

Ungulate Phylogeny: Molecular vs. Morphological Evidence

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Overview

Prothero, Manning, and Fischer (1988) published a phylogeny of ungulates that resolved their relationships according to morphological evidence. Both dental and nondental characters corroborated a phylogeny that placed artiodactyls as the first group diverging from the early ungulates, followed by the divergence of arctocyonids, hyopsodonts plus peripitychids, Cete (whales and mesonychids), phenacodonts, uinatheres, tethytheres (proboscideans, sirenians, and desmostylians), hyraxes, and perissodactyls. More recent evidence has further corroborated most of this hypothesis, especially in showing that arsinotheres are tethytheres, and that tethytheres, hyraxes, and perissodactyls form a natural group of higher ungulates, the Altungulata of Prothero and Schoch (1989a). Evidence for the affinities of hyraxes with either tethytheres or perissodactyls is discussed elsewhere in this volume by Fischer and Tassy (Chapter 16), although Prothero and Schoch (1989b) considered the evidence for hyrax-perissodactyl affinities so strong that they reduced the order Hyracoidea to a suborder of the Perissodactyla, as originally conceived by Owen (1848).

Much molecular evidence, on the other hand, has been ambiguous, primarily because it consists of only a few protein sequences from a limited selection of taxa. Where data are available, many proteins cluster whales, perissodactyls, and proboscideans, to the exclusion of artiodactyls (hyraxes, sirenians, and aardvarks are rarely sampled). This agrees with our hypothesis based on morphology. For example, α -hemoglobin clusters higher ungulates to the exclusion of artiodactyls, with only one substitution clustering whales, elephants, and hyraxes. β -hemoglobin clusters all ungulates to the exclusion of other mammals, but does not resolve their relationships. Pancreatic ribonucleases, cytochrome c, and fibrinopeptides A

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and B cluster artiodactyls, perissodactyls, and sometimes whales or elephants. Myoglobin strongly clusters ungulates and places artiodactyls at the most primitive node, with the next most derived groups being whales, elephants, and perissodactyls. Only lens α -crystallin A separates tethytheres and hyraxes from artiodactyls, perissodactyls, and whales, but many of the character substitutions and polarities for this arrangement can be reinterpreted. The molecular evidence corroborates the morphological evidence that (1) ungulates are a natural monophyletic group; (2) artiodactyls are the first living group to diverge; (3) whales are the next most derived group; and (4) tethytheres, hyraxes, and perissodactyls form a natural group of higher ungulates, whose mutual interrelationships are still controversial.

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Introduction

Among the most familiar of the living mammals are the hoofed mammals, or ungulates. Most larger terrestrial herbivores are ungulates, so in biomass and body size, they are usually the dominant group in any mammalian ecosystem. Ungulata also includes aquatic whales, which feed on fish, squid, or plankton, as well as sirenians, which are aquatic herbivores. Some extinct ungulates were bear-like or raccoon-like, and probably omnivorous. Ungulates include many huge graviportal animals, such as elephants, rhinos, hippos, and extinct uinatheres, arsinoitheres, titanotheres, pyrotheres, toxodonts, and liptopterns. Many ungulates were highly cursorial, including many artiodactyls, perissodactyls, and litopterns. The tree hyrax is one of the few arboreal ungulates, as were some of the extinct archaic ungulates.

The major living groups consist of the "odd-toed" perissodactyls, which include horses, zebras, donkeys, rhinoceroses, and tapirs, as well as many extinct forms; the "even-toed" artiodactyls, which include pigs, peccaries, hippopotamuses, camels, llamas, deer, giraffes, pronghorns, antelopes, cattle, sheep, and goats, as well as many extinct forms; and the proboscideans, or elephants. Although they are secondarily aquatic and no longer possess hooves, both whales and sirenians (manatees and dugongs) have fossil relatives that are clearly ungulates. Finally, the hyraxes (also known as coney or dassies), which faintly resemble a woodchuck with hooves and are today found in Africa and the Near East, are also ungulates.

In addition to these living groups, there are many extinct families of ungulates in the fossil record. Most of the archaic ungulates were once dumped in the wastebasket order "Condylarthra," which was explicitly paraphyletic (Prothero et al., 1988). Six families were once placed in this order. Three (arctocyonids, hyposodonts, and periptychids) are clearly very primitive, although artiodactyls diverged from their common ancestor even earlier. Two others (phenacodonts and meniscotheres) are unrelated to these families, but are clearly members of the higher ungulates (along with tethytheres and perissodactyls). The mesonychids have long been recognized as the sistergroup of whales and clearly show the terrestrial ungulate origins of whales. Prothero, Manning, and Fischer (1988) argued that the concept of "Condylarthra" has long been obsolete, and more recent works on early ungulates (e.g., Archibald in press) have abandoned "Condylarthra" and adopted a more phylogenetic classification.

A complete discussion of the phylogeny of both living and fossil ungulates was presented by Prothero, Manning, and Fischer (1988), and there is no need to repeat most of that paper here. Instead, I update that phylogenetic hypothesis with more recent data and, in par-

ticular, discuss the conflict and agreement between morphological and molecular data. Since molecular data are unavailable for extinct forms, I emphasize the living taxa in this chapter.

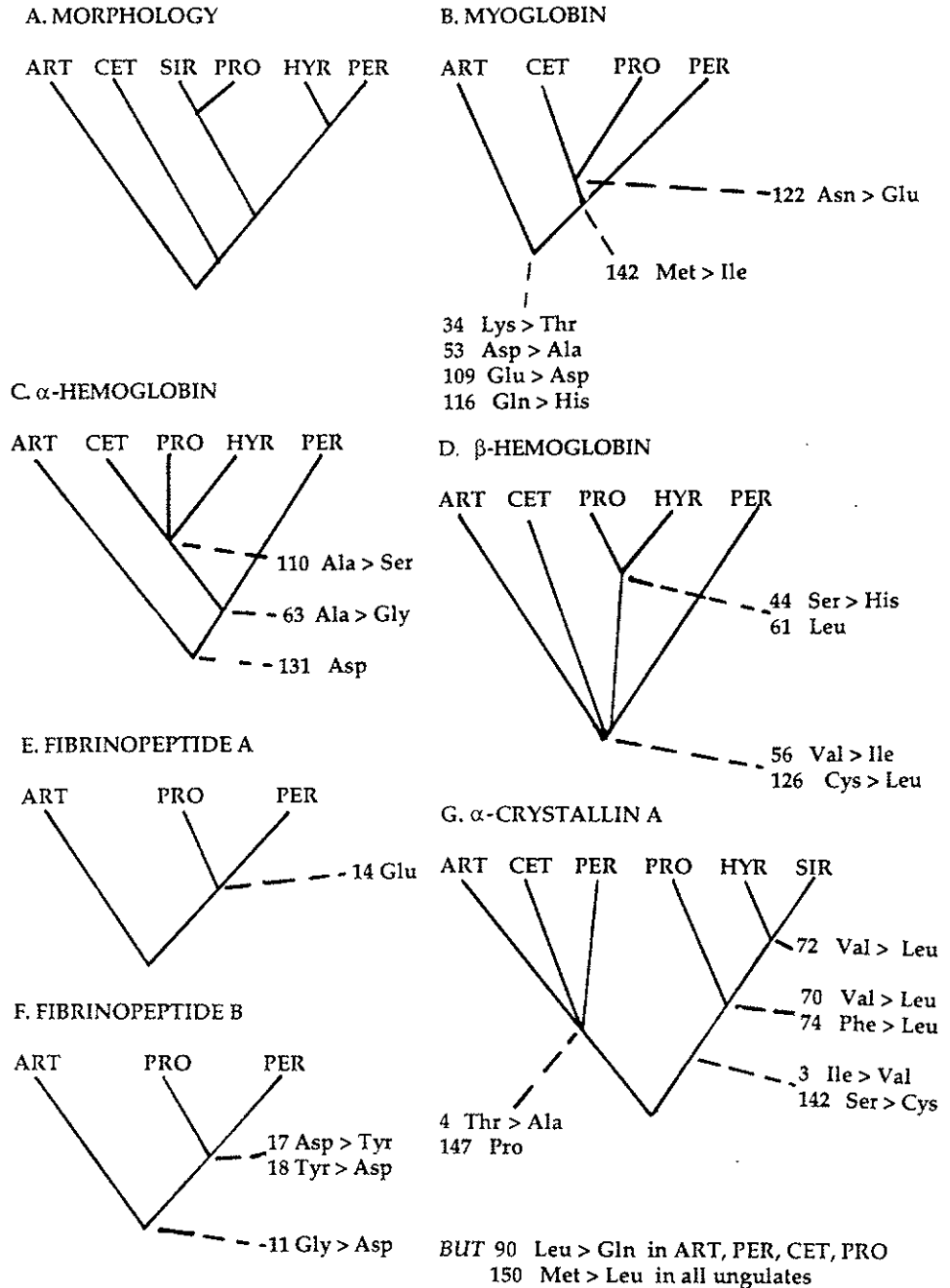
Morphological Evidence

Prothero, Manning, and Fischer (1988) presented a wide range of morphological characters in support of their ungulate phylogeny. Originally these were mostly dental characters collected by Earl Manning and presented by him in an unpublished cladogram in 1975. His hypothesis placed artiodactyls as the first group to diverge from the hypothetical ungulate common ancestor, followed by arctocyonids, periptychids plus hyposodonts, Cete (mesonychids plus whales), phenacodonts plus meniscotheres, uinatheres, arsinoitheres, tethytheres (proboscideans, sirenians, and desmostylians), and hyraxes plus perissodactyls. In preparation for the Tetrapod Phylogeny Symposium in 1987 (Benton 1988), Prothero began examining nondental characters, particularly those of the cranium and postcranial skeleton, in 1984. These data were remarkably congruent with the dental data produced by Manning. Later, Fischer (1986), Novacek (1986), and Novacek and Wyss (1986) produced a similar phylogenetic topology based on different data. By the time of the Tetrapod Phylogeny Symposium, there was remarkable consensus among all these authors that ungulates constituted a natural group; that artiodactyls were the first group to diverge, followed by whales; and that elephants and perissodactyls were the most closely related living ungulate groups. However, in more recent papers, Novacek and others (Novacek et al. 1988; Novacek 1989, 1990) have been less confident in the monophyly of ungulates.

Nevertheless, a number of new studies have come along that have corroborated our original hypothesis. For example, Archibald (in press) examined the "Condylarthra" and found our hypothesis to be very robust for the groups he examined. Shoshani (personal communication) examined characters of the musculature and apparently found a phylogenetic topology similar to ours. This is a big improvement over his earlier hypothesis based on an assortment of morphological characters (Shoshani 1986), which was plagued by incorrect character assessments and unnatural groups (Prothero et al. 1988, pp. 225–226). Court (1990) examined the ear region of the extinct arsinoitheres and found that they are nearly identical to proboscideans in their periotic anatomy. Interestingly, his study of ear regions also places artiodactyls at the most remote node, followed by hyraxes, and then perissodactyls as the nearest sistergroup of tethytheres, in good agreement with our hypothesis.

Rather than review all the nodes and characters discussed by Prothero et al. (1988), I concentrate on just a

FIGURE 13.1. Comparison of the topology of ungulate phylogeny based on morphological data (**A**) and on various amino acid sequences (**B–G**). Characters for the morphological cladogram are described in the text. Amino acid substitutions are indicated at each node. Abbreviations: ART, artiodactyls; CET, cetaceans; HYR, hyraxes; PER, perissodactyls; PRO, proboscideans; SIR, sirenians.



few key dichotomies in our hypothesis. As far as the living ungulates are concerned, there are only a few nodes to discuss (Fig. 13.1A): the monophyly of the ungulates; the early branching of the artiodactyls, followed by the whales; and the clade of "higher" ungulates (Altungulata of Prothero and Schoch 1989a, 1989b), which includes tethytheres, hyraxes, and perissodactyls.

UNGULATE MONOPHYLY. The most primitive known ungulates, such as *Protungulatum*, are known only from a few teeth, jaws, and fragmentary skulls and postcrania (Van Valen 1978). Thus, many of the characters apparent in the living ungulates cannot be shown for

their earliest fossil representatives. Nevertheless, in the Cretaceous, ungulates are quite distinct from other placentals, both in dentition and in available postcrania. Their teeth are more bunodont, with lower cusp relief, than other contemporaneous eutherians. The lower molar trigonids are shortened anteroposteriorly, and they have a large, posteriorly projecting hypoconulid on M_3 . Even though these animals are overwhelmingly primitive in most of their anatomy, they can still be recognized at the beginning of their divergence from other mammals. Besides their dental distinctiveness, ungulate feet are already distinct as well. The most striking feature is an astragalus with a shorter, more

robust head. In more advanced ungulates, the ankle complex is further modified to restrict lateral motion and promote rapid running in a sagittal plane.

In addition to these characters, comparisons of living ungulates with other living mammals reveals a number of characters that cannot be seen in the fragmentary Cretaceous and Paleocene fossils. Novacek (1986, p. 87) pointed out that the auditory bulla of ungulates, if present, is composed of the ectotympanic bone (although this also appears independently in some bats, rodents, and rabbits). Among living ungulates, only hyraxes appear to be exceptions, and their bullae are composed of both ectotympanic and entotympanic components. Novacek (1986, p. 88) observed that all living ungulates have lost the mastoid foramen, a feature that appears elsewhere only in marsupials. However, the most primitive artiodactyls retain a mastoid foramen (Russell et al. 1983), so the loss of this feature may be derived for non-artiodactyl ungulates. Wible (1987) showed that among animals with a superior ramus of the stapedial artery, the foramen is shifted to the petrosal, or lost altogether in living ungulates. Thus, there seems to be relatively strong support for the idea of ungulate monophyly from dental, cranial, and postcranial characters. Contrary to Novacek et al. (1988, p. 52) and Novacek (1990), I find that the character support for the ungulate clade is as strong as any other on the eutherian cladogram. There appears to be no strong evidence for a contrary hypothesis, as the discussion of the lens α -crystallin data will show below.

ARTIODACTYLS. Despite the fact that artiodactyls are the most abundant, successful, and specialized group of living ungulates, the evidence is quite strong that they were among the earliest to diverge from the common ungulate ancestor. The most primitive artiodactyls known, such as *Diacodexis* and *Dichobune*, lack many of the synapomorphies found in all other ungulates. Unlike other ungulates, their femora have very weak third trochanters, and they still retain the clavicle, which is lost in all higher ungulates (and some of the more derived artiodactyls). Their teeth never develop a true hypocone, but instead have a lingually shifted metaconule that takes its place in making a quadrangular tooth. In all other ungulates, the tympanic aperture of the facial canal is anterior to the fenestra ovalis (Cifelli 1982). Wible (1987) found that primitive artiodactyls retain the proximal stapedial artery, which is lost in all other ungulates (and eventually lost in artiodactyls as well). *Dichobune* is the only ungulate with a mastoid foramen. Its loss appears to be derived for both advanced artiodactyls and non-artiodactyl ungulates.

Even more striking is the overwhelming evidence that artiodactyls form a natural monophyletic group. This is supported by a wide array of unique and bizarre morphological specializations from every part of the anat-

omy. They have a unique morphology in the facial and orbital region, where the facial portion of the lacrimal is enlarged, and the orbitosphenoid is expanded, separating the frontal from the alisphenoid. Their teeth are very distinctive, with narrow lower molar trigonids resulting from closely appressed paraconids and metaconids. Finally, the artiodactyls are most easily recognized by their unique paraxonic foot (Schaeffer 1947), with the central axis between the third and fourth digits. This results in symmetrical third and fourth metapodials, and symmetrical reduction of second and fifth metapodials, giving an "even-toed" foot of either two or four digits. Their most distinctive bone is the astragalus, with its unique "double-pulley" configuration that permits efficient parasagittal motion for running, but restricts lateral rotation. Many of these features have been recognized as diagnostic by Blainville (1816), Cuvier (1800), and Owen (1848) early in the nineteenth century. Further work has made the Artiodactyla possibly the best-substantiated order within the Mammalia.

It is surprising, then, to find molecular data that occasionally put pigs closer to whales than to ruminants (Sarich, Chapter 8 this volume). Most of these data, however, are molecular distance data, which do not distinguish between shared primitive and shared derived similarity. Rather than adopting the grossly unparsimonious idea of clustering whales with pigs, there is a much simpler explanation. Since pigs are the most primitive living artiodactyls and whales are the next most primitive node on the ungulate cladogram, both must share much of the primitive ungulate genetic and molecular pattern. Ruminants, on the other hand, are highly specialized artiodactyls. It would not be surprising if they had picked up more molecular specializations separating them from the original ungulate molecular pattern than pigs or whales have. All three groups had diverged by no later than the Middle Eocene and have had long separate histories since then.

WHALES PLUS "HIGHER" UNGULATES. To most people, the idea that whales are ungulates seems incredible. After all, they lack hooves or grinding teeth, they have front flippers, and they have no hind limbs (although they have a vestigial pelvis and femora buried in their streamlined bodies). However, the most primitive whales very closely resemble a group of large terrestrial omnivores, the mesonychids (Van Valen 1966, 1968; Szalay 1969; Gingerich et al. 1983). Although they are superficially like some carnivores or creodonts, mesonychids lack the carnassial specialization characteristic of these groups. They have a fully ungulate skeleton (with hooves in some taxa). A number of derived features found in the Cete (mesonychids plus whales) strongly ally them with higher ungulates. These include the loss of the proximal stapedial artery (Wible 1987) and an inflated tegmen tympani in the ear region (Cifelli 1982). As Novacek (1986) pointed out, all Cete

plus Altungulata have a large posterior lacerate foramen that coalesces with the cochlear fissure, a weak occipital exposure of the mastoid, and a small or absent postglenoid foramen in the jaw joint.

There are a number of postcranial specializations uniting cetans and altungulates. These include a reduced acromion and coracoid process on the scapula, a straight or concave ventral border of the ulna (primitively convex), a reduced deltoid crest on the humerus, and the loss of the clavicle. Some people may dismiss these postcranial features as adaptations for large body size or graviportality, but they are found in a wide variety of locomotor types, including cursorial, aquatic, and even arboreal forms (e.g., *Dendrohyrax*). The clavicle and many of these forelimb features have long been argued to be essential for arboreality, especially in primates. In fact, the inability of tree hyraxes to redevelop any of these features, in spite of their return to the trees, strongly shows that these animals are not infinitely labile under changes in function. They simply cannot redevelop a bone like the clavicle once it is lost. Thus, the loss of the clavicle is no less valid a character than many cranial characters that are not so clearly tied to habitus.

ALTUNGULATA. Of all the suggested groupings of ungulates, the strongest support seems to be accumulating for a group that includes tethytheres, hyraxes, perissodactyls, and possibly some extinct forms, such as uinatheres, phenacodonts, and meniscotheres. This idea was suggested by Gregory (1910) and revived by Szalay (1977), Fischer (1986), and Tassy and Shoshani (1988). Prothero et al. (1988) originally labeled this group the "Pantomesaxonia," following Fischer (1986), who had resurrected the term from Franz (1924). However, it seems that Franz's group was a heterogeneous, paraphyletic wastebasket of non-artiodactyl ungulates, so Prothero and Schoch (1989a, p. 510) coined the term "Altungulata" for a taxon at grandorder rank (Prothero and Schoch, 1989b, p. 530) for tethytheres (including arsinotheres), hyraxes, and perissodactyls.

A wide variety of characters can be found in support of this grouping of taxa. Wible (1987) pointed out that the infraorbital ramus of the stapedia artery lies in the alisphenoid canal. A distinctive feature is the tuber maxillaris (the inflation of the maxilla around the posterior dental arcade) found in all these groups. Altungulates have a lacrimal process in the anterior border of the orbit. One of their most surprising and distinctive features is the presence of nineteen to twenty-one thoracic vertebrae, whereas primitively most mammals have twelve to fifteen (Gregory 1910, p. 275). The humerus has a reduced medial condyle and entepicondylar foramen. In the tarsus, altungulates have a flattened navicular facet on the astragalus and a reduced astragalus/

glandis with a projecting processus urethralis in the penis. There are a number of dental specializations in the living and fossil higher ungulates, including M^3/M_3 larger than M^2/M_2 ; P^4 protocone and metacone enlarged; metaconule moved posteriorly, losing connection with protocone; entoconid and hypoconid opposite one another, at right angles to axis of ramus; and a hypolophid formed between the hypoconid and entoconid (McKenna and Manning 1977; Prothero et al. 1988).

Further support for the relationship of arsinotheres, tethytheres, and perissodactyls comes from the discovery of *Radinskya* from the Late Paleocene of China (McKenna et al. 1989). Although McKenna and others tentatively placed this animal with the phenacolphid arsinotheres, they noted many derived similarities with the primitive tethythere *Minchenella* and with the most primitive perissodactyls. As Prothero and Schoch (1989a) argued, it is now quite clear that the altungulates were diverging in Asia and/or Africa during the Paleocene and later spread to North America or became isolated in Africa.

THE HYRAX CONTROVERSY. The position of hyraxes within the scheme of ungulates has become very controversial. Based on teeth and foot structure, Cuvier (1800) and Blainville (1816) placed hyraxes with rhinos, tapirs, and palaeotheres. When Owen created the order Perissodactyla in 1848, he included *Hyrax*. For over a century, however, classifications tended to place them with elephants and other primitive "taxeopode" ungulates following Cope (1882). The hyrax-perissodactyl clade was revived by McKenna (1975) and McKenna and Manning (1977) and extensively defended by Fischer (1986, 1989). As this old notion was being revived and defended, Novacek, Wyss, and McKenna returned to the idea of hyrax-tethythere affinities (Novacek 1982, 1986, 1989, 1990; Novacek and Wyss 1986; Novacek, Wyss, and McKenna 1988; Wyss, Novacek, and McKenna 1987). Although they base this conclusion on morphology, they admit to being influenced by the data from molecular biology.

Fischer (1986, 1989), Prothero et al. (1988), and Prothero and Schoch (1989a) have discussed both the molecular and morphological evidence and found the hyrax-perissodactyl connection more persuasive. Indeed, Prothero and Schoch (1989b) were so convinced that they included hyraxes as a suborder of the Perissodactyla (reviving Owen's original concept) and included them in a symposium volume on perissodactyl evolution (Prothero and Schoch 1989c), along with additional papers on hyraxes (Rasmussen 1989). Fischer and Tassy (Chapter 16, this volume) present this evidence in much greater detail.

As far as the morphological evidence goes, the case for hyrax-perissodactyl affinities still appears strong, as I

Of the five characters used by Novacek et al. (1988, table 3.1) to support hyrax-tethythere affinities, only two (posterior extension of the jugal and bifurcate styloglossus muscle) are unique. Amastoidy occurs in pangolins, dermopterans, whales, some suids, and rhinoceroses (Novacek 1986). Zonary placentation also occurs in aardvarks and carnivores (Fischer 1986). The much-touted serial carpus ("taxeopody") also occurs in some rodents, insectivorans, and *Hyaenodon* and is variably developed within the genus *Phenacodus* (Gregory 1910, p. 452; Radinsky 1966). Fischer (1986, 1989) argued that the serial carpus in hyraxes was a consequence of their carpal rotation for grasping, but Rasmussen et al. (1990) showed that even large graviportal (and clearly not arboreal and grasping) hyraxes from the Fayum Oligocene had a serial carpus.

Contrary to the weak morphological evidence for hyrax-tethythere affinities, the preponderance of the morphological evidence still seems to favor hyrax-perissodactyl affinities. Their most bizarre synapomorphy is the inflated eustachian sac (Fischer 1986, 1989), although Fischer and Tassy (Chapter 16, this volume) have apparently not located this in the rhinoceros (it does occur in tapirs and horses). There are many other unusual cranial synapomorphies, including an extrabulbar internal carotid artery (Wible 1986), the loss of the promontory and stapedia sulci (although this occurs elsewhere in the Mammalia), a large bridged tympanohyal, and a long tympanic process (Cifelli 1982). Hyraxes and perissodactyls retain the tuber maxillaris after tooth eruption (Fischer 1986, 1989). The peculiar appendages of the iris in the eye also seem to be unique to these two groups, as is the shoulder musculature (Fischer 1986). Finally, the foot of the hyrax is essentially identical to the mesaxonic foot of perissodactyls, with reduced first and fifth metapodials and enlarged weight-bearing third metapodials. The teeth of many hyraxes are especially similar to primitive perissodactyls, such as the palaeotheres (Prothero et al. 1988).

In summary, I feel that the evidence for hyrax-perissodactyl affinities is still much stronger than the alternative. The molecular evidence, as discussed below, is much weaker than most proponents will admit.

Molecular Evidence

In recent years, much new data of possible phylogenetic relevance have come from molecular biology. At face value, these data seem to be the "magic key" that should unlock secrets undecipherable by a century of anatomical studies. In reality, molecular data are plagued by just as much difficulty of interpretation and similar problems with parallel evolution and homoplasy. In addition, such molecular data have been studied in only a limited number of ungulate taxa, and with only a few biochemical systems, so the data base is very incomplete. Nevertheless, a number of authors

have extended these data to the limits of their usefulness, even going so far as to generate a new classification of the mammals (Miyamoto and Goodman 1986).

Without examining the original data in detail, however, it is difficult to judge the strength of the evidence for such conclusions. Most paleontologists, when faced with the daunting task of reading biochemistry, skim only the final phylogeny from a paper without fully understanding the data on which it was based. A close examination of the original data yields some surprising results. Scanning the amino acid sequences by eye reveals that there are remarkably few shared derived substitutions to support the most parsimonious trees presented in molecular papers. In fact, most nodes have at best only one or two shared derived substitutions, far fewer than are found on the cladograms based on morphological evidence. Thus, the phylogenies are not very robust: just a few new data points can radically change the topology of the tree. For example, the myoglobin sequence strongly supports a clustering of elephants, perissodactyls, artiodactyls, and whales (Dene et al. 1983 fig. 3). When this is mixed with data from another protein (lens α -crystallin A), however, a completely different tree results (Dene et al. 1983, fig. 4). Any reader who consults only the final figure would not be aware that it is completely contradicted by all the rest of the data in the same paper!

Prothero et al. (1988) surveyed the molecular data then available and pointed out that, except for one system (again, lens α -crystallin A), most proteins did not contradict the ungulate phylogeny advocated here. Since that time, I have gone over the original amino acid sequences of each of these proteins and discovered just how sparse the original data were. Wyss et al. (1987) did the same and found that several nearly equally parsimonious cladograms could be generated with the available proteins.

In the discussion below, I have used the original amino acid sequences as summarized by Wyss et al. (1987) or, when necessary, in Fasman (1976). Following Wyss et al. (1987), I looked only at amino acid substitutions that seemed shared derived for the appropriate groups of mammals and generated my own most parsimonious arrangement, using MacClade software. In most cases, I was able to generate one or two nearly equally parsimonious cladograms with minimal branch swapping. The most parsimonious cladograms are shown in Figure 13.1, with the specific shared derived substitutions labeled at each node.

MYOGLOBIN. As mentioned above, Dene et al. (1983, fig. 3) generated a phylogeny from myoglobin data that was quite concordant with the hypothesis of Prothero et al. (1988). Four substitutions support the monophyly of artiodactyls, whales, proboscideans, and perissodactyls (Fig. 13.1B). One substitution clusters the other three and excludes artiodactyls. Only one substitution

disagrees with my hypothesis in clustering whales and proboscideans. Thus, myoglobin seems to provide excellent support for the idea that ungulates are monophyletic and that artiodactyls are the most ancient branch.

HEMOGLOBINS. Very few sites are variable in the hemoglobins of mammals, so relatively few could be extracted for ungulate phylogeny. In α -hemoglobin, one substitution supports ungulate monophyly, and another excludes artiodactyls from the group including whales, proboscideans, and hyraxes (Fig. 13.1C). Only one substitution contradicts my hypothesis by clustering hyraxes and proboscideans with whales rather than perissodactyls. In β -hemoglobin, even fewer shared derived substitutions are relevant. Two support the monophyly of artiodactyls, whales, proboscideans, hyraxes, and perissodactyls (Fig. 13.1D), and two more cluster hyraxes and proboscideans. Thus, hemoglobins provide fairly strong support for the monophyly of ungulates, weak support for artiodactyls being the most ancient branch point, and some support for hyrax-proboscidean relationships.

CYTOCHROME C. According to Baba et al. (1981) and Goodman et al. (1982, fig. 3), cytochrome c clustered whales and artiodactyls, with perissodactyls on the next most remote node; no sequences were available for hyraxes, proboscideans, or sirenians. The original data, however, show that there are virtually no relevant substitutions on which to base this conclusion (Fasman 1976). The sequences for cow, pig, sheep, horse, donkey, and whale are virtually identical except for autapomorphic substitutions; there are no shared derived substitutions that separate these mammals from other non-ungulates. Indeed, this is shown by the zero branch lengths in all the relevant ungulate branches in figure 3 of Goodman et al. (1982). Thus, cytochrome c provides no data of relevance to ungulate phylogeny.

FIBRINOPEPTIDES. Goodman et al. (1982) reported that fibrinopeptides A and B placed proboscideans nearer to artiodactyls than to perissodactyls; no other ungulates were sampled. However, examination of the original sequence data (Fasman 1976) does not give the same result. By my arrangement (Fig. 13.1E), fibrinopeptide A has one substitution clustering proboscideans and perissodactyls and several that support the monophyly of all three orders. However, no substitutions uniquely support ungulate monophyly. Fibrinopeptide B has one substitution that supports the monophyly of ungulates and two that unite proboscideans and perissodactyls, as well as several that support the monophyly of all three orders. Thus, fibrinopeptides weakly support ungulate monophyly (Fig. 13.1E, F) and strongly ally proboscideans with perissodactyls (*contra* Goodman et al., 1982).

LENS α -CRYSTALLIN A. Most of the proteins surveyed to this point have given roughly concordant results. Ungulate monophyly seems strongly supported (myoglobin, both hemoglobins, and fibrinopeptide B), as does the early branching of artiodactyls (myoglobin, α -hemoglobin, both fibrinopeptides). Some proteins weakly cluster whales and proboscideans (myoglobin, α -hemoglobin), but others cluster perissodactyls and proboscideans (both fibrinopeptides). Hyraxes were known only from hemoglobins, which weakly cluster them with proboscideans.

It is jarring, therefore, to discover the discordance in the data from lens α -crystallin A. According to the conventional protein phylogeny (de Jong et al. 1977; de Jong and Goodman 1982; de Jong 1982), aardvarks, hyraxes, manatees, and proboscideans were clustered in one group at the base of the Eutheria, and whales, perissodactyls, and artiodactyls fall in a completely different place. As Wyss et al. (1987) and Prothero et al. (1988) have shown, however, there are several nearly equally parsimonious interpretations of the protein sequence that do not force this discordant topology (Fig. 13.1G). At locus 150, for example, all ungulates have methionine (as do opossums). De Jong et al. (1977) unparsimoniously derive this methionine independently in the two different ungulate clades, but it could be interpreted as uniting them into one clade. If so, it would also account for the substitution of leucine by glutamine at locus 90 in artiodactyls, perissodactyls, proboscideans, and whales (but not hyraxes). When the lens α -crystallin A data matrix is manipulated on MacClade, the arrangement that clusters the ungulates has a tree length of 33 substitutions and a consistency index (CI) of 0.50. This is negligibly less parsimonious than the arrangement presented by Wyss et al. (1987), which had a tree length of 30 and a CI of 0.47. The hypothesis presented by de Jong and others is no more parsimonious (only two substitutions support their arrangement in conflict with my interpretation), and their hypothesis goes against the consensus of all the other proteins reported above. Thus, lens α -crystallin A could be interpreted to support ungulate monophyly, with several amino acid substitutions that seem to support monophyly of tethytheres and hyraxes.

Conclusions

The discussion above clearly shows that most of the proteins sampled are in good agreement with the Prothero et al. (1988) hypothesis, so far as the evidence goes. Only the lens α -crystallin A seems to conflict, and it too can be reinterpreted to agree with the other proteins. Ungulate monophyly is strongly supported, as is the early branching of artiodactyls. Some proteins cluster whales and proboscideans, others cluster perissodactyls and proboscideans. Hyraxes are only known from three proteins so far (both hemoglobins and lens α -

crystallin A), which seems to place them with proboscideans. However, only four substitutions support hyrax-proboscidean affinities. In my opinion, this is not as strong as the morphological evidence to the contrary.

None of these protein sequences provides more than three or four substitutions per node, and most are supported by at most one substitution. This is in striking contrast to the morphological data, where the key nodes are supported by a much larger number of unique, striking synapomorphies from many different parts of the anatomy. It seems that the molecular data are not strong enough in their current state to effectively falsify the topology based on the morphological data. Indeed, most aspects of the molecular data corroborate this topology, despite the interpretation of Miyamoto and Goodman (1986).

The biggest problem is the lack of sequence data for many key taxa (only one protein for aardvarks, three for hyraxes, and whales or proboscideans are missing from many data sets). Determining such sequences might be worthwhile, although the limited number of substitutions in such data sets will probably make it less important than other projects. Interest seems to have shifted away from amino acid sequences, however, and into RNAs and DNA (Chapter 18, this volume). Indeed, the latest manual on molecular systematics neglects protein sequencing altogether, and freely admits (Hillis and Moritz 1990, p. 10) that it has been replaced by nucleic acid sequencing. I hope that these molecules will provide better answers, but I suspect that even at the level of the nucleic acid sequences, there will be the usual problems with homoplasy and character conflict. Clearly, no data set is a magical "black box" that gives revealed, unadulterated truth. The data presently available, however, seem to indicate that ungulates are monophyletic, that artiodactyls are the most ancient branch, and that proboscideans, hyraxes, and perissodactyls are very closely related.

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