticus*, MCZ 23179): incompletely fused metatarsals, incomplete distal keels. **(bii)** Giraffid (*Okapia johnstoni* MCZ 38105) showing fused metatarsals with open metatarsal gully, and complete distal keels. **(biii)** Bovid (*Tragelaphus scriptus* MCZ 33886) showing fused metatarsals with open metatarsal gully, and complete distal keels. **(biv)** Cervid (*Pudu puda* MCZ 5180) showing fused metatarsals with closed metatarsal gully, and complete distal keels. MCZ = Museum of Comparative Zoology, Harvard University.

the interpretation of loss of the artery being in any way related to the presence/absence of the grooves. Further dissection and taxonomic sampling is needed to better interpret promontory grooves in extinct taxa, and the polarity of this character is currently problematic.

The shallow subarcuate fossa is shared by most pecorans, but that of *Dremotherium* is reportedly moderately deep (Webb & Taylor 1980), and the shallow morphology is also found in suoids (O’Leary 2010) and protoceratids (contra O’Leary 2010, which relied on an isolated petrosal; Theodor in prep.), and O’Leary argues the shallow condition to be ancestral within artiodactyls (note that O’Leary uses a binary additive coding strategy, and this corresponds to characters 2-4). Tragulids, hypertragulids, leptomerycids and *Archaeomeryx* all show a deep subarcuate fossa (Fig. 11 illustrates this condition), as does *Lama*, which suggests quite a complex history for this character. Luo & Gingerich (1999) note that subarcuate fossa size and depth are not necessarily tied to the underlying morphology of the semicircular

canals; however, Costeur (2011) and personal observations (Theodor) suggest that they might be more consistently related to semicircular canal geometry within terrestrial artiodactyls. Further quantification of this relationship is necessary to better establish whether or not subarcuate fossa geometry is a good predictor of the anatomy of the underlying canals.

2.7 Characters defining clades within the Pecora

2.7.1 Metastylids on lower molars

Janis & Scott (1987) used this character (see Fig. 8) to unite all Pecora above the level of *Gelocus*. Dental characters such as this are subject to variation and parallelism, especially as this is one of the features of “greater selenodonty” of the cheek teeth, relating to the adoption of a more fibrous diet, and tends to be lost in the more simplified crown morphology of hypsodont molars. This character is not a particularly strong one to use as a synapomorphy.

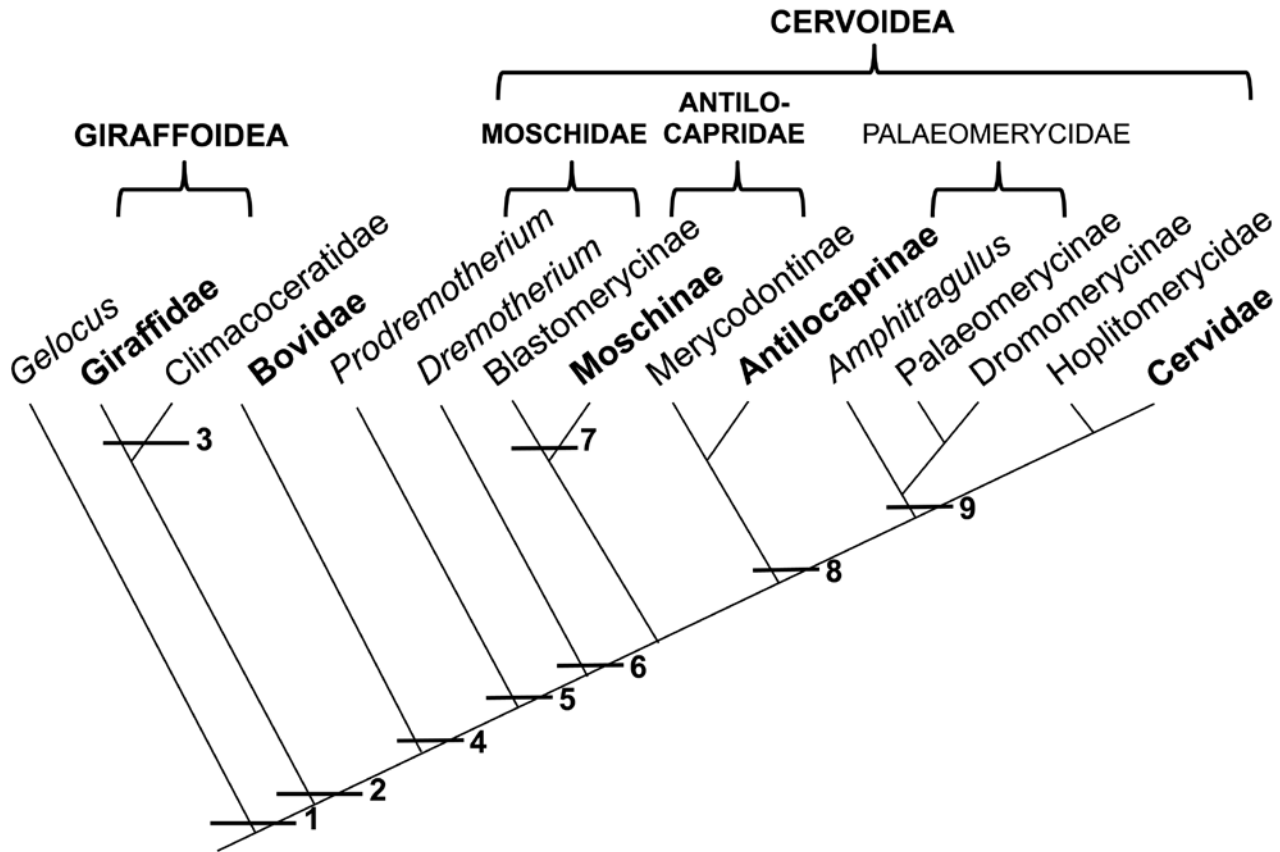


Figure 10: Phylogeny of the Pecora (following Janis & Scott 1987). Key: bold Roman = extant family or subfamily; plain Roman = extinct family or subfamily; italics = extinct genera. (Not all extinct taxa shown.) Key to characters: **1**, Compact, parallel-sided astragalus, plus a suite of basicranial characters. Extant families (and some extinct ones) all possess complete metapodial keels and fused metacarpals. **2**, Metastylids on lower molars. **3**, Bilobed lower canine. **4**, Enclosed, subcentral tympanohyal on the petrosal bone. **5**, Closed metatarsal gully. **6**, *Palaeomeryx* fold, sabre-like upper canines in males. **7**, Entostyle formed from anterior wall of metaconule. **8**, Double lacrimal orifice on the orbital rim. **9**, Posterior tuberosity on the metatarsus.

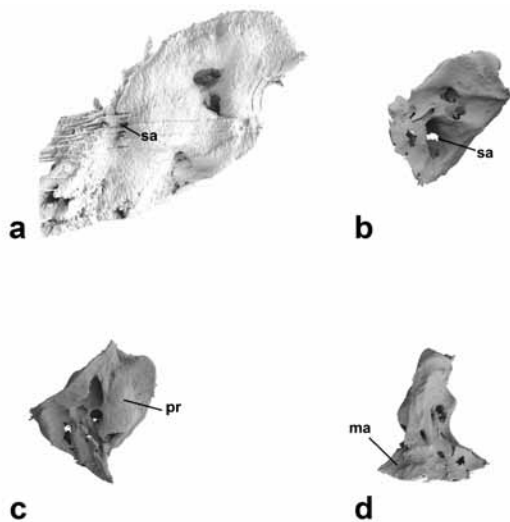


Figure 11: Basicranial characters. **(a)** Dorsomedial view of left petrosal of *Protoceras celer*, AMNH-VP 53523, showing shallow subarcuate fossa. **(b-c)** Right petrosal of *Hypisodus minimus*, AMNH-FM 9354. **(b)** Dorsomedial view showing deep subarcuate fossa. **(c)** Ventrolateral view showing promontorium lacking grooves. **(d)** Ventromedial view showing wedge shaped mastoid region. **sa**, subarcuate fossa; **pr**, promontorium; **ma**, mastoid region.

2.7.2 Cranial appendages

Pecorans are commonly termed “horned ruminants”, but not all extant pecorans possess horns or other cranial appendages (they are absent from the Moschidae, although the absence of antlers in the cervid *Hydropotes* is now considered to be secondary, due to its recently revealed phylogenetic position nested within the cervid subfamily Capreolinae (Cap et al. 2008; Hassanin et al. 2012). Despite advances in our understanding of the development of pecoran cranial appendages, any possible homologies between the pecoran families remain obscure (see Davis et al., 2011, for review).

2.7.3 Bilobed lower canine

This character (see Fig. 6c), originally described by Hamilton (1973) is an excellent one for uniting extinct families (such as the Climacoceratidae) with the Giraffidae into the Giraffoidea. However, this character is of little utility outside of the Giraffoidea.

2.7.4 Entostyle

An entostyle in the upper molars (see Fig. 8) formed from the anterior wall of the metaconule was used as a character by Janis & Scott (1987) to unite the Bovidae and Cervoidea (to the exclusion of the Giraffoidea). This morphological feature is seen in more basal, brachydont members of lineages within this grouping but, as with the metastylids, it tends to be lost in more hypsodont taxa. Janis & Scott (1987) considered the absence of an entostyle in the Giraffoidea (although it can occasionally be seen in individuals of *Giraffa* and *Palaeotragus*) to represent a phylogenetic signal. However, an entostyle also evolved convergently in *Hypertragulus* and *Lophiomeryx*. Thus, this is not a strong character.

2.7.5 Enclosed, subcentral tympanohyal vagina on the petrosal bone

This character was proposed by Webb & Taylor (1980) to unite an expanded family Moschidae, including the extant moschids with the Miocene North American blastomerycids, and the Oligo-Miocene European *Dremotherium*. However, while the blastomerycids do have a petrosal like that of extant moschids (although Sánchez et al. [2010] consider this to be due to convergence), this feature is not really evident in *Dremotherium* (see Costeur 2011, especially Fig. 3). Sánchez et al. (2010) note that the enclosure in *Hispanomeryx* and *Micromeryx* (Sánchez & Morales, 2008) is not complete. They argue that the subcentral position of the tympanohyal vagina is a synapomorphy of bovids + moschids. However, their data matrix codes only for the family level of Bovidae, Giraffidae, Cervidae and Tragulidae, and for the genus level for *Dremotherium*, *Blastomeryx*, and extinct moschids. Given the homoplasy in other characters, this character requires a broader taxonomic sampling to determine the condition across the breadth of Bovidae before accepting this as a bovid + moschid synapomorphy. *Dremotherium* is clearly a true pecoran, possibly a cervoid (see Janis & Scott 1987), but its affinities remain obscure. This petrosal character, if the more traditional interpretation withstands further scrutiny, is an excellent one for assigning extinct hornless taxa to the Moschidae, but is of limited use outside of this activity.

2.7.6 Condition of the metatarsal gully

The metatarsal gully is formed when the metatarsals fuse (see Fig. 9b). As the more general condition is for an open gully (as seen in *Gelocus*, and most other “gelocids”) it has been assumed that this is the primitive condition, from which a closed gully (i.e., with a distal bony bridge) has been derived (see discussion in Janis & Scott 1987). Leinders (1979; Leinders & Heintz 1980) used this character to distinguish cervids (with a closed gully) from bovids (which is

also seen in giraffids), and aligned antilocaprids and moschids with cervids on the basis of the character of a closed metatarsal gully. Janis & Scott (1987) extended this to include various extinct hornless forms (e.g., *Prodremotherium*, *Dremotherium*, *Amphitragulus*) within the same clade (Cervoidea). However, the phylogenetic tree of Sánchez et al. (2010) suggests that the closed gully evolved convergently in the Cervidae and the Moschidae (they did not include antilocaprids in their analysis). Sánchez et al. (2010) also provide an informative discussion of the soft anatomy (the position of digital artery) associated with different morphological states of the metatarsal gully.

Janis & Scott (1987) provide an extensive discussion of this character: while it is invariant among the living pecorans (with the exception of a single observed specimen by the authors of *Moschus moschiferus*), this reliability breaks down when fossil forms are included. Variability (i.e., some forms having an open gully, and some a closed gully) is seen within the Blastomerycinae (Moschidae?), the Merycodontinae (Antilocapridae), and the genera *Amphitragulus* and *Dremotherium*. Webb (2008) also reported a closed metatarsal gully in the North American “gelocids” *Pseudoceras* and *Floridameryx*. The utility of this character as a synapomorphy to unite families is thus called into question, especially as the grouping of extant taxa with this character is at variance with the molecular phylogeny.

2.7.7 *Palaeomeryx* fold

A *Palaeomeryx* fold on the lower molars (on the postero-labial surface of the paraconid; see Fig. 8) is actually fairly widespread amongst extinct pecorans (rather than limited to the palaeomerycids as the name suggests) including Oligo-Miocene taxa such as *Prodremotherium*, *Amphitragulus*, and *Dremotherium*, as well as in basal moschids and basal cervids. It is absent from any basal bovid or giraffoid, and Janis & Scott (1987) used this as a character to unite a grouping of “cervoids”, that also had a closed metatarsal gully. The problem with this character, like many other details of tooth anatomy, is that it is lost in more hypsodont forms, and a *Palaeomeryx* fold is unknown in any living taxon (or in any of the extinct members of the Antilocapridae, all of which are fairly highly hypsodont). Thus this character may be of some utility to include (e.g., *Eumeryx*) or exclude (e.g., *Propalaeoryx*, possibly basal bovids such as *Eotragus*) extinct brachydont taxa from this cervoid grouping, but that is about the extent of its usefulness.

2.7.8 Saber-like upper canines

Janis & Scott (1987) also used the feature of saber-like upper canines in the males (see Fig. 6e) to unite the Cervoidea, noting that these elongated canines were different from the thinner, more laterally

flaring canines of tragulids (see Fig. 6b, and fig. 4 in Janis & Scott, 1987). However, while saber-like canines are seen in extant hornless forms, such as moschids and the Chinese water deer *Hydropotes*, they are primarily a feature of forms that lack cranial appendages (although upper canines are retained in some extinct horned forms, palaeomerycids and in the muntiacine cervids [although note that Sánchez et al., 2010, consider the morphology of the muntiacine canines to be different from the moschid type]). As with the *Palaeomeryx* fold, this character may be useful to unite extinct hornless taxa with a cervoid grouping, but its utility outside of this is limited.

2.7.9 Double lacrimal orifice on the orbital rim

Leinders & Heintz (1980) noted this character as a means of distinguishing cervids from bovids (see Fig. 7bi, ii), although they did also note that bovids variably have a double lacrimal orifice (which is usually placed within the orbit or outside of the orbit rather than on the rim: see Fig. 7biii). Giraffids, moschids and tragulids have a single lacrimal orifice within the orbit (although the condition is also variable in *Moschus*), and this morphology is thus likely the primitive one. Leinders & Heintz (1980) used this character to group *Antilocapra* with the Cervidae, but there is significant variability among antilocaprids in general (merycodontines have only one orifice), and also within the extant *Antilocapra*, and the morphology is not identical to that seen in cervids (see discussion in Janis & Scott 1987). (This contrasts with the condition in dromomerycines, where the morphology is cervid-like and appears to be invariable, although few specimens with an intact orbital rim are known.) Thus this character suffers from similar problems to the closed metatarsal gully in its utility to unite clades within the Pecora.

2.7.10 Posterior tuberosity on the metatarsus

This character was originally used by Heintz (1963) to distinguish cervids from bovids. A tuberosity is invariably present in cervids, and its variable presence in palaeomerycids led Janis & Scott (1987) to use this as a character to unite the two groups. However, this anatomy can also be seen in some moschids, including *Moschus* (and it is absent in *Hoplitomeryx*), so its utility to unite extinct forms with the Cervidae is questionable.

Heintz (1963) also noted differences in the articular morphology of the metatarsals between bovids and cervids, but a brief survey by the senior author into the range of variation among extant taxa showed that there is little consistent difference between bovids and cervids, and that the condition in moschids and antilocaprids resembles that of cervids. Giraffids are certainly different in their articular morphology from other pecorans, but this is likely an apomorphy of the family.

2.7.11 Other nodes on the pecoran phylogeny

Janis & Scott (1987) united *Amphitragulus* with the palaeomerycids based on dental characters (see Fig. 10), which are notoriously variable. No good feature unites the merycodontines with the antilocaprids: they are grouped together on the basis of “cursorial” limb characters and hypsodonty (which have evolved in parallel many times within the Artiodactyla), plus their biogeographic and temporal proximity in North America. The cranial appendages of the two groups are also very different, although they may share a common ontogenetic origin (see discussion in Janis & Manning 1998).

2.8 A note of caution about hypsodonty

Hypsodonty has evolved multiple times convergently in mammals (see Janis & Fortelius 1988), and every lineage shown in Fig. 10 has members with a degree of hypsodonty (as is also seen in the hypertragulid *Hypisodus*), although extremely hypsodont forms are only found within the Bovidae and the Antilocapridae. Janis & Scott (1987) discussed extensively the reasons for excluding hypsodonty from ruminant phylogenetic analysis, a warning that is even more pertinent now all analyses are done using computer algorithms. Yet hypsodonty continues to be used as a character, much to our dismay (although hypsodonty might retain some utility at lower taxonomic levels, such as species within a genus, as the condition is not usually reversed [but see Bärmann et al. 2013]).

Additional problems exist in terms of the skull and dental features that invariably accompany hypsodonty. Note that hypsodonty is not necessarily related to eating grass per se, as is long been assumed, but rather to the mode of feeding. Hypsodonty relates to the abrasive properties of the diet, which are probably largely caused by ingested soil in animals feeding close to the ground. This explains, for example, why the pronghorn, *Antilocapra americana*, is highly hypsodont despite only taking around 10% of grass in its diet: it has rates of tooth wear similar to those of the horses and cattle grazing on the same ranges (see Damuth & Janis 2011). We use *Antilocapra* as an example of the influence of hypsodonty and foraging posture on the skull in Fig. 12, to show that this is independent of the effects of a grazing diet that involves a lot of mastication (which also results in convergent changes in skull anatomy, such as the enlargement of the angle of the mandible and the elongation of the masseteric ridge in the skull).

We noted before how hypsodonty will result in simplification of molar form, such as the loss of the *Palaeomeryx* fold, metastylids and the entostyle. Hypsodont ruminants and camelids (but not equids) also shorten their premolar row (see Janis 1990), so this should not be used as a character independent of hypsodonty. Fig. 12 illustrates cranial differences

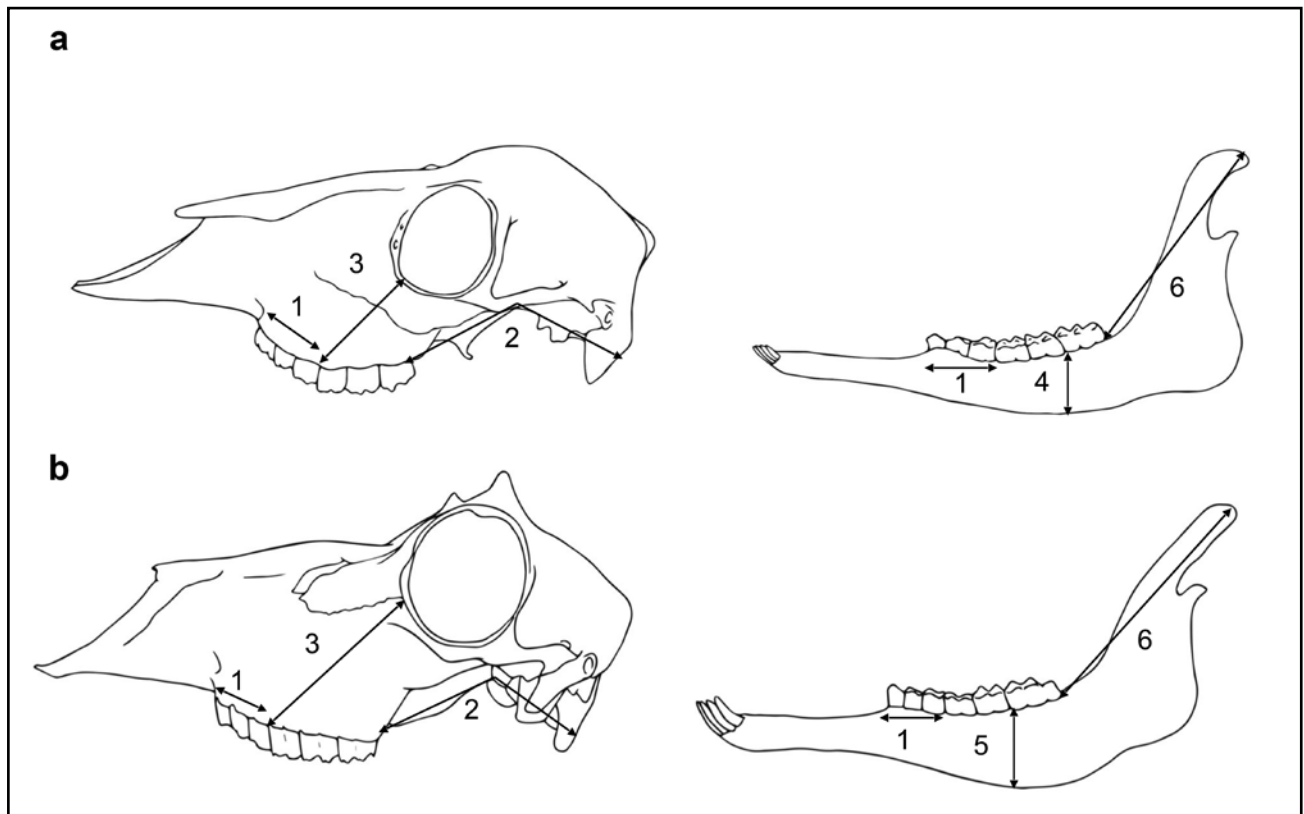


Figure 12: Cranial features associated with hypsodonty. **(a)** Skull and lower jaw of a brachydont form (*Odocoileus virginianus*, based on MCZ 68198). **(b)** Skull and lower jaw of a hypsodont form (*Antilocapra americana*, based on MCZ 121). Differing features (in hypsodont form): 1, Shorter premolar row. 2, Orbit more posteriorly placed and elevated. 3, Basicranial angle more acute and shorter basicranium. 4, Deeper ramus of mandible. 5, More posteriorly-projecting coronoid process. MCZ = Museum of Comparative Zoology, Harvard University.

between a brachydont deer and a hypsodont pronghorn. In the skull, in addition to the shorter premolar row in *Antilocapra*, the basicranium is shorter, the skull more flexed on the face (more acute basicranial angle), and the orbit is postero-dorsally displaced from the tooth row. The basicranial characters are likely due to the more derived feeding posture with the head close to the ground. The displacement of the orbit is more problematical: this has traditionally been thought to be associated with allowing room for the roots of hypsodont cheek teeth (Radinsky 1984), but the orbit is not greatly displaced in highly hypsodont camelids, and it is displaced posterodorsally in large brachydont ruminants such as moose (*Alces*) and giraffe (*Giraffa*) (personal observations of senior author). In *Antilocapra* the orbital displacement may be related in part to the reorganization of the skull with the change in basicranial anatomy. In any event, all of these skull characters should be viewed with caution in terms of phylogenetic relevance, and there should be the realization that these features are likely correlated with each other and with hypsodonty.

In the lower jaw the ramus of the mandible is deeper in *Antilocapra* than in the brachydont *Odocoileus*: this morphology probably is functionally related to the need to house deeper cheek teeth. But a difference also exists between the two forms with regards

to the form of the coronoid process, which is more posteriorly-projecting in *Antilocapra*, and with the posterior mandibular corpus having a “swept back” appearance. This morphology is related to the need to fit the jaw onto a skull with a displaced orbit and more angled basicranium. Again, these morphological features should be understood as being part of a character complex, and should not be considered as independent characters in phylogenetic analyses.

3. Discussion and conclusions

An examination of the morphological characters used in ruminant phylogeny reveals that the great majority of them are subject to variation and homoplasy. Notable exceptions (although none is completely free from these problems) include the fusion of the cuboid and navicular bones in the tarsus (uniting the Ruminantia), the fusion of the magnum and trapezoid bones in the carpus (uniting the Ruminantia above the level of the Hypertraguloidea), and the compact parallel-sided astragalus (uniting the Pecora). Other potentially reliable characters include the form of the malleolar articulation on the calcaneum (different morphologies uniting the Hypertraguloidea, the Tragulidae with the Lophiomerycidae, and the Ruminantia above this level), the restriction of the mastoid to

the occipital region of the skull (uniting the Ruminantia above the level of the Tragulidae), and a spout-like odontoid process of the axis (uniting the Ruminantia above the level of the Archaeomerycidae). It is somewhat ironic that almost all of these characters unite groups below the level of the Pecora, where all families with the exception of the Tragulidae are extinct, so there can be no corroboration (or refutation) of the phylogeny resulting from these characters (Fig. 5a) with molecular information.

The evolution of the Ruminantia set against the background of Cenozoic climatic change (Fig. 4) provides an understanding of why so many of the traditional characters used in ruminant phylogeny are subject to convergence. Reduction and/or loss of lateral digits, loss of the distal ulna, reduction of the fibula to a malleolar bone, elongation and fusion of the metapodials, and evolution of complete metapodial keels, are all related to the evolution of longer limbs more restricted to movement in the parasagittal plane, better adapted for efficient locomotion in the more open habitats of the late Palaeogene and Neogene. Likewise many aspects of dental anatomy are related to the acquisition of a more fibrous diet in these more open habitats: hypsodonty is an obvious issue here, but also note that hypsodonty carries with it the loss of some previous features of dental occlusal complexity (e.g., the *Palaeomeryx* fold), and is also associated with changes in skull morphology (see Fig. 12). Other aspects of dental change, such as reduction of the premolar row, and features relating to the development of more selenodont occlusal morphology, are also associated with changing diets with changing climatic conditions. Similar changes in postcranial and dental morphology can be seen to occur at the same time in other ungulate lineages, such as the Camelidae and the Equidae. Thus details of dental morphology relating to occlusal function, or limb morphology relating to elongation and restricted plane of motion of the limbs, are unlikely to be reliable features in phylogenetic analyses.

Within the Pecora, various morphological features that were deemed invariant in extant lineages are seen to be more variable if fossil taxa are taken into account, or even if a greater number of individuals are examined for the trait. For example, while a double lacrimal orifice appears to be invariant among species in the Cervidae, this character is variable in the pronghorn, *Antilocapra americana* (and to a lesser extent in the musk deer, *Moschus moschiferus*), and can also be seen to have evolved convergently within some bovid lineages. The condition of the metatarsal gully (closed in Cervidae, Moschidae, and Antilocapridae, open in Bovidae and Giraffidae) indeed typifies extant forms (although an open gully has occasionally been observed in *Moschus*), but shows high variability within extinct lineages (e.g. the merycodontine antilocaprids). Thus neither of these features is reliable for uniting a grouping of “cervoids” (cervids, moschids, and antilocaprids) and the

molecular data do not support this association.

Webb & Taylor (1980, tab. 1) identified thirteen basicranial features that they used to support their phylogeny of ruminants, scored for *Hypertragulus*, *Tragulus*, *Hyemoschus*, *Archaeomeryx*, *Leptomeryx*, *Gelocus*, *Dremotherium*, *Blastomeryx* and *Moschus*. Of these, many are still used in artiodactyl systematics, especially within ruminants and pecorans - however, many of these turn out to have more complex and homoplastic distributions among non-ruminants and further investigation is needed (O’Leary, 2010).

O’Leary (2010) detailed forty-two petrosal characters used in the Spaulding et al. (2009) phylogenetic assessment of the position of whales within the terrestrial artiodactyls, sampling only *Leptomeryx* and tragulids among non-pecoran ruminants. Of these forty characters, most were either highly homoplastic or were diagnostic of more basal groupings within artiodactyls, leaving three character complexes germane to the Ruminantia: the subarcuate fossa and transpromontorial sulci discussed above, and a wedge-shaped mastoid (seen in all ruminants scored with the exception of *Tragulus*).

Sánchez (2010) used approximately ten of these basicranial characters for their analyses, but coded many taxa at the familial level.

None of these analyses have yet considered character independence or ontogeny of basicranial characters, nor have they yet addressed analyses at the species or specimen level to assess variability in these characters. Based on the degree of homoplasy found in the rest of the skull and postcrania, more detailed character comparisons must be made, including species level coding, a wider sampling of non-ruminant outgroups, and careful consideration of character independence, before we can be assured that basicranial morphology is more reliable or less prone to convergence than other systems.

Can anything be gained from this assassination of the reliability of morphology? We note that molecular data also present problems, and are of no use in understanding the placement of extinct taxa within the phylogeny. Basicranial and ear region characters hold some promise for providing characters less subject to convergence due to climatic change, although they are not without homoplasy. In many cases, the basicranial characters that have been used have not been adequately surveyed because of reluctance to pursue destructive analysis, and in some cases limited preservation in the back of the skull. The advent of CT allows non-destructive sampling of the ear morphology of many more taxa than have been available until now, which should eventually result in more complete taxon sampling for many characters, and a better idea of the degree of homoplasy in these characters.

We think that one point that emerges from this examination of morphological characters is a cautionary tale about reliance on parsimony algorithms to do the character sorting. Such algorithms are one

of several approaches for dealing with large quantities of molecular data, but with morphological data, while parsimony is the most widely used algorithm, we can benefit from the wisdom and judgment of the systematist in the consideration of appropriate characters to use, and which characters may be more appropriate than others at various levels in the phylogeny. Sometimes retained primitive characters can overturn a phylogeny based on derived ones (see earlier comments about the differences in the hand-drawn and computer-derived phylogenies of Métais & Vislobokova 2007). A computer-generated phylogeny is not the end point of the study: the characters are, first and foremost, hypotheses of homology, and must be revisited when an analysis indicates homoplasy among characters. The characters must be carefully chosen and examined for character independence, and when there is significant conflict, then we must return to the character analysis and seek a better understanding of the morphology.

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4. References

- Bärmann EV, Rössner GE, Wörheide G. 2013. A revised phylogeny of Antilopini (Bovidae, Artiodactyla) using combined mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution* 67, 484-493.
- Cap H, Deleporte P, Joachim J, Reby D. 2008. Male vocal behavior and phylogeny in deer. *Cladistics* 24, 1-15.
- Cifelli RL, Dias JG. 1989. New remains of *Prothoatherium colombianus* (Litopterna, Mammalia) from the Miocene of Colombia. *Journal of Vertebrate Paleontology* 9, 222-231.
- Clauss M, Rössner GE. 2014. Old world ruminant morphophysiology, life history, and fossil record: exploring key innovations of a diversification sequence. *Acta Zoologica Fennica* 51, 80-94.
- Costeur L. 2011. A partial skull of *Dremotherium feignouxii* from the Aquitanian of France (MN2, Saint-Gérard-le-Puy, Allier). *Acta Geologica Slovakia* 3, 105-112.
- Damuth J, Janis CM. 2011. On the relationship between hypodonty and feeding ecology in ungulate animals, and its utility in palaeoecology. *Biological Reviews* 86, 733-758.
- Davis EB, Brakora KA, Lee AH. 2011. Evolution of ruminant headgear: a review. *Proceedings of the Royal Society B* 278, 2857-2865.
- Erfurt J, Métais G. 2009. Endemic European Paleogene artiodactyls. In: DR Prothero, SE Foss (Eds), *The Evolution of Artiodactyla*. Baltimore, MD, The Johns Hopkins University Press, 59-88.
- Frick C. 1937. Horned ruminants of North America. *Bulletin of the American Museum of Natural History* 69, 1-669.
- Hamilton WR. 1973. On the Lower Miocene ruminants of Gebel Zelten, Libya. *Bulletin of the British Museum (Natural History)* 21, 75-150.
- Hassanin A, Douzery EJP. 2003. Molecular and morphological phylogenies of Ruminantia and the alternative position of the Moschidae. *Systematic Biology* 52, 206-228.
- Hassanin A, Delsuc F, Ropiquet A, Hammer C, van Vuuren BJ, Matthee C, Ruiz-Garcia R, Catzeflis F, Areskoung V, Nguyen TT, Couloux A. 2012. Pattern and timing of diversification of Cetartiodactyla (Mammalia, Laurasiatheria), as revealed by a comprehensive analysis of mitochondrial genomes. *Comptes Rendus Biologies* 335, 32-50.
- Heintz E. 1963. Les caractères distinctifs entre métatarses de Cervidae et Bovidae actuels et fossils. *Mammalia* 27, 200-209.
- Janis CM. 1982. Evolution of horns in ungulates: ecology and palaeoecology. *Biological Reviews* 57, 261-318.
- Janis CM. 1987. Grades and clades in hornless ruminant evolution: the reality of the Gelocidae and the systematic position of *Lophiomeryx* and *Bachitherium*. *Journal of Vertebrate Paleontology* 7, 200-216.
- Janis CM. 1990. Correlation of cranial and dental variables with dietary preferences: a comparison of macropodoid and ungulate mammals. *Memoirs of the Queensland Museum* 28, 349-366.
- Janis CM, Fortelius, M. 1988. On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. *Biological Reviews* 63, 197-230.
- Janis CM, Manning E. 1998. Antilocapridae. In: CM Janis, KM Scott, LL Jacobs (Eds), *Evolution of Tertiary Mammals of North America*. Cambridge, UK, Cambridge University Press, 491-507.
- Janis CM, Scott KM. 1987. The interrelationships of higher ruminant families with special emphasis on the Cervidae. *American Museum Novitates* 2893, 1-85.
- Joeckel RM, Stavas JM. 1996. Basicranial anatomy of *Syndyoceras cookii* (Artiodactyla, Protoceratidae) and the need for a reappraisal of tylopod relationships. *Journal of Vertebrate Paleontology* 16, 320-327.
- Leinders JJM. 1979. On the osteology and function of the digits in some ruminants and their bearing on taxonomy. *Zeitschrift für Säugetierkunde* 44, 305-318.
- Leinders JJM, Heintz E. 1980. The configuration of the lacrimal orifice in pecorans and tragulids (Artiodactyla: Mammalia) and its significance for the distinction between Bovidae and Cervidae. *Beaufortia* 30, 155-160.
- Luo, ZX., Gingerich, PD. 1999. Terrestrial Mesonychia to aquatic Cetacea: transformation of the basicranium and evolution of hearing in whales. *University of Michigan Papers on Paleontology* 31, 1-98.
- Mazza PPA. 2013. The systematic position of Hoplitomerycidae (Ruminantia) revisited. *Geobios* 46, 33-42.
- Mennecart B, Métais G. 2014. *Mosaicomeryx* gen. nov., a ruminant mammal from the Oligocene of Europe and the significance of "gelocids". *Journal of Systematic Palaeontology*. DOI: 10.1080/14772019.2014.948505
- Métais G, Vislobokova I. 2007. Basal ruminants. In: DR Prothero, SE Foss (Eds), *The Evolution of Artiodactyla*. Baltimore, MD, The Johns Hopkins University Press, 189-212.
- Norris CA. 2000. The cranium of *Leptotragulus*, a hornless protoce-

- ratid (Artiodactyla: Protoceratidae) from the middle Eocene of North America. *Journal of Vertebrate Paleontology* 20, 341-348.
- O'Leary MA. 2010. An anatomical and phylogenetic study of the osteology of the petrosal of extant and extinct artiodactylans (Mammalia) and relatives. *Bulletin of the American Museum of Natural History* 335, 1-206.
- Pilgrim GE. 1941. The dispersal of the Artiodactyla. *Biological Reviews* 16, 155-158.
- Price SA, Bininda-Emonds ORP, Gittleman JL. 2005. A complete phylogeny of the whales, dolphins and even-toed hoofed mammals (Cetartiodactyla). *Biological Reviews* 80, 445-473.
- Radinsky L. 1984. Ontogeny and phylogeny in horse skull evolution. *Evolution* 38, 1-15.
- Romer AS. 1966. *Vertebrate Paleontology*, 3rd edition. Chicago, IL, University of Chicago Press, viii + 468 p.
- Rössner GE, Heissig K. 2013. New records of *Dorcatherium guntianum* (Tragulidae), stratigraphical framework, and the diphyletic origin of Miocene European tragulids. *Swiss Journal of Geosciences* 106, 335-347.
- Sánchez IM, Morales J. 2008. *Micromeryx azanzae* sp. nov. (Ruminantia: Moschidae) from the middle-upper Miocene of Spain, and the first description of the cranium of *Micromeryx*. *Journal of Vertebrate Paleontology*, 28, 873-885.
- Sánchez IM, Domingo MS, Morales J. 2010. The genus *Hispanomeryx* (Mammalia, Ruminantia, Moschidae) and its bearings on musk deer phylogeny and systematics. *Palaeontology* 53, 1023-1047.
- Simpson GG. 1945. The principles of classification, and a classification of mammals. *Bulletin of the American Museum of Natural History* 85, 1-350.
- Taylor B, Webb SD. 1980. Miocene Leptomerycidae (Artiodactyla, Ruminantia) and their relationships. *American Museum Novitates* 2596, 1-22.
- Webb SD. 2008. Revision of the extinct Pseudoceratinae (Artiodactyla: Ruminantia: Gelocidae). *Bulletin of the Florida Museum of Natural History* 48, 17-58.
- Webb SD, Taylor BE. 1980. The phylogeny of hornless ruminants and a description of the cranium of *Archaeomeryx*. *Bulletin of the American Museum of Natural History* 167, 117-158.
- Wilkie HC. 1936. The acoustic organ of the ox (*Bos taurus*). *Proceedings of the Zoological Society of London* 2, 985-1009.
- Zachos J, Pagani M, Sloan L, Thomas E, Billups K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292, 686-693.
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