

8. The phylogeny of the ungulates

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Abstract

Cladistic analysis of the major living and extinct ungulates, including the living hoofed mammals, was performed on dental, cranial, and postcranial characters. Both dental and non-dental characters clearly show that hyraxes and perissodactyls are a monophyletic group, followed by progressively more distantly related outgroups in the following order: tethytheres (proboscideans, sirenians, and desmostylians), arsinotheres, uinatheres, phenacodonts and meniscotheres, whales and mesonychids, hyopsodonts and peripatichids, arctocyonids, and artiodactyls. Molecular phylogenies of living ungulates typically cluster artiodactyls, perissodactyls, and whales, but differ from the morphologically-based phylogeny in that they separate hyraxes and tethytheres as 'paenungulates'. We find several derived characters that support a closer affinity of hyraxes with other perissodactyls than with tethytheres. Indeed, Owen included hyraxes in his original definition of the Perissodactyla. Contrary to common assumption, perissodactyls are closer to whales and elephants than they are to artiodactyls. There are characters of the skull, dentition, and postcranial skeleton that support the monophyly of ungulates and conflict with the molecular

phylogenies that place 'paenungulates' at more primitive nodes within the Eutheria. The phylogenetic pattern supported here clearly shows that the 'Condylarthra' is a paraphyletic waste-basket taxon that has long outlived its usefulness, and should be abandoned.

Introduction

The ungulates, including the living hoofed mammals, are the largest, most diverse, and ecologically most dominant group of mammals. According to Simpson (1945), ungulates make up over a third of the named genera (1049 out of 2864) and families (97 out of 257) of mammals. In this respect, they outnumber even the rodents. Outside Australia and Antarctica, ungulates have been the dominant large herbivores since the beginning of the Cenozoic. The largest known animal (the blue whale), the largest land mammal that ever lived (the extinct hyracodontid rhinocerotoid *Paraceratherium*), and the largest living land mammal (the African elephant) are all ungulates. There were very primitive housecat-sized Late Cretaceous ungulates, but even then they were the largest placental mammals around.

Although they dominate the large herbivore niche in most ecosystems, ungulates are much more ecologically diverse. The mesonychids and arctocyonids were probably bear-like omnivores, and whales feed on fish, squid, or plankton. Whales, desmostylians, and sirenians have secondarily become aquatic. Some ungulates became huge and graviportal, such as elephants, arsinoitheres, uiltatheres, pyrotheres, toxodonts, rhinoceroses, titanotheres, and hippopotami. Others became highly cursorial, especially among the litopterns, perissodactyls, and artiodactyls. There is even an arboreal ungulate (*Dendrohyrax*). A few ungulate groups, particularly the early ones, retain unspecialized patterns of feeding and locomotion.

Living ungulates are best known from the abundant 'even-toed' artiodactyls (pigs, hippos, peccaries, llamas, camels, chevrotains, deer, giraffes, pronghorns, antelope, cattle, sheep, goats, musk oxen), the 'odd-toed' perissodactyls (horses, tapirs, rhinos), and elephants. Although not usually considered 'hoofed mammals', whales (including dolphins and porpoises), sirenians (manatees and dugongs), and hyraxes are also grouped in the Ungulata. In the fossil record, ungulates are even more diverse; 75% of the families and 87% of the genera of ungulates are extinct (Simpson 1945). Any discussion of ungulate phylogeny based solely on living groups neglects their great diversity, and may be misled by limited character information (*contra* Patterson 1981).

In spite of the great number of fossil and living ungulates, and their

abundance and excellent preservation in the fossil record, there have been remarkably few comprehensive statements about their phylogeny. Some of the earliest efforts were reviewed by Gregory (1910), who was one of the first to sketch a phylogenetic diagram of the major groups of ungulates. Mammal classifications, from Linnaeus (1758) to Simpson (1945) to McKenna (1975), have suggested phylogenetic hypotheses, but none was fully supported by character evidence. The most explicit recent hypotheses (Sloan 1970, 1987; Van Valen 1978*b*) show only ancestor–descendant sequences of taxa, with no supporting evidence. Novacek (1982, 1986), and Novacek and Wyss (1986) have presented cladograms of the major eutherian groups, but have dealt only with the living ungulate groups. Our own phylogenetic work began in the 1970s, culminating in an unpublished cladogram using mainly dental characters by Manning in 1975, which was widely circulated. Part of this work was published by McKenna and Manning (1977). As an independent test of the 1975 cladogram, Prothero and Fischer collected non-dental evidence for the relationships of the major ungulate groups. Finally, we examined the evidence presented by molecular phylogenies of recent years. In this paper, we compare the three hypotheses generated from independent data sources by different authors. In this way, we hope that the resulting hypothesis will be well tested and robust.

Phylogenetic analysis

Materials and methods

There are many reasons for the confusion and lack of explicit hypotheses of ungulate relationships. Part of the problem is that ungulate groups are often strangely derived (e.g. uinatheres, elephants, arsinotheres, whales, and sirenians) or almost completely primitive (most of the so-called ‘condylarths’). In very specialized groups, it is often difficult to screen out unusual characters and find underlying common patterns. In groups with few specializations, it can be difficult to find anything that would be clearly synapomorphic.

A more significant problem with previous phylogenetic schemes is methodological. Too often, previous researchers have presented diagrams or classifications with no explicit character analysis in support. When evidence is presented, the great majority of the resemblances are clearly symplesiomorphic. For many Early Tertiary lineages, the phylogeny consists of ancestor–descendant sequences of genera allied only on dental features. This prevents any comparison or analysis of non-dental features, which are known for most ungulate genera. ‘Tooth phylogenies’ often degenerate to a ‘join up the dots’

approach that has been widely criticized (McKenna *et al.* 1977). Since major ungulate groups have migrated among Africa, Eurasia, and the Americas throughout the Early Cenozoic, a 'tooth phylogeny' of a single basin or continent (e.g. Sloan 1970, 1987; Van Valen 1978*b*) is not likely to produce good results (Lazarus and Prothero 1984). Such phylogenies not only emphasize similarity based on shared primitive features, but also neglect the non-dental evidence and the taxa from other areas. Certainly, dental evidence is important, and for many genera teeth are all that we have. The same patterns of relationship should also be evident from the rest of the anatomy.

Most of the dental features discussed here were examined in the excellent collection of fossil and living ungulates in the American Museum of Natural History. A number of very primitive ungulates were very briefly described and named by Van Valen (1978*b*); some of this material has also been described by Archibald (1982; Archibald *et al.* 1983*a*, 1983*b*). Unfortunately, the most important specimens, the skulls, have not been described. When the material is more completely described and illustrated, it will be possible to test some of our hypotheses. Non-dental comparisons were based on the specimens and sources in Table 8.1. The matrix of non-dental characters was analysed using the MacClade software package for the Apple MacIntosh, developed by Wayne Maddison at the Museum of Comparative Zoology, Harvard University.

Outgroup

Cifelli (1983*b*) has shown that *Kennalestes* and other Late Cretaceous eutherians make the best outgroups for determining character polarity with the Eutheria. Where appropriate, primitive carnivores (e.g. *Oodectes*), rodents (e.g. *Paramys*), primates (e.g. *Purgatorius*), and certain 'insectivores' (e.g. *Didelphodus*) were examined to determine whether a character state is widely distributed outside the ungulates. Many authors have suggested that *Protungulatum* (Sloan and Van Valen 1965; Van Valen 1978*b*) is primitive in all known features with respect to the other ungulates. We disagree, and prefer to use comparisons outside the ungulates.

Simpson's (1945) concept of the 'Ferungulata' has been used widely to suggest a close relationship between carnivores and ungulates. The influence of this concept can be seen in mammalogy literature, notably in Walker *et al.* (1975), where carnivores are placed next to the ungulate orders. Unfortunately, 'Ferungulata' was based entirely on the erroneous placement of certain ungulates. Cope (1884) greatly expanded his taxon 'Creodonta' (which previously included only carnivores, hyaenodonts, and oxyaenids) to include the arctocyonid

(*sensu lato*) *Triisodon* and the mesonychids. Even though these primitive ungulates were later distinguished from all other creodonts by Matthew (1909) as 'Acrodi', they were still considered to be related to carnivores. Thus Simpson (1945) connected carnivores and ungulates because of the connection between 'arctocyonid carnivores' and ungulates. Simpson (1953) even used this mistaken connection as a defence for horizontal classification. According to Simpson (1953, p. 345), 'there is one genus, *Protogonodon*, in which on balance of resemblance in small details some species would be classified as carnivores and others as ungulates'. When arctocyonids were later removed from the Carnivora (Patterson and McGrew 1962), all basis for the 'Ferungulata' disappeared (see Chapter 3).

Anatomical characters

The majority of Palaeogene fossil ungulates have been identified exclusively from their teeth. The cladogram in Fig. 8.1 is an attempt to reduce the complexity of dental variation to a meaningful pattern of derived character states. Some primitive ungulate genera were not included due to lack of space, but enough are shown to suggest a framework of relationships. Non-dental characters are summarized in Table 8.1. Much of this evidence goes back to the classic work of Gregory (1910, 1920), although Gregory did not always distinguish primitive from derived features.

Ungulate skulls bear the hallmarks of their relationships in many ways, in addition to their teeth. In the preorbital region, most artiodactyls show an unusually large facial portion of the lacrimal, which often contains a preorbital fossa or vacuity. Artiodactyls also have an unusually large orbitosphenoid bone, which separates the frontal from the alisphenoid (Russell *et al.* 1983). Perissodactyls (except some hyraxes, tapirs, and certain rhinocerotids) have developed a broad contact between the nasals and lacrimals, separating the frontals from the maxillaries.

In the ear region, there are many striking and unique characters, which were analysed in an excellent study by Cifelli (1982). Their distribution (Cifelli 1982, tables 1 and 2) is placed in the context of the present hypothesis in Table 8.1. Wible (1986, 1987) has analysed a number of characters of the cranial circulation. According to Wible (1987), in all ungulates the superior ramus of the stapedia artery no longer lies between the petrosal and squamosal; it either passes through the tegmen tympani of the petrosal (in *Arctocyon*, *Arctocyonides*, and *Pleuraspidothierium*, according to Russell 1964) or is absent altogether (all other ungulates). In addition, cetaceans, perissodactyls, hyracoids, and tethytheres are distinguished from artiodactyls by the loss of the

Table 8.1. Distribution of non-dental features in selected ungulate taxa

Character	Taxa										
	Art	Arc	Hyp	Prp	Mes	Cet	Phe	Men	Uin	Ars	Pro
<i>Cranial characters</i>											
Posterior petrosal epitympanic sinus	-	-	-	?	-	-	+	+	?	?	?
Lose promontory sulcus	-	-	-	?	?	?	-	-	?	-	-
Ventral, slit-like aqueductus cochleae	-	-	-	?	?	?	+	?	?	?	+
Inflated tegmen tympani	-	-	+	?	?	?	+	+	?	?	+
Tympanic aperture facial canal anterior to fenestra ovalis	-	+	+	?	?	?	+	+	?	?	+
Large, bridged tympanohyal	-	-	-	?	-	-	-	-	?	?	+
Long tympanic process (also Tu)	-	-	-	?	-	-	-	-	?	?	+
Lose stapedial sulcus	-	-	+	?	-	+	-	-	?	+	+
Lose proximal stapedial artery	-	-	-	?	+	+	+	+	?	?	+
Superior ramus of stapedial in petrosal or lost	+	+	+	?	+	+	+	+	?	?	+
Bulla (if present) made of ectotympanic only (also Ro, La)	+	?	?	?	?	+	?	?	?	?	+
Weak occipital exposure of mastoid (also Ch, Ed)	+	-	-	?	+	+	+	+	+	+	+
Lose mastoid foramen	+	+	+	?	+	+	+	+	+	+	+
Postglenoid foramen small or absent (also Tu)	-	-	-	?	+	+	+	+	+	+	+
Large posterior lacerate foramen coalesces with cochlear fissure (also De, Ch)	-	-	-	?	+	+	+	?	+	?	+
Ethmoid foramen above posterior palate	-	?	?	?	?	-	?	?	?	?	+

Eustachian sac	—	?	?	?	?	?	?	?	—	+	+	+
Extrabullar anterior internal carotid artery (also some Ro, La)	—	—	?	—	?	—	?	?	?	+	+	+
Lose carotid sulcus	—	?	?	+	—	—	—	—	—	+	+	+
Tuber maxillaris	—	—	—	—	—	—	?	?	+	+	+	+
<i>Postcranial characters</i>												
Lose clavicle	—	—	—	+	+	+	+	+	+	+	+	+
Reduced acromion, coracoid process on scapula	—	—	—	+	+	—	+	+	+	+	+	+
Reduced medial epicondyle, entepicondylar foramen	—	—	—	—	—	+	+	+	+	+	+	+
Ventral ulna straight or concave (some No)	—	—	—	+	+	+	+	+	+	+	+	+
Weak deltoid crest on humerus	—	—	—	+	+	+	+	+	+	+	+	+
19 or more thoracic vertebrae	—	—	—	—	—	—	—	—	—	—	—	—
Reduced astragalus/cuboid contact (also Tu, Pa)	—	—	—	?	+	+	+	+	+	+	+	+
Large, distally shifted third trochanter on femur (also Tu, Pa)	—	+	+	+	+	+	+	+	?	+	+	+

(-) Indicates primitive condition; + = derived condition; ? = condition unknown or not yet examined. Petrosal characters based on Cifelli (1982); vertebral characters from Gregory (1910); skull characters based on Novacek (1986) and Gregory (1920), plus personal observations. Sources for specific taxa include Rose (1982, 1985), Russell *et al.* (1983) for artiodactyls; for artocyonids: Russell (1964) and *Arctocyon ferax*, American Museum of Natural History (AMNH) 16542, 16543; hyposodonts: Gazin (1965); peripitychids: Matthew (1937) and *Peripitychus rhadodon*, AMNH 17075; mesonychids: Scott (1888) and *Pachyaena* (1962); *Mesonyx obtusidens*, AMNH 12643; whales: Kellogg (1936), Kumar and Sahni (1986); phenacodonts: Matthew (1937), Radinsky (1966), and *Phenacodus wortmani*, AMNH 4378, *P. primaeus*, AMNH 4369; meniscotheres: Gazin (1968); uinatheres: Flerov (1957); arsiniotheres: Andrews (1906); Proboscidea: Andrews (1906); hyraxes: recent material of *Procavia capensis*; perissodactyls: MacFadden (1976), Radinsky (1966). Abbreviated taxa listed below in the following order: artiodactyls, artocyonids, hyposodonts, peripitychids, mesonychids, Cetacea, phenacodonts, meniscotheres, uinatheres, arsiniotheres, proboscidea, hyraxes, and perissodactyls (excluding hyraxes). Abbreviations for other taxa showing some of these features in parallel arc: Dj = didelphids, De = dermopterans, Ch = bats, Ro = rodents, La = lagomorphs, Ed = edentates, Tu = aardvarks, Pa = pantodonts, No = some notoungulates.

proximal stapedia artery. Perissodactyls and hyraxes share an extra-bullar path of the internal carotid artery, a feature found only in some Glires within the Eutheria. All living ungulates, except hyraxes and some perissodactyls, have an auditory bulla composed of the ectotympanic bone, although this feature occurs in some rodents and rabbits (Novacek 1986). Many fossil ungulates do not have an auditory bulla, although in some cases this may be due to lack of preservation. Cranial foramina, particularly in the orbital and basicranial regions, were reviewed by Novacek (1986), and many have relevant distributions. The most striking is the loss of the mastoid foramen on the occiput between the mastoid and the supraoccipital. The mastoid foramen secondarily reappears in some artiodactyls and a few palaeotheres. Outside the ungulates, this feature is found only in didelphids (Novacek 1986).

Several characters are also available in the postcranial skeletons of members of most ungulate groups. Surprisingly, very few of these have been used as indicators of phylogenetic relationship. Some have an erratic distribution that shows no phylogenetic pattern. For example, the astragalar foramen is lost in nearly every ungulate group, apparently independently. Many features, however, have been described, discussed, and then ignored. We suspect that this may be due to an inherent functional bias. When organisms have very similar functional anatomy, there is reason to suspect that similarities are due to convergence. Yet many important characters have been dismissed or ignored, even when they occur widely in groups with completely different ecologies. We feel that each character should be examined initially without *a priori* weighting or biases, and rejected when its distribution within or between groups clearly leads to unparsimonious hypotheses.

It is very striking that living ungulates are among the few mammals that lack a clavicle. Among fossil ungulates, only primitive artiodactyls, arctocyonids, hyopsodonts, and peripitychids retain this feature; advanced artiodactyls lose it. Cifelli (1983b) doubted the value of this character, but we are impressed with its consistent distribution within the ungulates. Once the clavicle is lost, it never reappears in a group. Its loss seems to be independent of functional considerations as well. Even though cursorial ungulates lack a clavicle, so do many (but not all) graviportal, aquatic, and arboreal ungulates. According to the primate literature, a clavicle is essential to arboreality, yet the tree hyrax does not have one. Although organisms are influenced by functional considerations, their anatomy is not infinitely flexible. Once a feature is lost, it never reappears, despite functional demand for it.

The ungulate scapula is also distinctive. Mesonychids and all higher ungulates (except whales and meniscotheres) have greatly reduced the

acromion and coracoid processes of the scapula in concert with the loss of the clavicle. Some artiodactyls have independently reduced these processes. In the humerus, most higher ungulates have reduced the deltopectoral crest. Primitive ungulates have a large knob-like medial epicondyle with a large entepicondylar foramen. This is highly reduced or lost in all higher ungulates. The ventral border of the ulna is curved and posteriorly convex in most mammals, including primitive ungulates. The olecranon flexes toward the limb axis, accentuating this curvature. In mesonychids and higher ungulates, the ulna has a posterior border that is straight or posteriorly concave, with the olecranon flexed away from the limb axis. Although this feature can be related to limb efficiency, it also occurs in animals that seem to have no functional similarity.

The carpal region has long featured in discussions of ungulate relationships. In most mammals, the carpal elements overlap one another in a 'brickwork' fashion, known as the 'alternating' or 'diplarthral' carpus. Certain ungulates have shifted the carpal elements so that they are in line or 'serial'. Cope (1897) considered the serial (or 'taxeopod') carpus to be primitive for ungulates, based on the complete skeleton of *Phenacodus primaevus*, which had the most complete postcranial material of any fossil 'condylarth' known at the time. As a result, Osborn (1898) placed the peripitychids (with their alternating carpus) with the pantodonts in the waste-basket taxon 'Taligrada', as part of another waste-basket taxon 'Amblypoda' (which then included pantodonts and uinatheres). Many later authors kept this arrangement, largely on Osborn's authority.

Ironically, in the same year that Cope argued for a primitive serial carpus, Matthew (1897) showed that the alternating carpus is primitive for ungulates, based on the skeleton of *Tetraclaenodon* (= '*Euprotopia*') *puercensis*. Matthew's and Simpson's classic monographs of 1937 finally cleared up the confusion over alternating versus serial carpus. Although the serial carpus and the corresponding loss of the lunar-unciform contact is still used (Novacek and Wyss 1986, character 62) as a derived character supporting some phylogenetic arrangements, there are reasons to doubt its usefulness. As Gregory (1910, p. 452) showed, it occurs in some rodents and insectivores, *Hyaenodon*, and certain ungulates (some phenacodontids, meniscotheres, elephants, sirenians, hyraxes). It might be used to unite these ungulate taxa at node 38 in Fig. 8.1, except that it does not occur in primitive members of some of these groups (such as the phenacodont *Tetraclaenodon*), and even varies within genera. For example, *Phenacodus primaevus* is serial, but *P. copei* is alternating (Radinsky 1966). Similarly, a free centrale occurs in a number of primitive forms, but the fusion of this element with the scaphoid appears to have happened in several groups independently

(Gregory 1910). By the Oligocene, the carpals and tarsals of all main ungulate groups are easily distinguished.

As early as 1816, Blainville used the relative proportions of their podial elements to group ungulates. Artiodactyls are united by their 'paraxonic' foot, with the main axis between digits 3 and 4. These two digits have become symmetrical by the enlargement of the fourth metapodial and digit, and give artiodactyls their diagnostic 'even-toed' foot. Digits 2 and 5 are also equal in proportion to each other, and if they are reduced, they are reduced equally. The first digit is reduced in the earliest artiodactyls to a non-functional nubbin, since it has no symmetrical counterpart in the paraxonic foot. Agriochœres, however, have apparently redeveloped the first metacarpal.

In most other ungulates, all five digits are present and approximately equal in length. Phenacodonts, hyraxes, and perissodactyls have strengthened the central digit (as well as metapodial 3) to various degrees. This produces a derived form of the mesaxonic foot. The reduction of the side digits in phenacodonts is not as extreme as it is in hyraxes and perissodactyls. In the last two groups, the first metapodials are extremely reduced (Radinsky 1963), and metatarsal 5 is lost. In more derived perissodactyls, metacarpal 5 is also lost and the third metapodial becomes enlarged at the expense of the lateral metapodials.

The features that give the ungulates their name are hooves, or unguals, the laterally broadened terminal phalanges that stabilize the feet on flat ground when the number of digits has been reduced. Unfortunately, associated phalanges are seldom preserved in most Early Tertiary fossil taxa. Several Early Tertiary ungulates had claws. Van Valen (1978b, p. 292) reported that *Protungulatum* had claws, although these have not yet been described. Claws occur in *Arctocyon* (Russell 1964), *Chriacus* (Rose 1987), *Hyopsodus* (Gazin 1968), and *Tetraclaenodon* (Radinsky 1966). More hoof-like phalanges occur in the most primitive members of nearly all the remaining groups, including the early artiodactyl *Diacodexis* (Rose 1982, 1985), the peripitychids *Eoconodon* and *Peripitychus* (Matthew 1937), *Phenacodus* (Radinsky 1966), *Mesonyx* (Scott 1888), *Meniscotherium* (Gazin 1965), and in primitive uinatheres, arsinotheres, proboscideans, hyraxes, and perissodactyls. Thus, hooves developed several times independently within the ungulates, and a few groups (such as chalicotheres, agriochœres, and homalodotheres) secondarily reverted to claws (Coombs 1983).

One feature of the axial skeleton seems phylogenetically significant. Primitively, most eutherian mammals have 12–15 thoracic vertebrae (Gregory 1910, p. 275). Hyopsodonts, uinatheres, elephants, sirenians (except manatees), hyraxes, and perissodactyls have all increased this number to 19–21 (Table 8.1).

Most advanced ungulate femora (except those of artiodactyls) are easily recognized by a well-developed, distally-shifted third trochanter, to which the superficial gluteus muscles attach. Among ungulates, only artiodactyls, hyraxes, and some gravi-grade forms lack an enlarged third trochanter. The most primitive artiodactyl, *Diacodexis*, had a faint ridge-like third trochanter, but all higher artiodactyls have lost it completely (Rose 1982, 1985).

Like the carpus, the tarsus can be difficult to interpret. Some features, such as the loss of the astragalar foramen mentioned above, show no phylogenetic pattern. As Szalay (1977) has shown, however, the ungulate calcaneum and astragalus are readily distinguished from those of other groups. The astragalus of *Protungulatum* is derived in having a relatively short, robust neck. The reduced contact between the astragalus and cuboid, indicating the beginnings of a 'serial tarsus', occurs in the phenacodonts, meniscotheres, and higher non-gravi-grade ungulates. Uintatheres, arsinotheres, elephants, hyraxes, and perissodactyls are also united by having a flat, rather than convex or knob-like, navicular facet on the head of the astragalus. Perissodactyls have further modified this by developing a concave navicular facet, and corresponding convex astragalar facet on the navicular. Artiodactyls, of course, are unique in having the famous 'double pulley' astragalus, with well-developed trochlea at both ends (Schaeffer 1947). Ungulates never developed a fully plantigrade tarsus (such as those of humans or bears), nor has any ungulate become fully bipedal (although the modern gerenuk, *Litocranius*, comes close).

Results

Dental and non-dental anatomical evidence produces a remarkably consistent phylogenetic pattern (Fig. 8.1). Considering that dental, cranial, petrosal, and postcranial features are largely functionally independent, this consistency is even more striking. Some of the dental and/or postcranial anatomy might be dismissed as being due to functional or ecological convergence, but this does not apply to most of the petrosal and cranial features. Because of the congruence of a wide variety of anatomical evidence, we conclude that the hypothesis is robust.

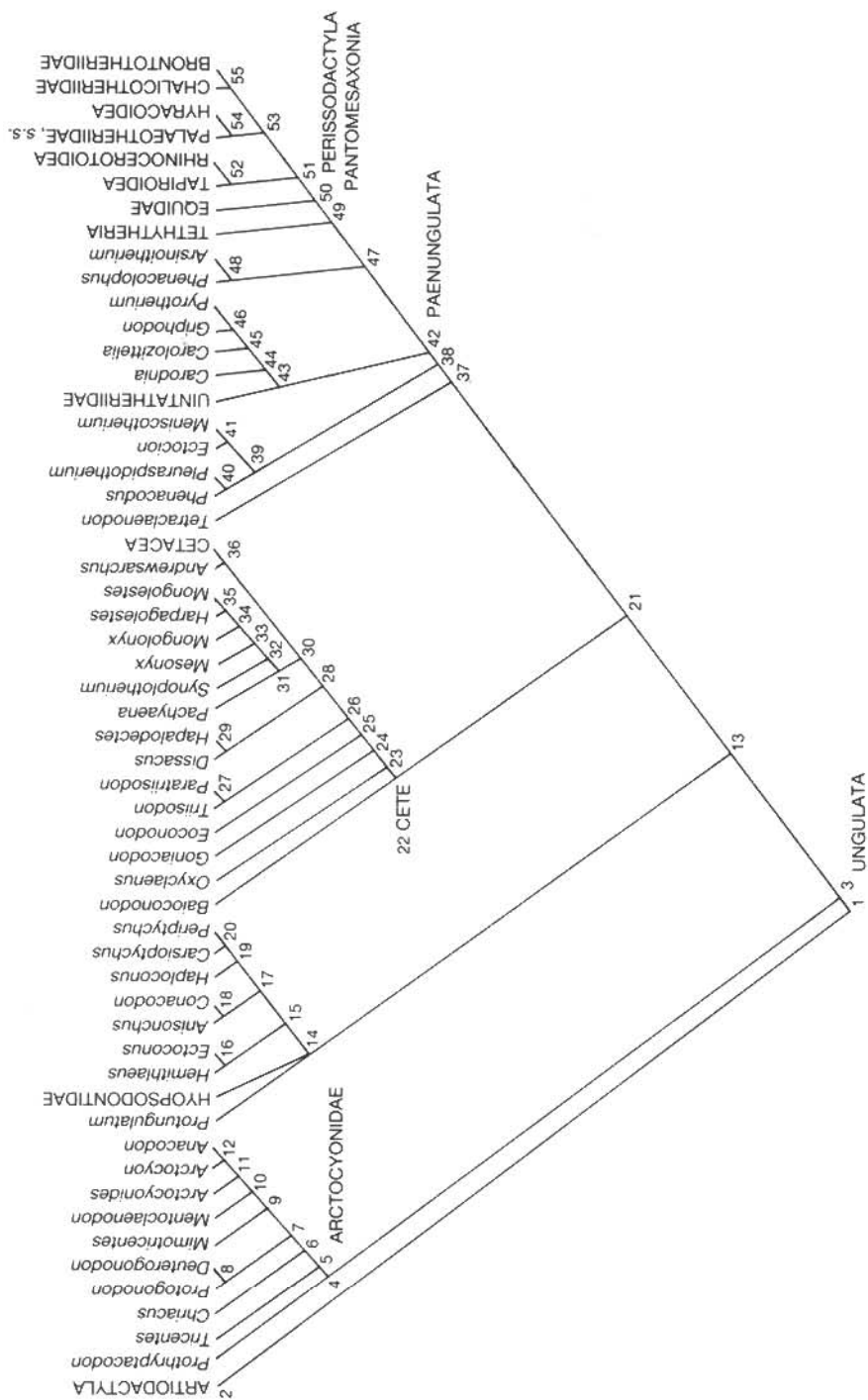


Fig. 8.1. Cladogram of selected ungulate higher taxa. Characters at numbered nodes as follows: 1. UNGULATA: superior ramus of stapedial artery shifted to petrosal or lost; mastoid foramen lost; bulla (if present) composed of ectotympanic; relatively bunodont teeth with low cusp relief; lower molar trigonids shortened anteroposteriorly; large, posteriorly projecting hypoconulid on M_3 ; astragalus with shorter, more robust head. 2. ARTIODACTYLA: lower molar trigonids very narrow, with paraconid and metaconid closely appressed; alisphenoid canal lost; pars facialis of lacrimal enlarged; enlarged orbitosphenoid, separating frontal from alisphenoid; paraxonic foot, with double-pulley astragalus, enlarged third and fourth metapodials, and symmetrically-reduced second and fifth metapodials. 3. Add hypocone to upper molars; third trochanter of femur enlarged and distally shifted; tympanic aperture of canalis facialis anterior to fenestra ovalis. 4. Complete lingual cingulum on upper molars. 5. Anterolingual cingulum on M^1 enlarged. 6. Size larger. 7. Parastyles and metastyles reduced. 8. Posteroangular cusp on M^3 . 9. Upper molars square. 10. Enamel crenulate. 11. Labial cingulum rounded. 12. Canines enlarged and saber-like, serrated posteriorly; mandibular condyle low; $P_{3,4}$ serrated posteriorly. 13. Inflated tegmen tympani. 14. $P_{3,4}$ protocone and paracone bulbous. 15. PERIPTYCHIDAE, s.l.: shallow lingual slope on protocone. 16. Mesostyle on M^2 . 17. Palate deep; hypocone shifted medial to protocone. 18. Hypocone region expanded. 19. P^4 becomes very large; protocone moved laterally between conules. 20. Enamel crenulate; hypocone moved laterally to level of protocone. 21. Weak occipital exposure of mastoid; lose proximal stapedial artery; large posterior lacerate foramen coalesces with cochlear fissure; postglenoid foramen small or absent; reduced acromion and coracoid processes on scapula; lose clavicle; ventral border of ulna straight or concave; reduced deltoid crest of humerus. 22. CETE: blunt, conical protocones. 23. M^3 small with small hypocone; posterolingual accessory cusp added to P^4 ; M^3 parastyle small and paracone large; P_4 paraconid deflected posteriorly. 24. M^3 metacone small. 25. $M^{1,2}$ parastyle lost. 26. Paracone larger; all cusps tall and conical; overall size increase. 27. TRIIODONTINAE: accessory cusp anterior to entoconid on M_1 . 28. ACREODI: trigonid high; entoconid very reduced. 29. HAPALODECTINI: lower cheek teeth narrow; $M^{1,2}$ parastyles long; $P_{2,3}$ diastema. 30. Mandibular condyle low, with pedicellate glenoid; mandibular angle small. 31. MESONYCHIDAE (amended): mandibular condyle below level of cheek teeth; P^4 protocone moved posteriorly. 32. M^3 very small. 33. M^3 lost. 34. P^2 short; labial cingula on upper molars absent. 35. Horizontal ramus arcuate. 36. Medial portion of lambdoid crest high; $I^{2,3}$ aligned with cheek teeth; elongated premaxilla. CETACEA: all incisors parallel with cheek teeth; medial lambdoid crest semicircular; nasals retracted; protocones small; accessory cusps large. 37. P^4 protocone area broadened. 38. P^4 protocone and metacone enlarged; ventral, slit-like aqueductus cochleae; reduced medial epicondyle and entepicondylar foramen on humerus; reduced astragalus/cuboid contact. 39. PHENACODONTIDAE (expanded): posterior petrosal epitympanic sinus; mesostyle on upper molars. 40. M^3 posterior cingular cusp expanded. 41. Metacarpal added between hypocone and metaconule. 42. PAENUNGULATA (amended): navicular facet of astragalus flattened; 19 or more thoracic vertebrae; M_3 larger than M_2 . 43. DINOCERATA (amended): M_3 metalophid high; V-shaped loph on M^3 ; lower incisors multicuspid. 44. PYROTHERIA (amended): $M^{1,2}$ fully bilophodont. 45. Cristid between M_3 hypoconid and entoconid. 46. P_4 fully bilophodont with metalophid. 47. Hypolophid forms between entoconid and hypoconid of lower molars; metaconule moves posteriorly and loses connection with protocone. 48. EMBRITHOPODA: M_3 hypoconulid small and merged with posterior cingulum. 49. PANTOMESAXONIA (*sensu* Franz 1924): entoconid and hypoconid opposite one another, at right angles to axis of ramus; lacrimal process in anterior border of orbit; fossa glandis with projecting processus urethralis in penis; ramus anastomoticus; ramus infraorbitalis of stapedial artery in alisphenoid canal; tuber maxillaris. 50. PERISSODACTYLA (*sensu* Owen 1848): lose promontory sulcus; lose stapedial sulcus; extrabullar internal carotid artery; large, bridged tympanohyal; long tympanic process; eustachian sac; tuber maxillaris persists after tooth eruption; reduced first metapodial and fifth metatarsals; enlarged third metapodials. EQUIDAE: foramen ovale and median lacerate foramen confluent; optic foramen and anterior lacerate foramen confluent; lengthened limbs; reduced lower canines. 51. Large parastyle; metaconule merges with metaloph. 52. CERATOMORPHA: paraconule merges with protoloph. 53. Mesostyle and metastylid present; anterior crista obliqua near metaconid. 54. M^3 expanded posteriorly; metastyle elongated. 55. Lower molars W-shaped (crista obliqua connects hypoconid to metaconid); centrale fused to scaphoid.

Discussion

The relationships of ungulates

The Ungulata are a monophyletic group recognizable in several features of their anatomy. They all share:

- (1) astragalus with a shorter, more robust head;
- (2) foramen for superior ramus of stapedial artery shifted to petrosal or lost;
- (3) auditory bulla (if present) composed of ectotympanic;
- (4) mastoid foramen lost;
- (5) more bunodont teeth with relatively low cusp relief (compared to *Purgatorius*, *Gypsonictops*, or other Late Cretaceous eutherians);
- (6) lower molar trigonids shortened anteroposteriorly;
- (7) a large, posteriorly-projecting hypoconulid on M₃.

The oldest known ungulate, *Protungulatum*, is as yet described only from teeth and tarsals, so some of these characters cannot be applied to it. More complete material (partially described by Van Valen 1978b) might be expected to show these features. Note that Novacek *et al.* (Chapter 3 of this volume) do not find strong evidence for a monophyletic Ungulata.

The artiodactyls appear to be the first of the ungulate groups to diverge, since they lack many of the specializations seen in all other ungulates. *Diacodexis* and *Dichobune*, for example, have very weak third trochanters, and lack the hypocone seen in all other ungulates. In higher artiodactyls, the metaconule takes the position of the hypocone. In some taxa, a lingual cingular cusp that may or may not be homologous with the hypocone also appears. Primitive artiodactyls can also be distinguished from all other ungulates by the following derived dental features: lower molar trigonids are very narrow, with the paraconid and metaconid closely appressed; M³ metacone enlarged; P⁴ with a small protocone crista; P³ broad. Artiodactyls are also united by a wide variety of unique non-dental features, including:

- (1) wide epitympanic recess;
- (2) anterior lacerate foramen confluent with foramen rotundum;
- (3) enlarged pars facialis of lacrimal, often developing a fossa or vacuity;
- (4) enlarged orbitosphenoid, separating frontal from alisphenoid;

- (5) paraxonic foot, with double-pulley astragalus, enlarged third and fourth metapodials, symmetrically reduced second and fifth metapodials, and vestigial first metapodials (except in the Tayasuidae) (see also Chapter 9).

At node 3 in Fig. 8.1 are several ungulate groups that developed a true hypocone. These include arctocyonids *sensu stricto*, hyopsodonts, peripitychids, and mesonychids. Non-dental evidence suggests that the arctocyonids are the most primitive of these groups. The arctocyonids have long been a paraphyletic 'waste-basket' taxon for many types of primitive ungulates that are not something else. We have relegated the 'triisodontines' (Fig. 8.1, node 22) to the Cete. At the core of this unnatural assemblage, however, is a monophyletic group united by the presence of a complete lingual cingulum on the upper molars. The relationships of selected genera of Arctocyonidae *sensu stricto* are shown in Fig. 8.1. Not all of the known genera are included, since the group is currently undergoing extensive revision and new taxa are being added (Van Valen 1978b; Cifelli 1983b).

The Arctocyonidae had long been included with the creodonts and carnivores, since they have a somewhat bear-like dentition, and a skull like some primitive carnivores. The lack of a true shearing carnassial, and the presence of ungulate limbs and feet, eventually led to their recognition as ungulates (Ameghino 1901; Patterson and McGrew 1962; Sloan and Van Valen 1965; Van Valen 1966). In addition to a typically ungulate bunodont dentition, which lacks the type of shearing seen in carnivores, arctocyonids have a number of other advanced ungulate features. These include an enlarged third trochanter, a typically ungulate astragalus, and the tympanic aperture of the facial canal that opens anterior to the fenestra ovalis (Cifelli 1982).

Hyopsodonts and peripitychids are two groups that were very abundant in the Early Tertiary. They are usually placed in the 'Condylarthra' on the basis of shared primitive similarities. In the past, they have been assigned to many different groups. Peripitychids were long associated with pantodonts and excluded from the ungulates, although they were part of Cope's (1881b) original definition of the Condylarthra. *Hyopsodus* has been considered a primate, an insectivore, an artiodactyl, or the ancestor of proboscideans or perissodactyls (Gazin 1968). Hyopsodonts and peripitychids share a number of derived dental similarities, especially the development of bulbous protocones and paracones on P^{3,4}. Some peripitychids are even more distinctive in having shallow lingual slopes on the protocones and, in more derived taxa, highly crenulated enamel. The relationships of hyopsodonts have been discussed by Van Valen (1978b), Rigby (1980), and Cifelli (1983b, pp. 36–8), yet the cladogram of these taxa is still in

flux. The peripitychids are currently being revised by Archibald (1982; Archibald *et al.* 1983a, 1983b). In the possession of an inflated tegmen tympani (Cifelli 1982), hyopsodonts and peripitychids are more derived than arctocyonids and are thus placed as sister-taxon to higher ungulates (Fig. 8.1, node 13).

Whales have traditionally been placed in their own Order Cetacea, with no apparent relationship to the rest of the Mammalia. In recent years, however, it has become clear that whales are related to a primitive omnivorous group, the Mesonychidae (Van Valen 1966, 1968; Szalay 1969a,b; Gingerich *et al.* 1983). Because of their bear-like skeletons and pointed teeth, mesonychids were long allied with creodonts and carnivores. Their fully ungulate skeleton (including hooves) and the lack of any carnassial modification strongly indicate that mesonychids are not related to creodonts or carnivores, but are in fact omnivorous ungulates. Several derived features, such as the loss of the proximal stapedia artery, loss of the clavicle, reduced coracoid and acromion processes on the scapula, reduced deltopectoral crest on the humerus, weak occipital exposure of the mastoid, small postglenoid foramen, and a large posterior lacerate foramen that coalesces with the cochlear fissure, suggest that mesonychids are actually quite derived ungulates.

McKenna (1975) resurrected Linnaeus' taxon, Cete, for whales and mesonychids. We would include not only these two groups, but also the triisodontines and some 'oxycloenine arctocyonids' (*sensu lato*) that share the derived feature of a blunt, conical protocone, which unites the Cete. The more derived cetans (Fig. 8.1, node 28) include *Dissacus*, *Hapalodectes*, mesonychids, and whales, which all had high trigonids and small entoconids. McKenna (1975) suggested Matthew's (1909) taxon 'Acreodi' for the Mesonychidae as a taxon equal in rank to the Cetacea. If the relationships shown in Fig. 8.1 are correct, however, this usage of Acreodi would be the same as the Family Mesonychidae used here, making the term redundant. We prefer to use the taxon as a hierarchical level above the mesonychids and cetaceans, and also include *Dissacus* and *Hapalodectes*.

The ecological gap between whales and other ungulates often seems unbridgable to mammalogists. Still, as living land carnivores and seals have a functional (rather than phylogenetic) intermediate in the otters, land and sea ungulates also have a functional intermediate. The transition can be made by a coastal scavenger that eats fish. If it is accustomed to eating fish washed up on shore, it is a relatively small step to adapt to catching live (probably weak, large, or slow-moving) coastal fish. After an otter-like semiaquatic stage, a whale could evolve. A fair approximation of this functional intermediate for whales is the living brown hyaena (*Hyaena brunnea*). When living along the coast of

South Africa (where it is called the 'strand wolf'), the brown hyaena is a large coastal scavenger (Walker *et al.* 1975).

The phenacodonts were the original nucleus of Cope's (1881*b*) concept of 'Condylarthra'. Cope (1881*a*, 1882) originally placed *Meniscotherium* with the phenacodonts in the 'Condylarthra'. Other authors (reviewed by Gazin 1965) have allied meniscotheres with chalicotheres, protheroheres, hyraxes, and artiodactyls (because of their precociously selenodont teeth). More recent authors (e.g. Gazin 1965) have shown that meniscotheres are most closely related to phenacodonts. They share a number of derived characters, including a well-developed mesostyle and a unique posterior petrosal epitympanic sinus (Cifelli 1982).

Phenacodonts and meniscotheres are the most derived groups formerly referred to the 'Condylarthra'. This is shown by a number of features. In the teeth, they are beginning to show the trend toward squaring and molarization of the premolars that is seen in higher ungulates. *Tetraclaenodon* had broadened the lingual side of the P^4 protocone, and *Phenacodus* and higher taxa have also enlarged the P^4 metacone. A number of non-dental characters clearly indicate that phenacodonts and meniscotheres are actually quite derived ungulates. These features include a reduced astragalus-cuboid contact (beginning the trend toward a serial tarsus) and a reduced medial epicondyle and entepicondylar foramen in the humerus. Phenacodonts and meniscotheres share with higher ungulates a ventral, slit-like aqueductus cochleae in the petrosal.

McKenna and Manning (1977) first suggested that the uinatheres (Dinocerata), arsinotheres (Embrithopoda), elephants (Proboscidea), sea cows (Sirenia), desmostylians, hyraxes, and perissodactyls (Fig. 8.1, node 42) formed a natural group of advanced ungulates. They expanded the 'Paenungulata' to include these taxa by adding the Perissodactyla and removing the Pantodonta. These groups all share the enlargement of M_3^3 , which is the beginning of the trend toward molars that are approximately equal in size—an advance which made lophodonty possible. In the primitive condition, the molar row tapers posteriorly. They also share a number of derived non-dental features, including a flattened navicular facet on the astragalus, and an increase to 19 or more thoracic vertebrae.

Of the first three groups listed, the uinatheres are clearly the most primitive. A number of features support the monophyly of the Dinocerata, including: a fully developed V-shaped loph on M^3 , a high M_3 metalophid, P_3 – M_3 metalophids obliquely oriented and posteriorly inclined, metastylids accentuated, paralophids lost, multicusped incisors, and an inframandibular flange (McKenna and Manning 1977; Tong and Lucas 1982). Tong and Lucas (1982) pointed out the

derived dental similarities between uinatheres and *Pseudictops*, and suggested that uinatheres might not be ungulates, but it is not only the astragalus that makes uinatheres ungulates. Nearly all the non-dental features found in more primitive ungulates (Fig. 8.1) are also found in uinatheres, particularly in the more primitive forms, such as *Mongolotherium* (Flerov 1957). Although the teeth of *Pseudictops* and uinatheres are somewhat similar, the strong evidence from the skull and postcranial anatomy clearly places the uinatheres within the ungulates.

Arsinoitheres are united with higher ungulates by the common possession of a hypophid between the entoconid and hypoconid of the lower molars, and a metaconule that shifts posteriorly and loses its connection with the protocone (McKenna and Manning 1977). The Embrithopoda was originally thought to include only the enigmatic Egyptian Oligocene *Arsinoitherium*, a rhino-like beast with paired pointed horns on its nasals and frontals. The group has been considerably expanded with the addition of *Crivadiatherium* from the Late Eocene of Rumania (Radulesco *et al.* 1976), *Phenacolophus* from the Late Palaeocene of Mongolia (McKenna and Manning 1977), other forms from the Late Palaeocene of China (Tong *et al.* 1976), and *Palaeoamasia* from the Late Eocene of Turkey (Sen and Heintz 1979). Apparently, arsiniotheres were an important element of the Early Tertiary large mammal fauna of the Old World, along with pantodonts and uinatheres.

McKenna (1975) united the proboscideans, sirenians, and desmostylians in his new taxon Tethytheria. Although he provided no evidence for this relationship, they are clearly a good monophyletic group, with a number of unique and striking synapomorphies. These were discussed by Domning *et al.* (1986) and Tassy (1981, 1982; Chapter 11 of this volume). The tethytheres are united with hyraxes and perissodactyls by the common possession of lower molars with entoconids and hypoconids opposite one another at right angles to the ramus, forming a more efficient bilophodont molar (McKenna and Manning 1977). This is further supported by the shared presence of a lacrimal process and the unique morphology of the tip of the penis, as discussed by Fischer (1986).

Several authors (Shoshani 1986; de Jong and Goodman 1982; Novacek 1982, 1986; Novacek and Wyss 1986; Chapter 3 of this volume) have suggested that hyraxes are more closely related to tethytheres than they are to perissodactyls. We feel that the anatomical evidence strongly supports the hypothesis that hyraxes and perissodactyls are most closely related. The dental similarities between primitive Fayum hyraxes and certain European 'palaeotheres' are very striking, and suggest that some perissodactyls share many derived dental

features with hyraxes. Indeed, the oldest known equoid was named *Hyracotherium* by Owen in 1841 because of this similarity. The list of non-dental features allying hyraxes and perissodactyls is even stronger. In the petrosal region (Cifelli 1982) they share a ventral hiatus fallopii, a large bridged tympanohyal, a long tympanic process, and a tympanic aperture of the canalis facialis at the fenestra ovalis. They both lose the stapedial sulcus, and instead share an extrabullar path of the internal carotid artery (Wible 1986; Fischer 1986). By far the most striking feature of hyraxes and perissodactyls is the inflated eustachian sac (Fischer 1986, 1988). Fischer (1986, 1988) lists additional characters of the course of the sternoscapular muscle, the details of the ungual phalanges, and the development of the tuber maxillare, which strongly suggest that hyraxes are perissodactyls. The feet of the hyrax are nearly identical with those of *Hyracotherium* and other primitive perissodactyls. Both groups have greatly reduced or have lost the first metacarpals, and first and fifth metatarsals. They emphasize the third metapodial, producing a strongly mesaxonic foot. Since Owen (1848) originally included *Hyrax* in his definition of the Perissodactyla, we suggest that the 'Order Hyracoidea' be demoted to a subgroup of the Perissodactyla.

The Perissodactyla has long been recognized as a monophyletic group. Several features support this relationship. In the skull, only perissodactyls (except certain hyraxes, advanced tapirs, and rhinos) have lacrimals that broadly contact the nasals. In the P^{3,4} of perissodactyls, the metacone is equal in size to the paracone. There are a number of derived postcranial similarities. The most striking is the concave navicular facet on the astragalus (and corresponding convex astragalar facet on the navicular). Perissodactyl and hyrax fibulae have lost their articulation with the calcaneum, and the third metapodials are even more enlarged than in hyraxes.

Other possible ungulates

Space limitations prevent us from more fully discussing several problematic groups. Aardvarks have long been allied with ungulates (Patterson 1975), but the evidence is ambiguous. They share a confusing mix of characters seen in ungulates, but also lack many key features. In their skull and ear features, they are clearly more primitive than any ungulate (Thewissen 1985; Novacek 1986; Novacek and Wyss 1986; Wible 1987). Molecular evidence (discussed below) tends to place aardvarks with other 'paenungulates' (and with tupaiids), where there are data available. The posteriorly inclined coronoid process and shallow mandibular symphysis of the peculiar pantodont *Pantolambdodon* may suggest a relationship of aardvarks to one group of

pantodonts. Further resolution of this problem requires a broader study than our space permits.

Because they are large and heavy-bodied, the pantodonts have frequently been placed with the ungulates. At one time, for example, they were grouped with the peripitychids and the uintatheres in the Amblypoda. Simpson (1937) and Patterson (1939) effectively demolished the Amblypoda, but proposed no alternative for pantodont relationships. Pantodonts do share a few features that are found in the ungulates, such as an enlarged femoral third trochanter and hooves in some of the more derived genera. Szalay (1977, pp. 354–5) argued that the pes of *Pantolambda* is like that of ungulates, but gives no specific features to support this contention. Our examination of primitive pantodont feet produced no derived ungulate features, only shared primitive similarity. More importantly, the teeth of pantodonts are specialized in a completely different manner from primitive ungulates. Instead of the transverse shear and low cusp relief that is diagnostic of primitive ungulates, pantodonts have specialized tribosphenic teeth with a high, W-shaped ectoloph formed on a broad styler shelf for vertical shearing. The hypocone, when present, is never large or high enough to produce the typically low, rectangular ungulate upper molar. For the present, we feel that *Deltatherium* is probably the closest sister-taxon of pantodonts, and suspect that pantodonts are closer to Ferae than Ungulata. The few derived features that pantodonts share with ungulates are probably convergent.

Schoch (1986) has provided convincing evidence that another Palaeogene large mammal group, the taeniodonts, is only distantly related to ungulates. Schoch indicates a relationship of taeniodonts to the leptictimorph group, including palaeoryctines, leptictids, and pantolestids (Schoch 1986, pp. 171–3).

South American ungulates

The enormous radiation of endemic ungulates in South America has long fascinated palaeontologists. Most authors thought that South American ungulates originated from a single primitive stock, and that they formed a monophyletic group. McKenna (1975) formalized this concept in proposing the 'Meridiungulata', although he provided no anatomical evidence for this taxon. A complete review of all the evidence is inappropriate here, but such work is currently in progress (Cifelli 1983a,b; *pers. comm.*). From Cifelli's work, it appears that didolodonts, litopterns, and notoungulates share derived features of the dentition and feet with hyopsodonts. Alternatively, *Didolodus* may be related to peripitychids, as suggested by the resemblance of its teeth to those of *Ectoconus*. Likewise, primitive notoungulates show similarities

to the enigmatic Chinese ungulate *Lantianius*. Astrapotheres and trigonostylopoids share more features with uinatheres than with any other group. The bizarre Palaeocene mammal *Carodnia* has frequently been united with pyrotheres, and both have derived dental similarities with uinatheres. For this reason, *Carodnia* and the pyrotheres have been united with the uinatheres here in an expanded Dinocerata (Fig. 8.1, node 43). *Carodnia*, however, has a peculiar type of serial tarsus, unlike that of uinatheres and pyrotheres. However, the serial tarsus has often been independently derived, as discussed above. At present, it appears that South American ungulates may be related to at least two different ungulate groups, the hyopsodonts (didolodonts, litopterns, notoungulates) and the uinatheres (astrapotheres, trigonostylopoids, pyrotheres, and maybe *Carodnia*). This suggests that the South American ungulates are not a monophyletic group. The 'Meridiungulata' appears to be merely a geographic construct (like the 'subungulates'), with no phylogenetic basis.

Comparison with molecular phylogenies

In the last decade, a new body of phylogenetic information has emerged from molecular biology. From crude immunological distances, to more sophisticated amino acid sequencing, to currently developing DNA analysis, molecular studies have provided a new source of data to test phylogenetic hypotheses based on traditional morphological features. As clearly shown by Goodman *et al.* (1979, 1982), however, the molecular evidence is no magical 'black box' that delivers unambiguous truth (see also Chapter 3 of this volume). Molecular sequences are also subject to parallelism and convergence, as well as insidious gene duplications (GD), and events that prevent gene expression (GE). For example, Joysey (*pers. comm.* 1985) has shown that the blood proteins of South American didelphids and primates show amazing convergence, which he attributes to some ecological crisis affecting all the mammals of this island continent in a similar fashion. This may explain some of the molecular similarities between endemic African forms, such as hyraxes and tethytheres.

In many cases, there are so few molecular differences that several possible arrangements are equally parsimonious. Phylogenetically-meaningful molecular differences can be overprinted by parallelism, back mutation, and other phylogenetic 'noise' (Goodman *et al.* 1982, p. 119). As a result, most molecular phylogenies are not simply the most-parsimonious arrangement of nucleotide replacements (NR) for a given array of taxa. Once a most-parsimonious tree has been produced and tested, a host of assumptions is added to the concoction. These *a*

priori assumptions (Goodman *et al.* 1979, p. 139) modify the clustering so that certain assumed monophyletic groups automatically become closely related. For example, in nearly all trees, the major orders of mammals are assumed to be monophyletic, and the Perissodactyla and Artiodactyla are automatically clustered. Within the artiodactyls, ruminants and tylopods are grouped together, excluding the suines. These *a priori* assumptions are often hard to decipher from the final, most-parsimonious tree given in the last figure of a paper, and sometimes their influence on the data can be misleading.

Consider, for example, the development of the myoglobin sequence. First presented by Romero-Herrera *et al.* (1973), the data set emphasized primates and included the horse, ox, sheep, and three cetaceans; all of these ungulate groups clustered together. A larger sample of these three orders (Goodman *et al.* 1979, figs. 16 and 17) provided the same arrangement, although three 'gene expression' events were required to hold ruminants together, and pigs clustered with insectivores. Goodman *et al.* (1982, figs. 1 and 2) added elephants to the pool; they clustered with the rest of the ungulates, as did the primate *Lepilemur*. Dene *et al.* (1983) added the aardvark to the arrangement, and the most-parsimonious NR tree with no *a priori* adjustments (Dene *et al.* 1983, fig. 3) clusters elephants with perissodactyls, followed by artiodactyls and then by whales. Except for *Lepilemur*, which once again clusters with elephants, this arrangement of monophyletic ungulates resembles ours. When *a priori* expectations from other protein sequences (primarily lens α -crystallin, as discussed below) were added to the pool, however, Dene *et al.* (1983, fig. 4) produced a completely different arrangement, with elephants widely separated from ungulates and placed near the base of the Eutheria.

Other protein sequences produced comparable results. α -haemoglobin (Goodman *et al.* 1979, figs. 6–9) clustered artiodactyls and perissodactyls with few GD or GE events required, but whales, elephants, and hyraxes were not sampled. β -haemoglobin (Goodman *et al.* 1979, figs. 10–13) cleanly clustered most artiodactyls and the horse, but the llama and elephant fell outside the ungulates. Judicious branch-swapping using GE and GD events where necessary finally placed the pig and llama within the artiodactyls, with elephants just outside the ungulates. We wonder if the further assumption that the elephant is also an ungulate would have produced an almost equally parsimonious arrangement. The β -haemoglobin tree of Goodman *et al.* (1982, fig. 6) showed similar results, although hedgehog and armadillo also cluster near the elephant at a node just more primitive than other ungulates. Fibrinopeptides A and B (Goodman *et al.* 1982) place the elephants nearest the artiodactyls.

The most-parsimonious arrangement of cytochrome *c* (Baba *et al.* 1981; Goodman *et al.* 1982, fig. 3) clustered whales and artiodactyls, and placed perissodactyls on the next most remote node. This arrangement required no GE or GD events. No data were available for hyraxes or elephants. Pancreatic ribonucleases (Beintema and Lenstra 1982) clustered artiodactyls and whales, with perissodactyls at the next most remote node; again, no data were available for elephants or hyraxes. From all the systems so far discussed, it is clear that artiodactyls, perissodactyls, and whales form a monophyletic group, and in most cases elephants cluster within or just outside this group. Goodman *et al.* (1982, p. 148) readily concede the ambiguous position of the Proboscidea.

Yet the most recent papers of the molecular phylogeneticists (Goodman *et al.* 1982, 1985; Miyamoto and Goodman 1986; Shoshani 1986) have strongly argued that elephants and hyraxes form a 'paenungulate' group not closely related to other ungulates, and have gone so far as to reclassify the mammals this way (Miyamoto and Goodman 1986). The basis for this abrupt switch appears to be the interpretation of yet another protein, eye lens protein α -crystallin A (de Jong *et al.* 1977; de Jong and Goodman 1982; de Jong 1982). This protein phylogeny (de Jong 1982, fig. 11) clusters aardvark, hyrax, and manatee with elephant as another outgroup near the base of the eutherian mammals, and places whales plus perissodactyls as closest sister-taxa, joined by the artiodactyls to form an ungulate group at the derived end of the phylogram.

On closer inspection, however, there appear to be some problems with the analysis. For example, de Jong (1982, table 2) shows that cetaceans, perissodactyls (except tapirs), proboscideans, hyraxes, manatees, aardvarks, and opossums all share methionine at locus 150. Since its distribution indicates that it is primitive for mammals, it would seem that clustering these groups would place them together at the base of the Eutheria. Instead, the algorithm uses methionine to valine substitution at locus 150 to set the 'paenungulates' in a node more primitive than all other eutherians (including edentates) and then requires a back substitution to account for the presence of methionine in whales and perissodactyls further up the tree. The separation of 'paenungulates' from other ungulates is supported by only two unique substitutions: threonine to alanine at locus 4, and aspartic acid to glutamic acid at locus 91. The argument of de Jong and Goodman (1982, p. 268) against a 'paenungulate'-ungulate grouping on the grounds that it requires 'five additional NRs' seems less impressive when the NRs that separate these groups in their arrangement include two changes in locus 150 mentioned above (which unite, rather than separate the groups), one back mutation, and two that

occur in parallel elsewhere. Only two unique substitutions support this separation.

So far, we have four proteins that support some sort of proboscidean-ungulate affinity (β -haemoglobin, fibrinopeptides A and B, myoglobin), one that separates elephants and hyraxes from other ungulates (lens α -crystallin), and the rest have not been sampled for all the relevant groups. Yet when all of these sequences are combined, the resulting phylograms (Goodman *et al.* 1985; Miyamoto and Goodman 1986) widely separate elephants from other ungulates. The lens α -crystallin has a disproportionate effect on the analysis, even though it is only one of seven proteins sampled. Apparently this is because lens α -crystallin has been sampled for a wider array of taxa than any other protein. When other proteins have not been sampled for the relevant taxa, they cannot outweigh the disproportionate effect of this one protein.

Finally, Weitz (1953) and Shoshani (1986) used the cruder immunological distance method to determine relative phylogenetic distances between taxa. Their results suggest that hyraxes and elephants are immunologically close, but horses are much less close. Since immunological distance cannot be broken down into discrete steps and analysed as above, it is difficult to assess the meaning of these data. It is not clear that immunological distance is always related to time of phylogenetic separation. Much of the similarity could be symplesiomorphic, and the horse could be different because it has diverged from a common ancestor with elephants much more rapidly than hyraxes have. This is analogous to uniting crocodilians with turtles because they share an overwhelming number of primitive similarities and only a few derived characters with birds. As has been shown many times, however, the fact that birds have diverged much more from their most recent common ancestor than crocodilians, does not justify placing crocodilians with turtles on shared primitive similarity. In this context, it is interesting to note that Buettner-Janusch *et al.* (1964) observed little similarity between hyraxes and elephants in an electrophoretic analysis of plasma proteins and haemoglobin.

In conclusion, we find no convincing evidence from the molecular data against our hypothesis that hyraxes and perissodactyls are sister-taxa, and that elephants belong with other ungulates in a monophyletic group. Indeed, it appears that four proteins (myoglobin, β -haemoglobin, and fibrinopeptides A and B) support this relationship, and only one (lens α -crystallin) appears to contradict it. The phylogenetic diagrams of Goodman *et al.* (1985) and Miyamoto and Goodman (1986) obscure this by throwing all proteins together, when many of the proteins have not been sampled for the relevant taxa (except lens

α -crystallin). In their discussions, Goodman *et al.* (1982, 1985) and de Jong and Goodman (1982) have apparently been strongly influenced by the long tradition of placing hyraxes and elephants together, separate from ungulates (Simpson 1945; Thenius 1969) and have only recently become aware of the growing body of evidence supporting hyrax-perissodactyl affinities (McKenna 1975; Fischer 1986, 1988) and ungulate monophyly (Novacek 1986; Novacek and Wyss 1986). Since their methods are explicitly dependent on *a priori* assumptions, we would be interested to see what new, perhaps even more parsimonious, solutions could be produced with different assumptions.

Other recent phylogenetic hypotheses

Novacek (1982, 1986) and Novacek and Wyss (1986) have provided the first testable phylogenetic analysis of the living ungulate groups, which is explicitly based on shared derived characters (see also Chapter 3 of this volume). Their arrangement independently corroborated our hypothesis, which was developed in 1985 and earlier, without knowledge of their work. Subsequently, we have incorporated many of their characters in our hypothesis. We differ from them only in that we place hyraxes closer to perissodactyls than to tethytheres. Our disagreements with their interpretation of the characters that support the 'paenungulates' are discussed above and by Fischer (1986, 1988). Although a few of their characters appear strong, we are more impressed with the uniqueness of the characters shared by hyraxes and perissodactyls (especially the eustachian sac), and by the overwhelming preponderance of characters that support this relationship. On the grounds of both uniqueness of characters and of parsimony, then, hyraxes are clearly closer to perissodactyls than to elephants.

Shoshani (1986) proposed a phylogeny based on morphological characters that was a condensed version of his doctoral dissertation. Unfortunately, in condensing the work for the PAUP phylogenetic program and for publication, there are many errors that invalidate the hypothesis. For example, the clavicle (node F2) is *not* lost in primitive artiodactyls, aardvarks, or most 'condylarths'. Node Q5 implies that artiodactyls have an odd number of digits in their feet. Some of the errors occur because only living members of the group were examined. For example, the astragalar foramen (node N5) is present in some primitive members of clade C, but is lost in the derived members. Besides, this feature is primitive for mammals. The tibia and fibula (node P2) and radius and ulna (node R8) are fused only in the more derived members of the perissodactyls and artiodactyls. Fewer than 14

thoracic vertebrae (node M3) is primitive for mammals (Gregory 1910). There are many more examples of the above, but space does not permit us to list them all here. Shoshani's clades B and C (his fig. 3) include most of the ungulate groups, but nearly all the characters at nodes H and I ('Paenungulata' and Tethytheria) also occur in nodes Q and R (notungulates, perissodactyls, and artiodactyls). Elsewhere, Shoshani indicates that it is only slightly less parsimonious to join clades B and C, eliminating these unnecessary parallelisms by postulating a monophyletic Ungulata. That hypothesis clearly approaches our own.

'Condylarthra' and other paraphyletic 'waste-baskets'

Unlike polyphyly (the grouping of taxa on the basis of shared convergent characters), paraphyly (the grouping of taxa based on shared primitive characters) has been a persistent problem in ungulate systematics. A few polyphyletic taxa were proposed in early classifications. Rhinos were united with rodents in an early version of the Glires on the basis of enlarged incisors. Elephants were grouped with hippos in an early Pachydermata on the basis of thick skin. Mercifully, these taxa were quickly dropped. Paraphyletic taxa, on the other hand, have increased within the Ungulata at an alarming rate.

In recent years, systematists have increasingly rejected the idea that paraphyletic taxa have any real meaning in nature, or are useful in phylogenetic analysis (e.g. Patterson 1977, 1981, 1982). The supposed 'biological reality' of 'adaptively unified groups' (Mayr 1974, 1981; Van Valen 1971, 1978a) does not stand up to the close scrutiny of either genetic or anatomical analysis (Patterson 1982). Paraphyletic groups are 'non-groups', defined by the common absence of derived characters, and few useful statements can be made about them. Even as non-phylogenetic, ecological groupings, paraphyletic taxa rarely provide useful information because of their emphasis on the *absence* of important (often ecologically significant) features.

The Mammalia, like most major taxa, has been subdivided into a mixture of monophyletic and paraphyletic groups. Most of the orders of mammals are clearly monophyletic, and were recognized as such from the time of Linnaeus. Bats, whales, carnivores, elephants, rabbits, and rodents, for example, have so many unique derived characters that even schoolchildren recognize them as natural groups. Unfortunately, many other groups have played the role of paraphyletic waste-baskets. Although there is a monophyletic core to the Insectivora, the Lipotyphla (Gregory 1910; McDowell 1958; McKenna 1975), many insectivorous mammals with no special relationships to the Lipotyphla

have been placed in an expanded 'Insectivora' because of shared primitive eutherian features (Van Valen 1978a).

The Ungulata has been burdened with a large number of paraphyletic groups. Apparently, the psychological need for 'ground-mass' taxa (to use Mayr's term) is so great that for every natural monophyletic group, there is an equal and opposite paraphyletic non-group. The most serious problem for ungulate systematics is the paraphyletic grouping of primitive ungulates—the 'Condylarthra'—which has resisted several attempts to break it (McKenna 1975; Cifelli 1983a,b). Cope (1881b) originally proposed the Condylarthra as a subunit of the Perissodactyla to include phenacodonts (*Phenacodus* and *Tetraclaenodon*), periptychids (*Anisomachus* and *Periptychus*), and a hyopsodont (*Mioclaenus*). He considered condylarths to be 'the ancestral type of the known Perissodactyla' (Cope 1881b, p. 1018). When it became clear that *Phenacodus* had feet quite unlike those of perissodactyls, Cope (1882) removed the 'condylarths' from the Perissodactyla. In 1884, he expanded the 'Condylarthra' to include additional periptychids, an arctocyonid (*Anacodon*), a meniscothere (*Meniscotherium*), a taeniodont (*Conoryctes*), and an artiodactyl (*Diacodexis*). With the revised contents, Cope gave the group a new meaning, as the 'most primitive type of the Ungulata' (Cope 1884, p. 793). Over the years, the concept of Condylarthra has expanded to include a great diversity of phenacodonts, meniscotheres, didolodonts, periptychids, hyopsodonts, mesonychids, and arctocyonids, with the last treated as the central 'stem group' (Simpson 1945; Van Valen 1978b; Cifelli 1983b). To retain Cope's name for a monophyletic group, the Condylarthra would have to be a synonym of nearly the entire Ungulata to fit his original concept, or a synonym of nearly the entire Eutheria to fit his 1884 concept. 'Condylarthra' has taken on such significance as a grouping of primitive ungulates that it has hampered the investigation of the interrelationships of the major ungulate groups for over a century.

It is much better to abandon the term 'Condylarthra' altogether, and with it all the erroneous connotations it has acquired. There are many good reasons for this. Although many 'condylarths' share primitive mammalian, eutherian, and ungulate characters, the far more important derived ungulate characters have been obscured by the use of a waste-basket term. Even some of these primitive similarities hide significant distinctions. General statements about 'condylarths' emphasize primitive ungulate morphology and hide important differences between early ungulate lineages. When we refer to 'condylarths', are we talking about arctocyonids, phenacodonts, meniscotheres, periptychids, or hyopsodonts? Each of these groups is different in detail from the others, likely to have major ecological

differences as well. Despite claims to the contrary (Van Valen 1978a), 'condylarths' are not a clear example of an 'adaptively unified group'. For example, the teeth of *Arctocyon* suggest an omnivore, while *Meniscotherium* was apparently a specialized herbivore that lived in herds.

A more serious problem with the persistence of a waste-basket taxon like 'Condylarthra' is its effect on the people who do not know the fossils first-hand. The waste-basket term not only obscures derived features, but it also hinders understanding by suggesting false relationships, and prevents serious discussion of relationships between taxa. Like the emperor's new clothes, horizontal groups obtain a reality in people's eyes they never really had. Shoshani's (1986) phylogenetic analysis vividly demonstrates the pitfalls of the 'Condylarthra'. By treating the mesonychids as 'condylarths' (along with *Arctocyon* and *Phenacodus*, to which they are only distantly related) rather than as a separate group, his analysis placed the mesonychids and the whales in completely different clades. Most of the characters Shoshani used for 'condylarths' are not true of the majority of the taxa concerned, since there are no derived characters that unite the group.

As this study has shown, there was an important substructure of nested, derived similarity hiding beneath the obscuring blanket of the 'Condylarthra' all along. It is hoped that the framework presented will begin to clear away the vagueness and confusion, and provide meaningful biological statements for further testing of the natural groups of ungulates. Sometimes it is useful to make statements about generalized or primitive ungulates, but no formal taxonomic term is required for such a concept. 'Primitive' or 'archaic ungulate' or some similar term is much more evocative than 'condylarth', and carries no misleading phylogenetic connotations. The time has come to relegate 'Condylarthra' to the waste-basket of forgotten and obsolete taxa, and move on to problems regarding *real* monophyletic taxa within the ungulates.

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