Primate Phylogeny: Morphological vs Molecular Results

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If Morris Goodman is correct in his conclusion, we will just have to go back to the anatomical evidence and find out what we've been missing. (Lewin, 1987, p. 273, attributed to Lawrence Martin).

As in murder investigations, reconstruction of phylogenetic history after the event has its difficulties. There may be several versions of what supposedly happened. Nevertheless, only one sequence of events actually occurred. (McKenna, 1987, p. 82).

Our comparative study of morphological (our data on selected living primates) and molecular characters (from the literature) confirms that, overall, phylogenetic reconstructions of Primates, and consequently their classifications, are more similar than dissimilar. When data from fossil Primates are incorporated, there may be several possible relationships among living Primates; the difference between most of them hinges mainly on the position of *Tarsius.* In one hypothesis, tarsiers are closely related to lemurs and lorises, and thus Primates is divided into Prosimii [lorises, lemurs, and tarsiers] and Anthropoidea [Platyrrhini and Catarrhini, i.e., monkeys, apes, and humans]. Two additional alternatives are that *Tarsius* is a sister group to the clade embracing lorises + lemurs and Anthropoidea and that in which all three lineages (*Tarsius,* lorises + lemurs, and Anthropoidea) form a polychotomy. In another hypothesis, tarsiers are closely related to anthropoids, giving these two branches: Strepsirhini [lemurs, lorises] and Haplorhini [tarsiers and Anthropoidea (Platyrrhini, the New World monkeys, and Catarrhini, Old World monkeys and Hominoidea)]. The first three alternatives gain some support from the fossil record, and the fourth from morphology of the living *Tarsius* and molecular data. It is emphasized that the morphological characters employed in this study for *Tarsius* are based on the only surviving genus of once-diverse tarsiiform primates known from the Eocene, and, although considered a "living fossil," it cannot represent all of them. Furthermore, *Tarsius* embodies derived features of its own which may affect its systematic position, but not necessarily the position of Tarsiiformes. Although the early Tertiary adapoids might have more nearly resembled anthropoids in their biochemistry and placental developments, this hypothesis is not testable from fossils, and any inferred relationships here must be based on characters of skeletal anatomy. Alternatively, anthropoids may be derived from certain omomyids or from some as yet undiscovered Eocene African taxon. Close relationships among *Homo, Pan,* and *Gorilla* have been confirmed during recent decades; *Pongo* is the sister group to this trichotomy. With increasing molecular data, *Homo* and *Pan* appear to be closer to each other than to any other living hominid taxon. *Gorilla* is a sister group to the *Homo–Pan* clade and *Pongo* is a sister group to all of them. Morphologists have given limited evidence for such a dichotomous grouping. In this study, we support the *Homo–Pan* clade, although with characters not as strong as for other clades. © 1996 Academic Press, Inc.

INTRODUCTION

Even though the quotes at the beginning of this paper do not seem to be in concert with each other, they are very much interrelated. The main thread connecting them and other similar ideas is that there is only one true phylogeny. Based on available evidence, it appears that, overall, results of intraordinal primate relationships from morphological characters correspond to those from molecular ones. A major discrepancy between the results obtained from morphological (of fossil taxa) and molecular characters relates to the taxonomic position of *Tarsius* (cf. Appendix 1 to Tables 1 and 2). Other disagreements concern classification on the family and subfamily levels. For example, *Aotus,* based on morphology, is classified in the family Aotidae, superfamily Ceboidea (Groves, 1991), whereas molecular data place it in a subfamily Aotinae, family Cebidae (Schneider *et al.,* 1993). As will be noted below, here we employ the subfamilial category, to correspond with those of Thorington and Anderson (1984, pp. 204–208), based on morphology, and of Schneider *et al.* (1993, p. 235, in part), based on molecular data.

Understanding intraordinal relationships within any given mammalian order may help in better understanding interordinal relationships within the class Mammalia and vice versa. Similarly, a better familiarity with the fossil record of a lineage helps in better understanding the polarity of a character, thus rooting the tree. For example, in the primitive state at the ordinal level of Mammalia, the orbital fissure and foramen rotundum are united as one common opening, character 39 in Appendices 2 and 3 [the orbital fissure is located in the cranium, pierces the orbitosphenoid and alisphenoid bones, and transmits cranial nerves III, IV, V_1, and VI; the foramen rotundum is located in the alisphenoid bone and transmits the maxillary branch—V_2—of the trigeminal cranial nerve]. This primitive condition also occurs in certain living primates, e.g., *Lemur, Daubentonia, Loris,* and *Nycticebus.* The derived state for this character (separate openings for the orbital fissure and the foramen rotundum) is found in *Tarsius* and all higher primates through *Homo.* Within Mammalia the primitive condition for this character is found in Monotremata and Marsupialia, and the derived condition is found within Eutheria (but not all eutherian taxa exhibit the derived condition). Within the Primates the derived condition of this character is one piece of evidence, a synapomorphy, for Haplorhini (Tarsioidea and Anthropoidea; Simiiformes is used instead of Anthropoidea by Groves (1991)). As discussed below, the age-old quandary regarding the phylogenetic position of *Tarsius* has not been resolved.

In this paper, we examine morphological characters for testing cladistic relationships within extant Primates, with discussion on the role of extinct taxa. The polarity of some of these characters was established based on character data sets for the class Mammalia (Shoshani and McKenna, 1995). Other characters were chosen from orders thought to be closely related to primates. Most characters, however, were chosen to represent the extant primates. This approach was decided upon because we wanted to compare our findings to those obtained from molecular data.

The importance of fossils in evaluating phylogenetic relationships cannot be overstressed (cf. Simons, 1972; Novacek, 1992; Tassy, 1993). A section on the fossil history of primates is included here for background and correlation of emergence of certain characters with geological dates. Although there are approximately 252 living species classified into 61 genera and 13 families (Groves, 1993a), the extinct genera of Primates greatly outnumber the living ones (218 fossil genera with approximately 405 species). Living Primates vary in size from 30.6 g for Western Rufous (or Pygmy) Mouse Lemur (*Microcebus myoxinus*) to 160,000 g for male gorilla (*Gorilla gorilla*) (Schmid and Kappeler, 1994; Tattersall *et al.,* 1988, p. 215).

THE FOSSIL HISTORY OF PRIMATES

Primate fossils, once thought to be rare, are now known to be common in the early Cenozoic wherever warm temperate to tropical forests existed. Fossil Primates vary in size from approximately 50 to 80 g for extinct *Teilhardina* to over 160 kg for extinct species of *Gigantopithecus.* Extinct genera of Primates provide an extensive basis for character evaluation that facilitates better understanding of evolutionary relationships within the order Primates. The earliest Primates date from the late Cretaceous period, and Primates became a taxon distinct from other mammals between about 90 million and about 65 million years ago (= Ma) (Simons, 1992b).

Africa has been suggested as the place of origin of Primates, but without any evidence from fossils. North America and Eurasia may be better places to search for origins of the Primates because fossils of this order are widespread and were abundant there during the Paleocene and Eocene. The evolution of Primates may be traced to two species of the archaic primate *Purgatorius unio* and *P. ceratops* (Van Valen and Sloan, 1965), which lived in the late Cretaceous and early Paleocene of eastern Montana (USA) at least 65 Ma. Molars and premolars of *Purgatorius* have sharp cusps, which may imply that it ate insects, as do small living insectivorous primates, e.g., mouse lemur (*Microcebus*) and the dwarf bushbaby (*Galagoides demidoff*). Based on the size of its teeth, *Purgatorius* was a mouse-sized animal whose skeleton and locomotor adaptations are so far unknown.

Major divisions within the Primates, living and extinct, include Plesiadapiformes, Adapiformes, Lemuriformes and Lorisiformes, Tarsiiformes, and Anthropoidea. Traditionally (Simpson, 1945; Simons, 1964), living primates were classified into Prosimii and Anthropoidea (higher primates or simians). Prosimians are generally divided into these groups: the archaic primates or proprimates (Plesiadapiformes), the tarsier-like primates (Tarsiiformes), and the lemur-like primates (Lemuriformes). The higher primates are modern-day Anthropoidea taxa, incorporating the platyrrhine and catarrhine clades or infraorders. Morphological characters of plesiadapiformes vs prosimians and prosimians vs simians are shown in Fig. 1. A classification of Primates, living and extinct is given in Appendix 1, and major lineages are depicted in Fig. 2.

Archaic Primates or Proprimates— the Plesiadapiformes

The fossil record suggests that the initial radiation of the archaic primates occurred in the Northern Hemisphere and that they probably originated there. By middle Paleocene (around 60 Ma), archaic primates had diversified into at least four families: the Picrodontidae, Carpolestidae, Plesiadapidae, Paromomyidae, and possibly the Microsyopidae. These "half-lemur" primates were mostly rat or mouse size, although some species reached domestic cat size. The archaic primates or Proprimates (Gingerich, 1989) might include extant
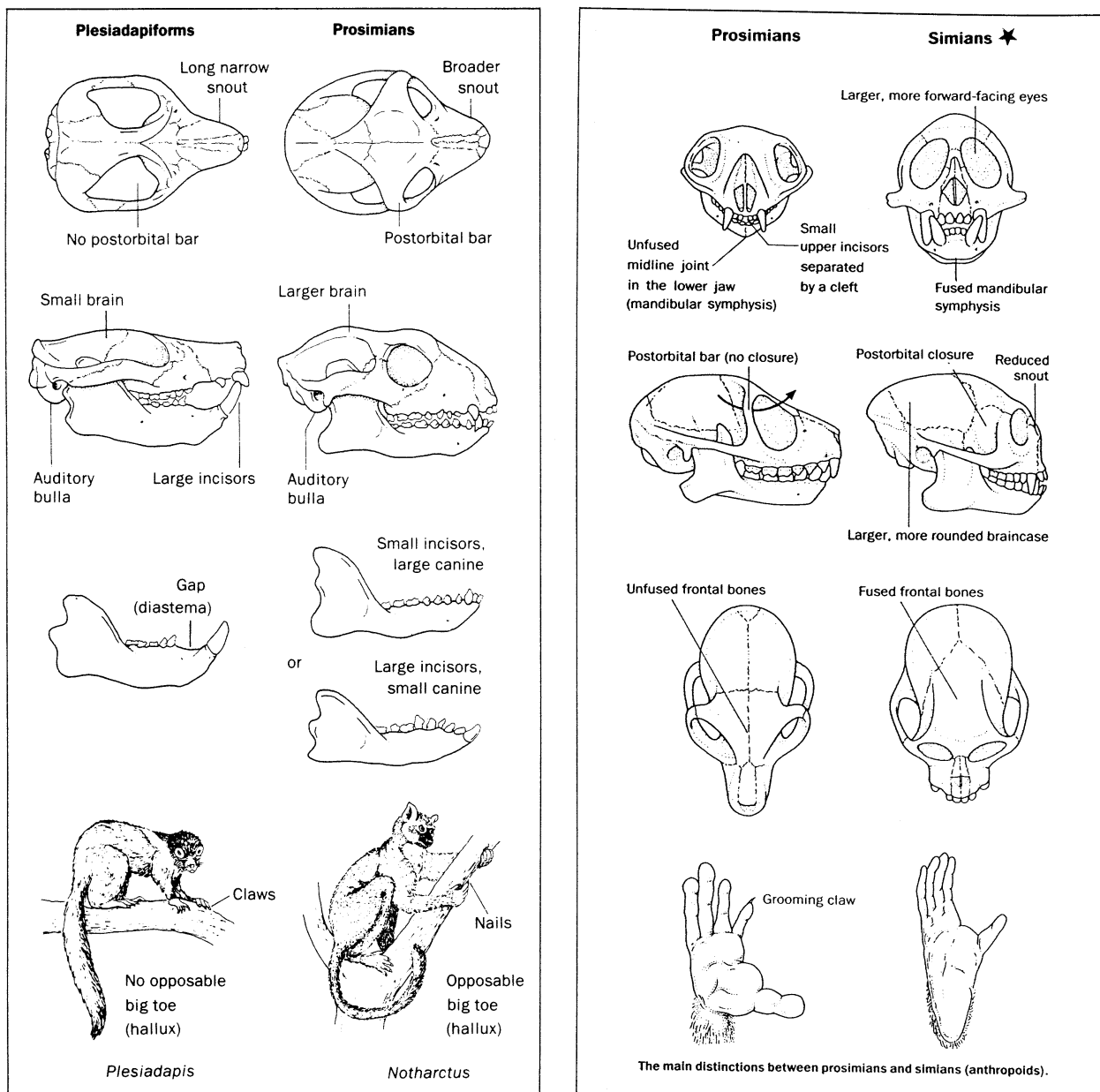
FIG. 1. Comparison of morphological characters of plesiadapiforms vs prosimians (left, after Gingerich, 1992), and prosimians vs simians (right, after Simons, 1992b). ★In this paper "Simian" is called "Anthropoidea." © Cambridge University Press 1992; Reprinted with the permission of Cambridge University Press.

tree shrews (Scandentia) and flying lemurs (Dermoptera) as descendants, but are otherwise extinct.

Dental characters of archaic primates indicate an evolutionary trend toward leaf- and fruit-eating specializations and away from the sharp-cusped, primitive dental patterns of their insect-eating predecessors. The view that the plesiadapiforms should be ranked with true Primates has been challenged because none had all the features that characterize later primates. Plesiadapiformes, for example, lacked postorbital bars, did not have expanded brains, possibly did not have opposable thumbs (pollexes) and great toes (halluces), and some seem to have had few obvious adaptations for life in trees. Most plesiadapiforms had large, pointed, anteriorly angled lower incisors, which may have been useful for opening seeds and fruits, and many had low-crowned cheek teeth with flattened, and sometimes multiple, cusps that resembled miniature versions of the cheek teeth of later folivorous and frugivorous primates (Fig. 1; Simons, 1992b).

The alternate hypothesis (for including plesiadapiforms within the true Primates) is supported by the
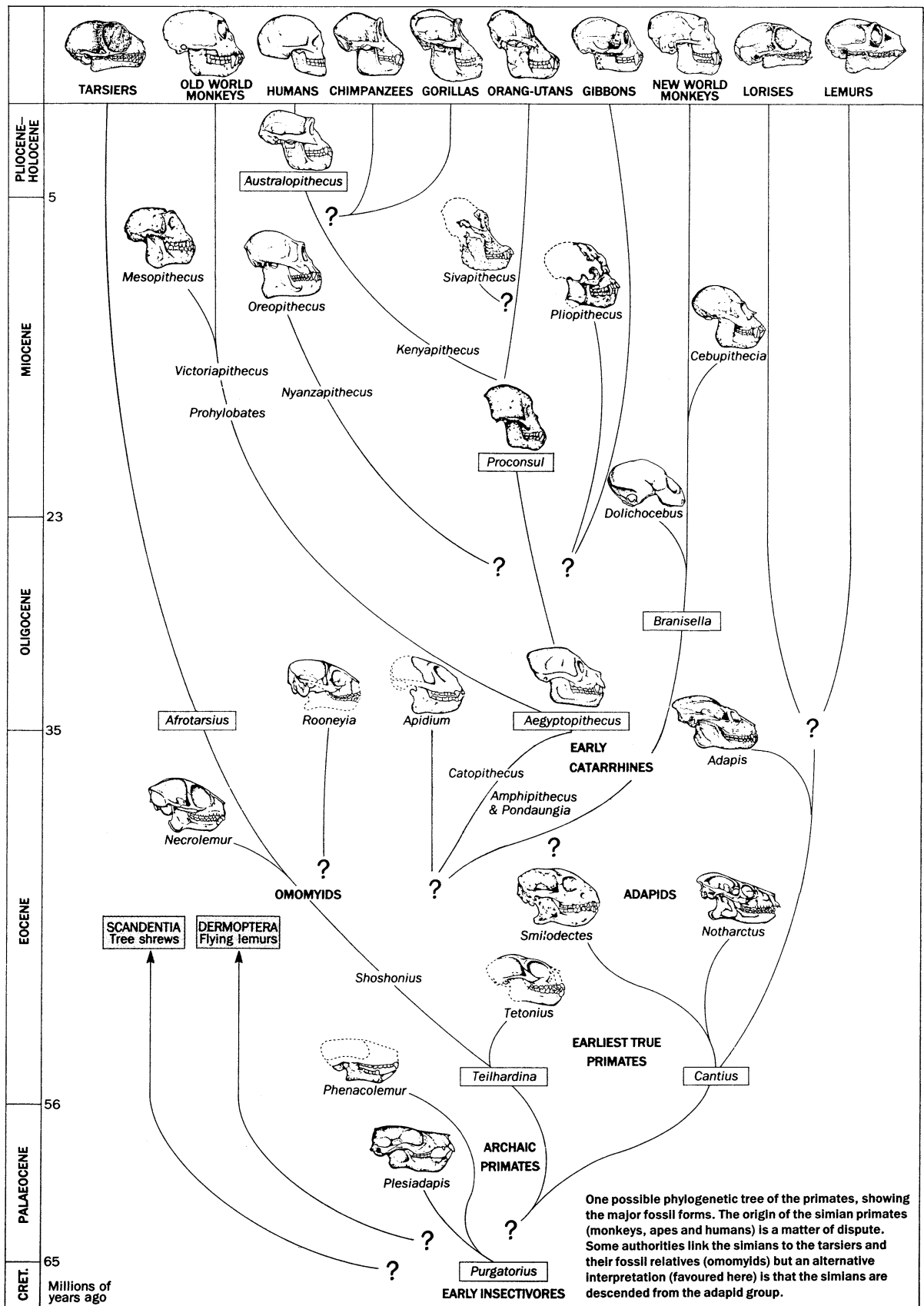
TARSIERS   **OLD WORLD MONKEYS**   **HUMANS**   **CHIMPANZEES**   **GORILLAS**   **ORANG-UTANS**   **GIBBONS**   **NEW WORLD MONKEYS**   **LORISES**   **LEMURS**

Australopithecus

Mesopithecus

Sivapithecus

Oreopithecus

Pliopithecus

Cebupithecia

Victoriapithecus

Kenyapithecus

Prohylobates

Nyanzapithecus

Proconsul

Dolichocebus

Branisella

Afrotarsius

Rooneyia   *Apidium*   *Aegyptopithecus*

EARLY CATARRHINES

Adapis

Necrolemur

Catopithecus

Amphipithecus & Pondaungia

OMOMYIDS

ADAPIDS

| SCANDENTIA Tree shrews | DERMOPTERA Flying lemurs |

Smilodectes

Notharctus

Shoshonius

Tetonius

EARLIEST TRUE PRIMATES

Phenacolemur

Teilhardina   *Cantius*

ARCHAIC PRIMATES

Plesiadapis

One possible phylogenetic tree of the primates, showing the major fossil forms. The origin of the simian primates (monkeys, apes and humans) is a matter of dispute. Some authorities link the simians to the tarsiers and their fossil relatives (omomyids) but an alternative interpretation (favoured here) is that the simians are descended from the adapid group.

Purgatorius

EARLY INSECTIVORES

PLIOCENE–HOLOCENE · MIOCENE · OLIGOCENE · EOCENE · PALAEOCENE · CRET.

5 · 23 · 35 · 56 · 65

Millions of years ago

FIG. 2. A phylogenetic tree of primates, showing the major fossil forms (after Simons, 1992b, p. 206). © Cambridge University Press 1992; Reprinted with the permission of Cambridge University Press.

strong similarity between the teeth of some Paleocene archaic primates (e.g., *Plesiadapis*) and later forms called adapids from the Eocene (e.g., *Notharctus*). Beard (1993), on the other hand, citing characters of the ear region and postcranial skeleton, observed that at least some plesiadapiforms may have been related to flying lemurs (Dermoptera). Beard (1993, p. 145) removed certain plesiadapiforms from the Primates and classified them as a suborder of Dermoptera (see, however, Krause (1991) and Runestad and Ruff (1995) for alternative views), but the ties to Dermoptera are far from established (cf. Kay *et al.,* 1990, 1992).

Plesiadapiformes is taken from the common Paleocene genus *Plesiadapis,* the best known and most widely distributed genus of the group (found in northwestern United States and in France). The name means "half toward the sacred bull," Apis, based on Georges Cuvier's misnomer for a lemur-like primate from the French Eocene, *Adapis,* which he thought was related to cattle. Most species of *Plesiadapis* were the size of squirrels, but a few were as large as small felids. *Plesiadapis* had molars that resemble those of *Adapis.* They had distinctive, pointed lower incisors. The large upper incisors, which in some taxa bore a single projection, opposed forward-inclined lower incisors, separated by a large diastema from the lemur-like cheek teeth.

Because it is so widespread in Europe and North America, *Plesiadapis* presumably migrated on the ground between forests. Dental specializations of plesiadapids suggest they were not direct ancestors of later primates; the resemblances of the front teeth to those of the aye-aye (*Daubentonia madagascariensis*), an aberrant Malagasy lemur, are clearly convergent features.

An early family of archaic primates, the Picrodontidae, resemble bats in the structure of their teeth. The Carpolestidae, with a name meaning "fruit-stealers," perhaps because of their specialized blade-like premolars, include small primates from Paleocene deposits in western North America. Like *Purgatorius,* these animals are about the same size as dwarf bushbabies (*Galagoides demidoff*), pygmy mouse lemurs (*Microcebus myoximus*), and pygmy marmosets (*Cebuella pygmaea*).

Because of gaps in the fossil record, microevolutionary transitions are not generally documented for extinct primates, but they are for carpolestids. For example, populations of these fruit-stealers show gradual enlargement through time of the back lower premolar into a large serrated blade such as that found in *Carpolestes* which cuts against upper premolars that are armed with multiple cusps. This mechanism has a parallel in the teeth of some living Australian marsupials, such as the vegetarian rat kangaroos (e.g., *Bettongia gaimardi*). The subtle but well-established changes in tooth anatomy among carpolestids provide some of the best examples of evolution in progress among primates, even though these plesiadapiforms left no descendants.

The Plesiadapiformes' greatest diversification was in the Paleocene epoch in North America, Europe, and perhaps Asia. By the early Eocene, around 50 Ma, they had begun to decline, perhaps because they were outcompeted as arboreal fruit and leaf eaters by rodent groups, which had an explosive adaptive radiation in the early Eocene. At the end of the Eocene, around 35 Ma, the plesiadapiforms were almost entirely replaced by rodents and certain primates.

Earliest Modern Primates—Lemuriformes and Lorisiformes

The first undisputable primates, resembling lemuriforms and tarsiiforms, appear in early Eocene deposits in Belgium, France, England, and Wyoming (USA). At this time, some 56 Ma, the North Atlantic had not yet fully opened and very early Eocene mammals could move freely between Europe and North America via the Faeroes corridor, Iceland and Greenland. The first of these early Primates are a mouse-sized form, *Teilhardina,* and a larger rat-sized form, *Cantius,* both found in Europe and western North America. Either *Cantius* (Notharctinae, Notharctidae, Adapiformes, in Appendix 1) or *Teilhardina* (Anaptomorphinae, Omomyidae, Omomyiformes, in Appendix 1) could be a direct ancestor of all later primates, including humans, but no links connecting either to the earliest Old World anthropoid primates of the Fayûm in the Egyptian Oligocene have yet been found.

About 40 genera of Eocene prosimians have been recognized (Simons, 1964; Beard, 1993, p. 145; Bown and Rose, 1987; cf. Appendix 1). They share many dental and postcranial features with modern prosimians. None of these northern Eocene forms have characters shared with the Anthropoidea, which strongly implies that anthropoids arose in the second half of the Eocene, very likely in Africa. *Altiatlasius* and *Azibius* from the Paleocene and Eocene of North Africa, respectively, may have been euprimates, but the fossil evidence is insufficient for a clear interpretation. Many Eocene prosimians had large, forward-directed eyes with fully developed postorbital bars; they were agile, tree-dwelling animals, specialized for eating fruit and leaves. In addition, these prosimians had distinctly larger brains for their body size than did most other Eocene mammals. Among living prosimians, nocturnal species can be distinguished from diurnal ones by their relatively larger eyes and hence larger orbits. This criterion has also been applied to Eocene prosimians.

Eocene primates have been divided into two principal groups—the "tarsier-like" and the "lemur-like" forms—however, there is growing evidence that this dichotomy is oversimplified. The former, supposed tarsier relatives, occurring in the Northern Hemisphere, are commonly allocated to the family Omomyidae, with three subfamilies: Anaptomorphinae, Omomyinae, and Microchoerinae (Appendix 1). Microchoerine taxa are known only

from Europe. These groups are traditionally considered to be closely allied with the living Southeast Asian tarsiers (family Tarsiidae), which are represented today by only one genus, *Tarsius. Tarsius* (although a "living fossil") obviously cannot represent the full diversity of tarsiiform primates known from the Eocene, but it does provide a reasonably good living model for the appearance of some early members of the tarsiiform group. It has, however, many derived features unique to the modern form alone. The Eocene lemur-like primates are classified in two families, Notharctidae (with four subfamilies, including Cercamoniinae) and Adapidae (with one subfamily, Adapinae).

Adapidae and Omomyidae differ in several respects. For example, the ear bones of adapids were not extended into a tube as in some omomyids [the extension of the ectotympanic bone into a tubular structure constitutes the external auditory meatus]. Adapids were usually larger than the squirrel-sized or smaller omomyids. Notharctines were between the sizes of a kitten and an adult domestic cat, coinciding with the range from the modern gentle lemurs (*Hapalemur*) through the brown lemur (*Eulemur fulvus*) to the ruffed or variegated lemur (*Varecia variegata*). Tarsier-like and lemur-like Eocene prosimians were specialized for leaping and jumping. The adapids (lemur-like) had some skeletal similarities to leaping indrid lemurs, whereas omomyids (tarsier-like), resembling the development in modern bushbabies and tarsiers, characteristically had an elongated tarsus (heel) and pes (foot).

About 20 living genera of lemuriform and lorisiform primates are recognized, including the lemurs of Madagascar and the lorises and bushbabies of Asia and Africa. Earliest known representatives of the modern family Lorisidae (or Loridae) were collected from deposits dating to the early Miocene of East Africa (Walker, 1978) and the middle to late Miocene of southern Asia, but recently a loris-like prosimian *Plesiopithecus teras*, has been described from the Fayûm Eocene (Simons, 1992a,b; Simons and Rasmussen, 1994a,b).

Tarsier-like Primates—Omomyidae

Fossil specimens of *Teilhardina* occur in the earliest Eocene deposits, ca. 56 Ma, of Belgium and Wyoming. Its teeth had a generalized, tarsier-like pattern and seem to have been adapted for chewing insects. *Teilhardina* may be near the base of the radiation that produced all living Primates (perhaps with the exclusion of lemurs and lorises). This genus is thus one of the two oldest, small, generalized true Primates, the other being the earliest species of *Cantius* (a notharctine), which has been found near London, England, and in the Eocene of Wyoming.

Simons (1992b, p. 203) noted that if *Teilhardina* is close to the origin of the anthropoid primates (Anthropoidea) and *Cantius* is near that of the prosimian primates (lemurs and lorises), then the first main division

among surviving primates must have occurred before 56 Ma, perhaps about 65 to 60 Ma. Nevertheless, the two genera are close to each other and could actually have had the reverse relationships: *Cantius* with anthropoids and *Teilhardina* with tarsioids. Another early North American omomyid (dated to ca. 56 Ma) with more advanced dentition than *Teilhardina* and *Cantius,* is the anaptomorphine *Tetonius,* which is known from many jaws and one, perhaps the oldest known, well-preserved skull. *Tetonius* has an enlarged brain and small face. Its cheek teeth suggest that it was insectivorous, like modern tarsiers, but was smaller than *Tarsius,* comparable in size to mouse lemurs or dwarf bushbabies. Tarsier-like primates appear to have been very diverse by the end of the early Eocene. This is exemplified by the occurrence of a somewhat younger omomyine *Shoshonius,* which dates to about 50 Ma, and is well documented through the discovery of six skulls in Wyoming. *Shoshonius* shares many similarities with *Tarsius,* some not found in other omomyids, a fact which may indicate a close relationship to tarsiers.

Features characteristic of a taxon at a higher level are not always preserved in one specimen. For example, many postcranial remains of *Hemiacodon* (an omomyine from the middle Eocene of North America) show that its heel was somewhat elongated and was probably adapted for powerful leaping. The metatarsal of the hallux shows that this digit could be opposed to the other digits, as is typical of euprimates. *Rooneyia,* another omomyine, is known from a well-preserved skull from the early Oligocene of western Texas (USA). *Rooneyia*'s cranium, like that of microchoerines of Europe, had an extended tubular ectotympanic bone (the external auditory meatus). This tube is lacking in the earliest known anthropoids, e.g., the somewhat older *Catopithecus* (Simons, 1995) or contemporary *Aegyptopithecus* from Egypt, and this structure was not acquired by the New World monkeys (Platyrrhini). We can hence safely hypothesize that the common ancestors of Anthropoidea (monkeys, apes, and humans) did not have this auditory tube.

One of the best known microchoerine primates is *Necrolemur* from the middle Eocene of south-central France (Quercy). Its cranium resembles that of tarsiers in several features. Like *Rooneyia* and *Tarsius, Necrolemur* had a long external auditory tube. This feature, when present in both omomyines and microchoerines at such an early date, disqualifies them from direct ancestry of monkeys and apes. Moreover, the structure of the auditory bulla and nearby blood vessels is unlike that of simians. The tibia and fibula of *Necrolemur* may have been fused, as in modern tarsiers, an adaptation otherwise unique among primates. In addition, *Necrolemur* had a forward-shifted foramen magnum, large forward-facing orbits, a large brain and a small face—features suggesting that it was a leaping form that, like *Tarsius,* held its body erect much of the time.

Lemur-like Primates (Adapids)

Both omomyids and adapids or adapoids have been proposed as progenitors for the higher primates. The adapids' smaller, unspecialized incisors, fused dentaries, and details of the cheek teeth better foreshadow higher primate teeth than do the same parts of the dentition of omomyids. *Adapis,* known from many specimens from France, was the first fossil primate to be described (in 1821). Since the turn of the century, however, the similarities between *Adapis, Leptadapis,* and the modern Malagasy lemurs have been emphasized. *Adapis* was probably a leaf eater, and its skeleton, with structures resembling those of lorises, but unlike that of any modern Malagasy lemur, indicates that it was a climber with relatively short hind limbs. Skeletons of *Notharctus* from North America, and of the closely related *Smilodectes,* are the most completely preserved of any primates older than the Pleistocene epoch. In comparison to modern lemurs, their feet were less specialized for grasping, clinging and leaping, but broadly their locomotor adaptations resemble those of *Propithecus.* These similarities may simply be shared-primitive features. Recently, Franzen (1994) has described postcranial skeletons with skulls of cercamoniines from the middle Eocene site at Messel, Germany.

Malagasy lemurs have a fossil record spanning only the past few thousand years. Subfossils of Madagascar showed that the island once supported many different types of lemur, including some giant forms (Vuillaume-Randriamanantena *et al.,* 1992; Simons *et al.,* 1992). Some of these fossils can be allocated to the modern families Lemuridae, Indridae, and Daubentoniidae and contribute little to understanding the evolutionary history of any of the living lemur families. Subfossil lemurs are more "advanced" than some extant generalized lemurs and are often convergent to the higher primates. Thus, these prosimians sometimes provide approximate models for the early stages of higher primate evolution. For instance, some have developed frontal fusion and fusion of the jaw at the symphysis, both otherwise anthropoid characters.

From the review above, the questions of whether Anthropoidea is derived from adapids, from omomyids, or from some as yet unknown African group is not resolved (cf. Simons, 1995; Culotta, 1992, 1995). Because early fossil anthropoids had unspecialized heels and limbs and lacked elongated auditory tubes, they probably cannot be derived from an omomyid with specialized foot bones or a tubular ectotympanic bone. This interpretation implies that, once again, convergence and/or parallelism (e.g., for a tubular ectotympanic bone) is lurking at every major node on a primate cladogram.

Primates from the Eocene and Oligocene of Africa

Late Eocene sedimentary deposits in the Fayûm Depression, about 60 km south of Cairo, Egypt, contain early relatives of tarsiers (*Afrotarsius*) and lorises, an omomyid species, and the earliest Old World anthropoids. Primates were first discovered in this rich fossil-bearing area in 1907; fossils of numerous other mammals, birds, reptiles and plants have also been found in these deposits at various sites in the Jebel Qatrani Formation. Redating of these rocks shows that they range from at least 31 million to as much as 36 or 37 million years old (late Eocene to early Oligocene); for dating, see Kappelman *et al.* (1992). Africa was then cut off from Eurasia by the Tethys seaway and the Fayûm primates lived in tropical forests close to the coastal outlet of a major river system, on a somewhat fluctuating shoreline of interdigitated deltaic environment (e.g., Bown *et al.,* 1982; Simons, 1992b). It is suggested that the primates in Africa diversified in the late Eocene, or perhaps much earlier.

Recently, remains of several primate genera and species have been recovered from deposits that probably represent the late Eocene in the Fayûm (Simons, 1992a; Simons and Rasmussen, 1994a,b). The cranium known for *Catopithecus* already shows distinctive anthropoid features, such as postorbital plates and frontal fusion. The earliest Oligocene primate site in the Fayûm quarries includes two genera: *Oligopithecus* and *Qatrania. Oligopithecus* resembles the later Fayûm anthropoids, *Aegyptopithecus* and *Propliopithecus,* in the structure of its canines and premolars. Similarities of the latter taxa to the Eocene *Amphipithecus* and *Pondaungia,* older genera from the Far East, could suggest a possible southern Eurasian origin for the Fayûm catarrhines, but an African origin is more likely. A separate and distinct family (Parapithecidae) that belongs in the Anthropoidea is represented in the Fayûm by *Serapia, Qatrania, Arsinoia, Parapithecus,* and *Apidium.* These monkey-like taxa are also found in the Fayûm, contemporary with the early catarrhines, *Oligopithecus, Catopithecus, Propliopithecus,* and *Aegyptopithecus* (Appendix 1, Fig. 2; cf. Harrison, 1987). Simons (1995) reported on 19 primate species from the Fayûm belonging to at least six families. In addition, poorly preserved specimens that may be euprimates have been found in Morocco and Algeria.

Lower molars of *Parapithecus* and *Apidium* are similar to those of guenons (*Cercopithecus*). Possible synapomorphies for *Apidium* and Old World monkeys are found in the molar with multiple, small cusps. The postcranial skeleton of *Apidium* suggests that it was an actively jumping and leaping animal of riverine and mangrove forests, a habitat similar to that of titi monkeys (*Callicebus*) today. *Apidium*'s feet were similar to those of some lemurs and New World monkeys. Many of the skeletal similarities between *Apidium* and New World monkeys consist, however, only of primitive retentions or convergent adaptations related to leaping (Simons and Delson, 1978).

Aegyptopithecus and *Propliopithecus* resemble apes

(Hominoidea) in many dental, cranial and facial features and are considered by some to be the earliest members of the Hominoidea, but others regard them simply as primitive catarrhines (e.g., Simons, 1972, 1992b). *Aegyptopithecus* is the best-known Oligocene anthropoid (Simons *et al.,* 1978). It almost certainly lived in the tall trees of a monsoon rain forest where fruits upon which it fed were abundant. *Aegyptopithecus* was a quadruped, with adaptations for climbing and leaping. Sexual dimorphism in body size, canine size, and jaw size suggest that a polygonous social system was prevalent in the one species of *Aegyptopithecus.*

Miocene Apes of Africa

One of the most completely known extinct apes is *Proconsul* from the early and middle Miocene (23 to 15 Ma) of eastern Africa. Its fossils from Kenya and Uganda show that it diversified into many species, and ranged in size from large monkeys, such as *Colobus,* to female gorillas. Another related genus, *Afropithecus,* with distinct links to *Aegyptopithecus,* has recently been described. *Micropithecus, Limnopithecus,* and *Dendropithecus,* the smaller east African Miocene apes, may be direct close relatives of modern lesser apes (Hylobatidae, gibbons, and siamangs), or they may merely be primitive catarrhines. These early apes appear to be sexually dimorphic, like those of the Fayûm (but unlike modern lesser apes).

As is often observed in basal forms, the skeleton of *Proconsul* shows a blend of primitive, advanced, and unique features. This primate was a monkey-like quadruped although it resembled apes in some features of its mani and pedes and it also lacked or had an extremely reduced number of caudal vertebrae. The pelvis had a combination of monkey-like, ape-like, and unique features, while the sacrum was flattened and ape-like. There are few skeletons of primates from the middle to late Miocene or the Pliocene; the particular lineage that led to *Homo* has not yet been discovered. Eurasian genera, *Sivapithecus* and *Gigantopithecus,* are related to the orang-utan (*Pongo*) and not to the radiation of African apes and humans. "*Ramapithecus,*" now considered by most primatologists (cf. Tattersall *et al.,* 1988, p. 474; Pilbeam, 1969, p. 1093; Andrews and Cronin, 1982; and Kelley and Pilbeam, 1986) to be a female *Sivapithecus,* was long thought to be an ancestor of *Australopithecus* on the basis of shared characters in teeth and jaws (Simons and Pilbeam, 1978), but its similarities to *Australopithecus* are now considered to be parallelisms. The conclusion that the *Sivapithecus* group and other Eurasian apes are not closely related to *Australopithecus* emphasizes that the split between apes and humans occurred in Africa. The African fossil record of higher primates, unfortunately, has a gap between about 13.5 and 5 Ma (see Pilbeam, in press). *Kenyapithecus* from Fort Ternan in Kenya, dated to 14 Ma, was once thought to be a *Ramapithecus*

from Africa whose dentition is similar to that of *Sivapithecus. Kenyapithecus,* in fact, almost certainly predates the splits among the African genera (*Gorilla, Pan*) and *Australopithecus.*

African Pliocene Hominids

Definite *Australopithecus* remains from 4.2 to 1 million years old have been found in eastern and southern Africa (e.g., Leakey *et al.,* 1995a). Its anatomy is well established from finds made for the period from 4 to 2.5 Ma, e.g., at Hadar (Ethiopia), Laetoli (Tanzania), eastern and western Lake Turkana (Kenya, e.g., Leakey *et al.,* 1995a), and also at Makapansgat and elsewhere in southern Africa (Howell, 1978; Tattersall *et al.,* 1988; Johanson and White, 1979). It is generally agreed that *Australopithecus* is the oldest known member on the specific lineage that includes *Homo* but no other hominoid genera. Even though it was fully adapted for bipedal locomotion, its brain ranged in size from that of a chimpanzee to little more than that of a gorilla. *Australopithecus* species had flat faces with flaring nostrils; at least some were markedly sexually dimorphic (e.g., Wolpoff, 1976). Recently, a more generalized relative of *Australopithecus, Ardipithecus,* has been proposed (White *et al.,* 1994, 1995).

Manufacture of stone tools by australopithecines had begun by about 2.5 to 2 Ma (Tattersall *et al.,* 1988, p. 543; Tattersall, 1995, p. 136). Concomitantly, radiation and diversification of certain branches of the *Australopithecus* group had given rise to new species such as *Homo habilis,* which first appeared at this time in both eastern and southern Africa. Apparently, sometime before 1.5 Ma, a larger species, *H. erectus,* emigrated from Africa into Eurasia. Perhaps descended from the latter species, *H. sapiens* is cosmopolitan and ubiquitous.

CHARACTER ANALYSIS OF CONTEMPORARY PRIMATES

Taxa Chosen

Outgroups chosen to study relationships within the Primates are extant members of the orders Insectivora (represented by *Solenodon paradoxus*), Scandentia (represented by *Tupaia glis*), Dermoptera (represented by *Cynocephalus volans*), and Chiroptera (represented by *Pteropus vampyrus*). More than one outgroup is included because of the uncertainty as to which is the closest living relative of Primates (cf. discussion in Novacek, 1992; Beard, 1993, and papers in the volume edited by MacPhee, 1994). In addition, one outgroup may give a false reading if it happened to have derived conditions for certain key characters. For these reasons, characters for the four outgroup species are actual data, not a pooling of character states for the ordinal level, or randomly assigning of character state (0) for the outgroup(s).

Within the Primates, we focus on 18 living genera which represent major lineages on the family level at least. These include *Lemur* (to represent the family Lemuridae), *Daubentonia* (Daubentoniidae), *Loris* and *Nycticebus* (Lorisidae or Loridae; see Table 1), *Tarsius* (Tarsiidae), *Leontopithecus, Aotus, Cebus, Saimiri* (Cebidae), *Macaca, Papio, Colobus, Presbytis* (Cercopithecidae), *Hylobates* (Hylobatidae), and *Pongo, Gorilla, Homo,* and *Pan* (Hominidae). Other primate taxa were also studied (e.g., *Indri, Brachyteles,* and *Cercopithecus*) but not included in the analysis. Since we are comparing our results to those obtained by molecular methods, the focus of this study is on living taxa, and, in addition, it is an extention of the work of Shoshani (1986b) who included the same taxa and data (here expanded to include the work of Groves, 1986).

Characters Chosen

Data for the living taxa which were analyzed are from two main sources: those of Groves (1986, revised in 1995) and of Shoshani (1986b). Data for the extinct taxa are from Simons (1992b); they are not included in the character matrix, or in the analyses, but under Results and Discussion. We also employed some characters from Beard (1993) and other sources (e.g., Simons, 1992b). Specific sources are provided with the listing of characters (Appendix 2).

Details about specific methodology (e.g., number of specimens studied per taxon, and methods of investigation of the characters) are given in Shoshani (1986b). In brief, whenever possible, at least three specimens were studied for each taxon (in most cases 10 or more were examined), and young as well as adult individuals were included. When a character was in doubt (mostly because of polymorphism), additional specimens were sought. When certain about the polarity of a character (based on the literature), we coded a polymorphic character as the primitive character state, even if it was not prevalent among the specimens studied. When uncertain, the majority rule (over 50% of the specimens—similar to the approach explained in Domning (1994); see also Appendix 2) was employed; that is, the character state exhibited by most specimens was used. Primitive versus derived conditions are difficult to evaluate; one has to consult the literature or rely on a large data set with a large number of taxa for the polarities there. The work of Shoshani and McKenna (1995) for studying relationships within Mammalia is based on 234 characters for 37 vertebrate taxa (3 reptiles, 1 mammal-like reptile, and 33 mammals; 20 extant and 13 extinct). Some characters from the character matrix of Shoshani and McKenna (1995) were used in this study.

Of the original 244 characters used in Shoshani (1986b), only 35 are used here, either because they do not apply to relationships within Primates (Shoshani's (1986b) work was on interordinal level), or because they were noninformative (contained data for only one primate, or were extremely homoplasic—see explanation below). To these characters, we added characters from the literature and the 164 characters of Groves (1986, 1995—includes data mostly for *Hylobates, Pongo, Gorilla, Pan,* and *Homo*), tallying to a total of 264 morphological characters (Appendices 2 and 3).

Character Analyses and Evaluation

Computer programs. Two computer programs were employed: PAUP (Phylogenetic Analysis Using Parsimony (Swofford, 1993)) and MacClade (Maddison and Maddison, 1992). Because there are two sets of characters (details above), we ran PAUP three times: one with the 100 characters of the first set for all 18 primate taxa, one with the 164 characters of the second set, and one with all 264 characters and all taxa.

With the combined data set, we ran PAUP using Heuristic from the Search menu with ACCTRAN (accelerated transformation) and DELTRAN (delayed transformation) settings from the Option menu under Optimization. We employed the Standard character option in which characters are unordered and unweighted, and the program allows reversals.

Once the consensus tree was obtained, a list of synapomorphies ("apomorphy list" option within the run of consensus tree) and their consistency indices was obtained. Bootstrap values—confidence limits for each node—were obtained from PAUP (from the Search menu), choosing 1000 replicates for testing (cf. Felsenstein, 1985).

MacClade program was used to test certain phylogenetic hypotheses by removing one clade from its position (as obtained from PAUP) and joining it to another clade. The length of the trees and the consistency indices for the new topologies are given. Employing the parsimony principle, one can then decide between and among trees, depending on the differences in the additional steps required.

Character description and coding. It is extremely important that characters are unambiguously described and clear distinction is made between primitive and derived character states. As presented in recent literature (e.g., Novacek and Wyss, 1986; Novacek, 1992; Beard, 1993; Fischer and Tassy, 1993; Shoshani, 1993; Domning, 1994; Simmons, 1993; Thewissen, 1994), condition (0) is coded for the primitive state, and condition (1) or any other states are derived. For binary characters [states (0) and (1)], coding is simple, but, for multistate characters, coding and deciding whether or not to make them ordered character states is, or can be, a complicated matter. Although not usually stated, the sequencing of the character states [i.e., deciding which is state (1), state (2), (3), and so on] seems to imply this transformation series: $(0) \rightarrow (1) \rightarrow (2) \rightarrow (3)$, which may or may not be the case, depending on many

factors, especially the topology of the tree. This topology reflects the characters used, their codings, weights, and ordering; once the characters were described and coded, we let the computer do the rest (no weighting or ordering systems were applied).

Character evaluation. Evaluation of characters for phylogenetic purposes may be conducted in one of the following approaches:

(1) strictly or mostly based on morphology—e.g., presence vs absence of a process on a bone—cf. Novacek and Wyss (1986), Shoshani (1986a,b), Fischer and Tassy (1993);

(2) strictly or mostly based on function—e.g., ability vs inability to pronate the palm—cf. Szalay (1981), Szalay and Decker (1974);

(3) combination of the two approaches—cf. Thewissen (1994);

(4) application of approach (1), but incorporated specific discussion on the functions of characters and their significance in the analysis—cf. Shoshani (1993), MacPhee (1994).

In addition, characters may be weighted or unweighted, ordered or unordered. Use of a weighting system was favored by Hecht and Edwards (1976) and Marshall (1977); ordering of characters (performed on multistate characters) forces the investigator to examine carefully the character state and to ensure that, indeed, the directionality of evolution of that character is as was coded by the character state. Sometimes, weighting for characters may be suggested but not included in the analysis (e.g., Shoshani, 1993). In this study we did not weigh the characters, nor did we use any ordering system. This is probably the safest and most objective approach, for the computer program "determines" the polarities of the characters.

Consistency index. In the process of evaluating morphological characters, one has no prior knowledge if a character is "good" or "bad" and, often, after some experience, there is a need to decide which characters to include or to exclude from the character matrix. Otherwise, there would be too much "background noise" which may not help, but retard, the analysis. A consistency index (CI) may be used as a criterion for helping to make such a determination; caution must be exercised to avoid subjectivity in this approach. One method of achieving this is to proceed in two stages. In the first stage, all the characters should be included in the analysis (using PAUP; Swofford, 1993). Once the program is run, obtain a list of apomorphies which includes consistency indices for each character for a particular node. Examinations of the CI at this stage may help in determining which characters are most homoplasic. In the second stage, the investigator may employ an option in PAUP program which allows one to delete a

character only from the analysis but not from the matrix. Deletion of a character from the analysis (e.g., one with a very low CI of 0.100 or less) permits the investigator to rerun PAUP and see what effect, if any, removal of that character had on the results. This procedure of testing with PAUP can be carried out one character at a time, beginning with the lowest CI, and may assist in determining at each stage which character to keep and which to delete.

Domning (1994) appeared to have applied a screening method in evaluating his characters for, as he stated (p. 178), he selected 62 of 158 original characters which he studied in detail. Such an approach is not uncommon, especially when a study comprises extinct taxa with many missing data and a large number of characters. The lowest CI of Domning (1994, p. 183) is 0.25, compared to 0.20 of Novacek and Wyss (1986, pp. 260–261).

Results Obtained with PAUP and MacClade

Results obtained with PAUP. Analyses of data for 18 primate taxa and four outgroups (*Solenodon, Tupaia, Cynocephalus,* and *Pteropus*) or with only one outgroup (*Solenodon*), produced, with one exception, similar branching patterns for relationships within Primates. The exception was the trichotomy of *Daubentonia, Lemur,* and *Loris + Nycticebus* (note, however, that one of the two trees obtained with only one outgroup was identical to that with four outgroups). With PAUP (of Swofford, 1993) we conducted four analyses and obtained these results.

[1] With the first 100 morphological characters on 18 primate taxa (PAUP settings were Heuristic, characters unweighted and unordered), there were three equally parsimonious trees with 198 steps each, a CI = 0.677, and a RI = 0.850 (RI, retention index); the consensus tree had the same tree length (TL), CI, and RI. There was one polychotomy in this tree: (*Pongo, Gorilla* (*Pan, Homo*)); other branches were similar to those shown in Fig. 3.

[2] With the remaining 164 morphological characters on 18 primate taxa {PAUP settings as in [1]}, there were 36 equally parsimonious trees, with 397 steps each, CI = 0.559, and RI = 0.590; the consensus tree (TL = 411) had a CI of 0.540 and a RI of 0.557. This consensus tree included three polychotomies: (1) all four outgroups and Primates, (2) *Aotus, Cebus,* and *Saimiri,* and (3) *Gorilla, Pan,* and *Homo.* In addition, *Daubentonia* was the symplesiomorphic sister group to all other Primates, *Tarsius* was a sister group to *Gorilla + Pan + Homo,* the clade of *Colobus + Presbytis* was a sister to platyrrhine monkeys, and *Macaca + Papio* in turn joined the latter cluster.

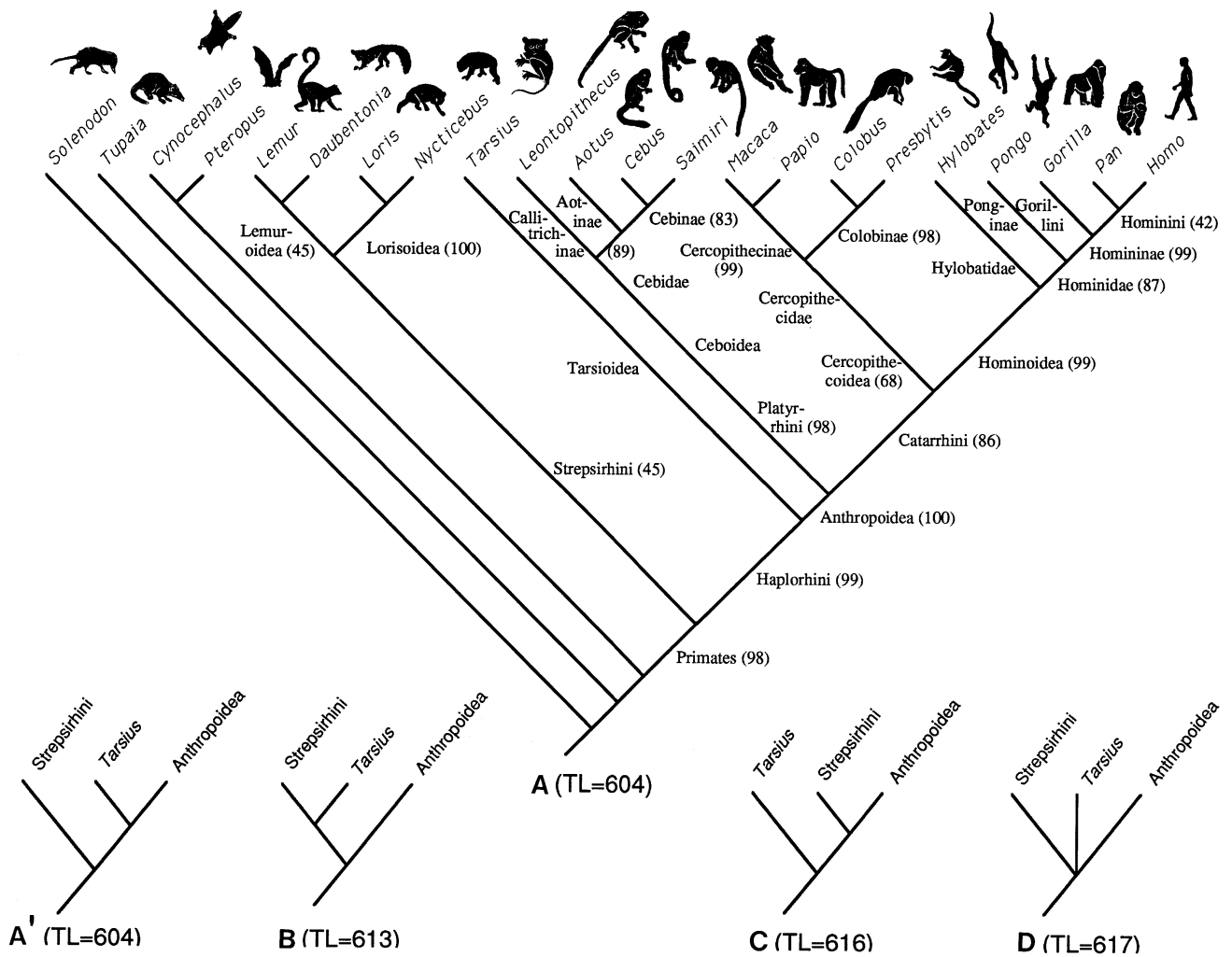[3] With all 264 morphological characters on all 18 primate taxa and four outgroups {PAUP settings as in

FIG. 3. (A) A cladogram obtained from PAUP analysis of 264 morphological characters on 18 primate taxa and four outgroups (PAUP settings were Heuristic search and tested in ACCTRAN and DELTRAN; characters unweighted and unordered); bootstrap values for 1000 replicates are in parentheses. TL, length of tree; 604 steps (cf. A'), CI = 0.589, RI = 0.711; these values apply to ACCTRAN and DELTRAN (CI of 0.613 and RI of 0.695 were obtained from only one outgroup). Results shown in this cladogram are very similar to those obtained from molecular characters. (B, C, D) Alternative hypotheses for the position of *Tarsius,* based mostly on the fossil record.

[1] and both ACCTRAN and DELTRAN used}, there were two equally parsimonious trees, with 604 steps each, and a CI of 0.589, and a RI of 0.711; these values apply to ACCTRAN and DELTRAN. The consensus tree had a TL of 607, with CI = 0.586 and RI = 0.708. The two trees differ in the position of the outgroups: one alternative was (*Solenodon* (*Tupaia* (*Cynocephalus, Pteropus*)) *Primates*) and the other was (*Solenodon* (*Tupaia* ((*Cynocephalus, Pteropus*) *Primates*))).

[4] With all 264 morphological characters on all 18 primate taxa and only one outgroup—*Solenodon* {PAUP settings as in [1]}—there was only one tree (as depicted in Fig. 3, but without *Tupaia, Cynocephalus,* and *Pteropus*), which required 552 steps, had a CI of 0.614, and a RI of 0.696; these values apply to ACC-TRAN and DELTRAN.

Analyses [1], [2], and [4] were conducted for better understanding the nature of parts of the data (see, for example, observations under "Synapomorphies for Haplorhini"), whereas analysis [3] was more comprehensive. Since the consensus tree for [3] required three more additional steps than the two equally parsimonious trees, and since this study focuses on intraordinal relationships within Primates, we opted to choose the second alternative to conduct tests with MacClade. This choice was made because the relationships of the outgroups to Primates are the same as the results obtained by Shoshani and McKenna (1995).

The most parsimonious tree chosen depicts these major divisions of living Primates (Fig. 3): Strepsirhini and Haplorhini. Strepsirhini includes Lemuriformes and Lorisiformes (Table 2). Haplorhini is divided into

TABLE 1

Results of Branch-Swapping within Primates

Relationship(s)	Length of tree	No. of extra steps
As depicted in Figs. 3A and 3A′	604 Steps	0[a]
Tarsius with Strepsirhini instead of with Anthropoidea (Fig. 3B)[b,c]	613 Steps	9
Tarsius as a sister group to all other primates, Strepsirhini joins Anthropoidea (Fig. 3C)[b]	616 Steps	12
Tarsius, Strepsirhini, and Anthropoidea join in a polytomy (Fig. 3D)[b,c]	617 Steps	13
Tarsius as a sister group to *Loris + Nycticebus*[d]	615 Steps	11
Tarsius as a sister group to *Daubentonia + Lemur*[d]	615 Steps	11
Daubentonia as a sister group to all strepsirhines[d]	606 Steps	2
Daubentonia as a sister group to all other primates[e]	607 Steps	3
Daubentonia, Lemur, Loris + Nycticebus join in a polytomy[d]	609 Steps	5
Loris + Nycticebus join Haplorhini[f]	605 Steps	1
Loris + Nycticebus, Lemur + Daubentonia and Haplorhini join in a polytomy[d]	606 Steps	2
Aotus join with *Leontopithecus* or *Aotus, Leontopithecus, Cebus + Saimiri* join in a polytomy[d]	607 Steps	3
Pan joined with *Homo* (as in Fig. 3)	604 Steps	0
Pan joined with *Gorilla*[g]	605 Steps	1
Gorilla joined with *Homo*[h]	606 Steps	2
Gorilla, Pan, and *Homo* joined in a trichotomy[d,h]	619 Steps	15
Pan joined with *Pongo, Gorilla* an outgroup[i]	621 Steps	17
Pongo joined with *Gorilla, Pan* with *Homo*[i]	622 Steps	18
Pongo, Pan, and *Gorilla* joined in a polytomy[i]	632 Steps	28
Pongo joined with *Homo,* followed by *Gorilla* and *Pan*[j]	632 Steps	28
Pongo joined with *Homo,* then by *Gorilla + Pan*[j]	622 Steps	18
Gorilla, Pan, Homo, and *Pongo* joined in a polytomy; *Hylobates* is an outgroup[d]	648 Steps	44
Hylobates, Pongo, Gorilla, and *Pan* joined in a polytomy; *Homo* is an outgroup[d]	675 Steps	71

[a] These extra steps are to the most parsimonious tree shown in Fig. 3. Consistency Index for this and all tests in this table is approximately 0.60.

[b] A hypothesis to accommodate the dilemma as to whether *Tarsius* is a strepsirhine or a haplorhine.

[c] A hypothesis suggested by Gregory (1910, p. 465), and by Simpson (1945, p. 63).

[d] An alternative hypothesis to that depicted in Fig. 3.

[e] A hypothesis implied by Groves (1974).

[f] A hypothesis proposed by Schwartz and Tattersall (1987).

[g] A hypothesis proposed or suggested by many authors as part of one of possible topologies; cf. Simpson (1945, p. 68), Schwartz (1984, p. 594), Andrews (1987, 1988, 1992), Groves (1991), and Barriel *et al.* (1993, p. 159).

[h] A hypothesis proposed or suggested by, e.g., Andrews (1987, 1988, 1992), Groves (1986, 1991), and Barriel *et al.* (1993, p. 159); see text for an explanation for the increase from one or two steps to 15 steps in this trichotomy.

[i] A hypothesis suggested by, or implied from, Simpson (1945, p. 68).

[j] A hypothesis proposed by Schwartz (1984, p. 594; 1987), cf. Groves (1987).

Tarsioidea and Anthropoidea, which, in turn, is divided into Platyrrhini (New World monkeys) and Catarrhini (Old World monkeys and Hominoidea). Hominoidea contains two clades, the Hylobatidae (gibbons and siamangs) and the Hominidae (*Pongo, Gorilla, Pan,* and *Homo*).

Results obtained with MacClade. Results of branch swapping within Primates with MacClade are shown in Table 1 and Fig. 3. It appears that with available morphological characters and the selected primate taxa, the topology in Fig. 3 is rather stable, with the exception of those branch swaps which required a small number of extra steps. These include the positions of *Daubentonia, Loris + Nycticebus, Aotus,* and among Homininae, all requiring between one and three extra steps to accommodate the branch swaps listed in Table 1. It is noted that even though the change in the position of these taxa required a small number of extra steps, when a polytomous arrangement was tested, the score raised was more than the dichotomous changes. For example, when *Pan* was joined with *Gorilla,* the score of the tree was raised by one step, and when *Gorilla* was joined with *Homo,* the score of the tree was raised by two steps, but when *Pan, Gorilla,* and *Homo* were joined in a polytomy, the score of the tree was raised by 15 steps (see also under Subfamily or Subtribe Relationships).

Primates and Primates Intraordinal Synapomorphies

Zoologists since Linnaeus (1758), have attempted to define the mammalian order Primates, but most have failed to provide shared–derived characters (e.g., Le Gros Clark, 1959; Napier and Napier, 1985). MacPhee (1981), followed by Thorington and Anderson (1984), and Beard (1993) provided these osteological synapomorphies for living and extinct Primates:

• Auditory bulla formed by outgrowth of petrosal and

TABLE 2

A Simplified Classification of Representative Living Primates Studied Based on Morphological Characters

Order primates
  Suborder Strepsirhini (or Strepsirrhini)[a]
      Infraorder Lemuriformes[b]
        Superfamily Lemuroidea
          Family Lemuridae—e.g., *Lemur*
          Family Daubentoniidae—e.g., *Daubentonia*
      Infraorder Lorisiformes[b]
        Superfamily Lorisoidea
          Family Lorisidae (or Loridae)[a]—e.g., *Loris, Nycticebus*
  Suborder Haplorhini (or Haplorrhini)[a]
    Semisuborder Tarsioidea[c]
    Infraorder Tarsiiformes
        Family Tarsiidae—e.g., *Tarsius*
    Semisuborder Anthropoidea[c]
    Infraorder Platyrrhini
      Superfamily Ceboidea
        Family Cebidae
          Subfamily Callitrichinae—e.g., *Leontopithecus*
          Unnamed taxon
          Subfamily[d] Aotinae—e.g., *Aotus*
          Subfamily[d] Cebinae—e.g., *Cebus, Saimiri*
    Infraorder Catarrhini
      Superfamily Cercopithecoidea
        Family Cercopithecidae
          Subfamily Cercopithecinae—e.g., *Macaca, Papio*
          Subfamily Colobinae—e.g., *Colobus, Presbytis*
      Superfamily Hominoidea
        Family Hylobatidae—*Hylobates*
        Family Hominidae
          Subfamily Ponginae—*Pongo*
          Subfamily Homininae
            Tribe Gorillini—*Gorilla*
            Tribe Hominini—*Pan, Homo*

Name of genera are those terminal taxa depicted in Fig. 3. Names of categories (suborders, semisuborders, infraorders, superfamilies) are included to correspond with the sister-groups on the cladogram; i.e., each node is named. This classification is similar in its overall hierarchy to that obtained from molecular data—e.g., Goodman (1962, 1963, 1976), Goodman and Moore (1971), Miyamoto and Goodman (1990), Bailey *et al.* (1992), Schneider *et al.* (1993), Goodman *et al.* (1994), and Porter *et al.* (1995); cf. Gingerich (1984).

[a] The alternative spellings in parentheses are after Jenkins (1987); also used by Corbet and Hill (1992). In Appendix 1 we used Lorisidae and Galagidae. One of us (CPG) thinks it unwise to preempt the decision of the International Commission on Zoological Nomenclature (ICZN) on this nomenclature, and prefers Loridae and Galagonidae, per Jenkins, 1987 recommendation. A petition for conservation of Lorisidae and Galagidae was submitted to the ICZN by Schwartz *et al.;* note, however, that names of animal taxa above the family group level are not regulated by the ICZN (Article 1[b][4]).

[b] Category of "Infraorder" was added to accommodate other taxa.

[c] Category of "Semisuborder" after Miyamoto and Goodman (1990, p. 200).

[d] Alternative category may be used with further research.

ectotympanic; entotympanic element is lacking (MacPhee, 1981; Thorington and Anderson, 1984; Beard, 1993).

- Dorso-ventral flattening and medio-lateral widening of nail-bearing distal phalanges (Beard, 1993).

- Patellar groove deeply excavated anteriorly with respect to the distal femoral shaft (Beard, 1993).

The last character may not be as strong as the other two due to homoplasy. This character was studied by Shoshani (1986b, character 93), in combination with other features of the patellar groove, and was found to be variable.

Given below are selected synapomorphies and a brief discussion for each major clade in Fig. 3 based on analysis in PAUP (Swofford, 1993; an apomorphy list can be obtained from the senior author). It is noted that because of the branching pattern on this cladogram (Fig. 3), some characters which are coded as primitive conditions turned out to be derived for a particular clade. These, of course, are reversals and their CIs are usually lower than for those which have no homoplasy (convergence, parallelism, and reversals). All changes on a given clade—synapomorphies and homoplasies—are called evolutionary changes (ECs).

Synapomorphies for Primates (cf. Fig. 3 and Table 2). Based on the analysis conducted in this study, there are 17 characters interpreted as synapomorphies, or ECs from the common ancestor of Primates and its closest relative(s) to the common ancestor of Primates. These characters (as they appear in Appendices 2 and 3, not in order of importance), with their CI in parentheses are 1 (0.33), 13 (1.0), 14 (0.67 R), 24 (1.0), 26 (1.0 R), 27 (0.50 R), 29 (0.43), 66 (1.0 R), 71 (0.33), 88 (0.50), 90 (0.75), 94 (1.0), 110 (0.25), 132 (0.25), 248 (0.50), 258 (1.0), and 260 (0.50). The letter "R" for characters 14, 26, 27, and 66 implies reversal. Those characters with CI of 1.0 (but without R) are considered good synapomorphies, and worthy of summarizing here. They are character 13—TYMPANIC FLOOR fully ossified, petrosal plate major element, it forms anterior, medial, and posterior walls; character 24—EPITYMPANIC WING of alisphenoid small, does not reach to the level of the anterior pole; character 94—EMBRYONIC DISC orthomesometrial; and character 258—MEISSNER'S CORPUSCLES present. Although a reversal, character 26 could have been a good character if only *Solenodon* had been used as an outgroup. If we consider these five characters and the "dorso-ventral flattening and medio-lateral widening of nail-bearing distal phalanges" noted earlier, we may have about six synapomorphies for Primates (see also Szalay and Delson, 1979; MacPhee, 1981; Andrews, 1988; Fleagle, 1988). The bootstrap value (BSV) for this node is 98% (cf. Fig. 3).

Synapomorphies for Strepsirhini (cf. Fig. 3 and Table 2). There are six ECs for this clade. These characters are: 17(R), 80, 82, 97(R), 259, and 260 (listed in Appendix 2). Characters 80 and 82 (after Gebo, 1986, pp. 423–425) have a CI of 1.0, and are considered good synapomorphies (shared–derived characters); they are as fol-

lows: ASTRAGALUS (TALUS) FIBULAR FACET is oblique (ch. 80), and the flexor of the POSTERIOR TALAR TROCHLEA is on the lateral side (ch. 82). The other four characters have CIs of 0.50. The BSV for this node is 45% (cf. Fig. 3; see also Schwartz and Tattersall, 1987; and Groves and Eaglen, 1988).

Synapomorphies for Haplorhini (cf. Fig. 3 and Table 2). There are 18 synapomorphies or ECs for this clade, one of them with CI of 0.29, two with 0.33, six with 0.50, one with 0.75, and eight with 1.0. Two of the characters are reversals (25, 129). This node is supported by good characters with CIs of 1.0—52, 55, 85, 86, 87, 96, and 224. A sample of these synapomorphies with CI = 1.0 includes character 52—RHINARIUM dry, and UPPER LIP partially, or not, split; character 55—TAPETUM LUCIDUM absent; character 96—ALLANTOIC DIVERTICULUM vestigial; and character 224—PUBERTY reached at about 3–5 years. Three or possibly four other good characters with CI of 0.5 are applied to this node, one is RETINA with central foveal spot (ch. 54), another is CHORIOVITELLINE PLACENTA absent (ch. 95), a third is hemochorial PLACENTA present (ch. 97), and the fourth is character 39. All have CI of 0.5 because the derived character states (CSs) appear in other taxa: *Aotus* (for ch. 54; see under Notes in Appendix 2), *Cynocephalus* (for chs. 95 and 97), and *Tupaia* (for ch. 39). The derived condition for character 39 (separation of FORAMEN ROTUNDUM and the ORBITAL FISSURE), we feel, is one of the best examples of morphological character without subjectivity because its polarity is well known in Mammalia (e.g., Gregory, 1910; Shoshani and McKenna, 1995). Although, PAUP analysis indicates that CS (3) of character number 42 is a synapomorphic character for Haplorhini, based on the available evidence from the extinct anthropoids and/or catarrhines, it appears that the complete and long auditory tube (EXTERNAL AUDITORY MEATUS) evolved independently in tarsiers and catarrhines; see discussion under Fossil History of Primates and Problems Encountered, Possible Considerations. Luckett (1980, p. 352) employed five characters uniting Haplorhini; some are used here. Schwartz (1978), on the other hand, challenged some of Luckett's shared–derived characters for Haplorhini. The BSV for this node is 99% (cf. Fig. 3).

Synapomorphies for Anthropoidea (cf. Fig. 3 and Table 2). There are 32 synapomorphies or ECs for this clade; of these 16 are with CI of 1.0 and the rest with CIs which vary from 0.167 to 0.750. There are four reversals—characters 71, 88, 116, and 159. The best characters for this node are characters 2, 4, 5, 7, 45, and 57 (after Gingerich, 1992, p. 201; cf. Fig. 4B), characters 81, 83–87 (of Gebo, 1986, pp. 423–425), and characters 11, 43 (after Shoshani 1986b), 92 (after Luckett, 1980, pp. 352–353), and 264 (after Groves,

personal observation, 1995). The clade of Anthropoidea is well-supported; it has a BSV of 100% (cf. Fig. 3).

Synapomorphies for Platyrrhini (cf. Fig. 3 and Table 2). There are 13 synapomorphies or ECs for this clade; one is a reversal. Nine synapomorphies have CI of 1.0, one has CI = 0.25, one with 0.33, and two with 0.50. The synapomorphies with CI = 1.0 are character numbers 8, 42, 64, 75–76, 98–100, and 147. The best of these nine synapomorphies are character 8—FRONTAL and ALISPHENOID contact is absent; character 42—EXTERNAL AUDITORY MEATUS, opening of external acoustic meatus is large, round with thickened margins forming a rim of ectotympanic all around the opening except on the dorsal posterior edge ("horseshoe shaped"), margin of tube opening is medial to the zygoma, opening faces diagonally from the ventral of bulla dorsally and laterally; character 98—INTRAPLACENTAL MATERNAL VESSELS present; character 99—PLACENTAL HEMATOPOIESIS present; character 100—OVARIAN INTERSTITIAL GLAND TISSUE DEVELOPMENT abundant; and character 147—HALLUCIAL TARSOMETATARSAL JOINT present. It is often stated in the literature (e.g., Thorington and Anderson, 1984, p. 204) that members of the family Cebidae are "distinguished from other Recent monkeys by retained primitive characteristics." The 13 ECs, and specifically the six summarized above (chs. 8, 42, 98–100, and 147) provide better support for this family (note that Thorington and Anderson (1984) used many of the synapomorphies mentioned here; see however, Rosenberger (1992b) for possible platyrrhine synapomorphies not included here). The Platyrrhini is a well-supported clade, with a BSV of 98% (cf. Fig. 3).

Synapomorphies for Catarrhini (cf. Fig. 3 and Table 2). There are 12 synapomorphies or ECs for this clade. These characters (as listed in Appendix 2), with their CIs in parentheses are: 10 (1.0), 31 (0.50), 33 (0.33), 41 (0.5), 43 (1.0), 48 (1.0), 49 (0.50), 73 (0.33), 122 (0.33), 125 (0.25 R), 244 (0.20), and 260 (0.50). Following are good synapomorphic characters for this clade: character 10—POSTERIOR PALATAL SPINE is large, slopes dorsally and is supported by the vomer which extends ventrally, postpalatine torus absent; character 43—FOSSA GENIOGLOSSI FORAMINA are clearly delineated and visible with a naked eye on the posterior end of the mandibular symphysis, inside the fossa genioglossi, just above the spina mentalis and the Simian Shelf. [This character may be associated with the fusion of the dentaries. These foramina are present in other mammals with well-fused symphysis, such as domestic pig (*Sus scroffa,* family Suidae, order Artiodactyla), but possibly also in mammals with unfused symphysis, such as beaver (*Castor canadensis,* family Castoridae, order Rodentia).]; character 48—HONING in males (back of upper canine sharpens against third

lower premolar) present; i.e., P_3 bilaterally compressed (sectorial) and modified for honing on C^1, P_3 larger than P_4 especially mesiodistally, also may involve honing C^1 on C_1. Other good characters (but with CI = 0.5 because they appear in other taxa) for this node are character 31—CORONOID PROCESS of mandible when teeth are fully occluded is not projecting dorsal to margin of zygomatic arch; character 41—POSTGLENOID FORAMEN very small or absent; character 49—having two upper and lower PREMOLARS present; character 260—deep stratum of FALCULA is about 0% of claw (this CS also appears in *Lemur, Loris,* and *Nycticebus*). As noted above, of the 12 ECs, only one is a reversal (R). A complete and long auditory tube (EXTERNAL AUDITORY MEATUS), character 42, CS (3), may be considered a synapomorphy for advanced catarrhines; see, however, notes under "Synapomorphies for Haplorrhini." The BSV for this node is 86% (cf. Fig. 3). Other possible synapomorphies for this clade may be found in Szalay and Delson (1979), Thorington and Anderson (1984), and Tattersall *et al.* (1988).

Synapomorphies for Cercopithecoidea (cf. Fig. 3 and Table 2). There are six synapomorphies or ECs for this clade; one with CI of 1.0 (ch. 50), the other CIs vary from 0.33 to 0.50. These characters are: 50, 120, 151R, 159, 164R, and 242, of which two are reversals. The BSV for this node is 68% (cf. Fig. 3). As expected, character 50 (with CI = 1.0), the presence of bilophodont MOLARS, appears to be the best. One other possible good Cercopithecoidea synapomorphy is character 159—mesial groove of male's CANINE extends into root; it has a CI of 0.50, possibly because of three CSs and inconsistency of states within a clade. Note, however, that only cercopithecoid taxa are coded with CS (1) [see Appendix 3], but because of the topology of the cladogram, the CI for this character is 0.5, instead of 1.0, as might be expected [see also Delson (1992) for possible catarrhine synapomorphies not included here].

Synapomorphies for Hominoidea (Hylobates, Pongo, Gorilla, Pan, Homo; cf. Fig. 3 and Table 2). There are 37 synapomorphies or ECs for this clade. Following is a complete list of ECs with transformation series (TS), e.g., $0 \Rightarrow 1$, and CI in parentheses, as obtained from PAUP (Swofford, 1993). The reason for providing the complete listing is that it will be easier to trace a change in a character state or a reversal in the succeeding sections (Synapomorphies for Hominidae, Homininae, and Hominini). Character definition and a brief explanation are given when we felt that it would help explain the TSs and the CIs. [An open arrow means that the change occurs in all possible reconstructions (i.e., is unambiguous). A simple right arrow indicates that change occurs under some reconstructions

but not others (Swofford, 1993, p. 120).] These characters are:

character 10 [TS of $2 \rightarrow 3$, CI = 1.0]; character 12 [$0 \rightarrow 2$, CI = 1.0]; character 29 [$1 \Rightarrow 2$, CI = 0.429]; character 30 [TS of $0 \Rightarrow 1$, CI = 0.33]; character 48 [$1 \rightarrow 2$, CI = 1.0]; character 61 [$0 \Rightarrow 1$, CI = 0.20]; character 74 [$0 \Rightarrow 1$, CI = 1.0]; character 112 [$0 \Rightarrow 2$, CI = 1.0]; character 131 [a reversal of $1 \rightarrow 0$, CI = 0.17]; character 133 [$0 \rightarrow 1$, CI = 0.67]; character 136 [$0 \rightarrow 1$, CI = 0.50];

character 138 [$0 \Rightarrow 1$, CI = 1.0], OS CENTRALE partially fused with scaphoid, a CS (1) which occurs in *Hylobates* and *Pongo;* CS (2), complete fusion of OS CENTRALE with scaphoid occurs in *Gorilla, Pan,* and *Homo;*

character 142 [$0 \Rightarrow 1$, CI = 1.0], HUMERAL TORSION increased; among living hominoids, *Gorilla* exhibits CS (2);

character 143 [$0 \Rightarrow 1$, CI = 1.0]; character 145 [$0 \Rightarrow 2$, CI = 0.67];

character 149 [$0 \Rightarrow 3$, CI = 1.0], relative length of UPPER LIMB increased further; this does not appear to be a good character because living hominoids exhibit all four CSs, yet it has a CI of 1.0;

character 157 [$0 \rightarrow 1$, CI = 0.50]; character 175 [$0 \Rightarrow 1$, CI = 1.0]; character 176 [$0 \rightarrow 1$, CI = 0.20]; character 177 [$0 \Rightarrow 1$, CI = 0.67]; character 186 [$0 \rightarrow 1$, CI = 0.67]; character 194 [$0 \Rightarrow 1$, CI = 0.67]; character 195 [$0 \rightarrow 1$, CI = 0.67];

character 200 [$0 \rightarrow 1$, CI = 0.67]; character 204 [$0 \rightarrow 1$, CI = 0.50]; character 205 [$0 \rightarrow 1$, CI = 1.0]; character 208 [$0 \rightarrow 1$, CI = 1.0]; character 209 [$0 \Rightarrow 1$, CI = 1.0]; character 210 [$0 \rightarrow 2$, CI = 0.67]; character 211 [$0 \rightarrow 1$, CI = 0.33]; character 212 [$0 \Rightarrow 1$, CI = 0.50]; character 215 [$0 \rightarrow 2$, CI = 0.67]; character 217 [$0 \rightarrow 1$, CI = 0.50];

character 224 [$1 \Rightarrow 2$, CI = 1.0], PUBERTY delayed, reached at about 6–7 years; this does not appear to be a very good character for Hominoidea because CS (2) changes to (3) within the clade;

character 234 [$0 \Rightarrow 1$, CI = 0.67], BACULUM reduced; among living Primates, *Tarsius, Pan,* and *Homo* have CS (2), baculum is tiny or absent;

character 245 [a reversal of $1 \rightarrow 0$, CI = 0.33];

character 252 [$0 \Rightarrow 1$, CI = 0.50] orifices of APOCRINE GLANDS nearer to body surface; among living hominoids, *Homo* has the primitive condition, CS (0).

Hominoidea is a well-supported clade, with a BSV of 99% (cf. Fig. 3). There are 13 characters with CI of 1.0, they are: 10, (12; not as good as characters without parentheses), (48), 74, (112), (138), (142), 143, (149), (205), (208), (209), and (224). The best characters for this node are numbers 10, 74, and 143. Other characters for hominoid primates not mentioned here may be found in Andrews (1987, 1988).

Synapomorphies for Hominidae (Pongo, Gorilla, Pan, Homo; cf. Fig. 3 and Table 2). There are 45 synapomorphies or ECs for this clade. Rather than list all the ECs for this clade, we select only those that appear in the preceding section (with different TSs) and those with CIs of 1.0.

These characters appeared as ECs for Hominoidea; now they appear, with different TSs as ECs for Hominidae. They are: 12 [2 → 3, CI = 1.0]; 133 [1 → 2, CI = 0.67]; 157 [1 → 2, CI = 0.50]; 195 [1 → 2, CI = 0.67]; 200 [1 → 2, CI = 0.67]; 205 [1 → 2, CI = 1.0]; 208 [1 → 2, CI = 1.0]. The 16 characters with CI of 1.0 for this clade are:

character 12 [2 → 3], SUBARCUATE FOSSA is very shallow to nonexistent;

character 36 [0 ⇒ 1], INCISIVE FORAMEN is directed diagonally, from anterior-ventral to posterior-dorsal; the opening is small, leads to a tube-like structure, and one cannot "see through" the foramina;

character 65 [0 → 1], ULNAR STYLOID PROCESS shortened; note that *Pongo* has CS (1), whereas *Gorilla, Pan,* and *Homo* have CS (2);

character 69 [0 ⇒ 1], PELVIS, size of acetabular fossa approximate size of obturator foramen;

character 128 [0 → 1], INCISIVE FORAMEN is reduced, note that *Pongo* has CS (2);

character 156 [0 ⇒ 1], TROCHLEA broad, and spool-shaped;

character 174 [0 → 1], preprotocrista of dP⁴ more developed;

character 182 [0 ⇒ 1], LONG TIBIAL FLEXOR withdrawn from digit I;

character 205 [1 → 2], FUNGIFORM PAPILLAE fully concentrated on apex of tongue;

character 208 [1 → 2], PALATINE ridges asymmetrical;

character 225 [0 → 1], OVUM enlarged, incomplete data for Hominidae;

character 226 [0 → 1], MITOCHONDRIAL COILS reduced in number, incomplete data for Hominidae;

character 227 [0 ⇒ 3], TESTES very small, <0.05% of body weight; note that polarity changes within the family;

character 240 [0 ⇒ 1], MAMMARY DEVELOPMENT IN FEMALE present, at least from first pregnancy;

character 250 [0 → 1], ECCRINE GLANDS increased over body surface; note that *Pongo* has CS (1), whereas other hominid have CS (2);

character 255 [0 → 1], HAIR DENSITY on back reduced, under 200/cm², note that *Pongo* has CS (1), whereas other hominids have CS (2).

Hominidae is a fairly well-supported clade, with a BSV 87% (cf. Fig. 3). The 16 characters with CI of 1.0 appear to be good synapomorphies. Other characters for hominid primates not mentioned here may be found in Andrews (1987, 1988).

Synapomorphies for Homininae (Gorilla, Pan, Homo; cf. Fig. 3 and Table 2). There are 58 synapomorphies for this clade. All these characters are from the data set covering mostly five primate taxa, characters 101–264 of Groves (1986, 1995). Of these 58 characters, 14 are reversals, and of the reversals, two have CI of 1.0. As expected, some characters which appeared on the Hominidae branch now appear, with different TSs as ECs for Homininae; they are: 65 [1 → 2, CI = 1.0]; 119 [0 → 2, CI = 0.4]; 179 [1 → 2, CI = 0.67]; 184 [1 → 2, CI = 0.67]; 230 [1 → 2, CI = 0.67]; 250 [1 → 2, CI = 1.0]; 251 [1 → 2, CI = 0.67]; 255 [1 → 2, CI = 1.0]; and 256 [1 → 2, CI = 0.67].

A total of 27 ECs have CI = 1.0, three of these are noted in the previous paragraph, and two are reversals; therefore, we will briefly list the remaining 22 ECs for this node. They are characters 102 [0 ⇒ 1], 104 [0 ⇒ 1], 106 [0 ⇒ 2], 111 [0 ⇒ 1], 137 [0 ⇒ 1], 138 [1 ⇒ 2], 139 [0 ⇒ 1], 152 [0 ⇒ 2], 153 [0 ⇒ 1], 155 [0 ⇒ 1], 175 [1 ⇒ 2], 192 [0 ⇒ 1], 197 [0 ⇒ 1], 202 [0 ⇒ 1], 207 [0 ⇒ 1], 209 [1 ⇒ 2], 214 [0 ⇒ 1], 216 [0 ⇒ 1], 219 [0 ⇒ 1], 231 [0 ⇒ 1], 238 [0 ⇒ 1], and 249 [0 ⇒ 1]. Most of these characters have only two CSs, and the derived CSs are easily recognized from Appendix 2. Homininae is a well supported clade (cf. Andrews, 1987, 1988, 1992), with a BSV of 99% (cf. Fig. 3).

Synapomorphies for Hominini (Pan, Homo; cf. Fig. 3 and Table 2). There are 29 synapomorphies or ECs for this clade, nine of which are reversals, and two appear on the line leading to Hominoidea; they are: 210 [0 → 1, CI = 0.67] and 215 [0 → 1, CI = 0.67]. There are nine synapomorphies with CI of 1.0, but two are reversals. The remaining seven characters are:

character 48 [2 ⇒ 3], HONING in males (back of upper canine sharpens against third lower premolar) is further reduced; P₃ about the same size as P₄ in length in occlusal view (see also under Catarrhini);

character 130 [0 ⇒ 1], PREMAXILLARY SUTURE obliterated in adult;

character 154 [0 ⇒ 1], ANKLE EPIPHYSES not delayed relative to elbow and hip;

character 187 [0 ⇒ 1], DIGASTRIC inserts on inferior transverse torus;

character 220 [0 ⇒ 2], ENCEPHALIZATION high, >11;

character 224 [2 ⇒ 3], PUBERTY further delayed, reached at >7 years; and

character 235 [0 ⇒ 1], PENIS, when erect, lengthened, over 80 mm.

Other good synapomorphies for Hominini, but with CI less than 1.0 include:

character 70 [1 ⇒ 2, CI = 0.67], PELVIS, obturator groove or notch is deep and well delineated;

character 186 [1 → 2, CI = 0.67], GENIOHYOIDEUS inserts above inferior transverse torus;

character 210 [0 → 1, CI = 0.67], ILEO-CAECAL VALVE widened; and

character 215 [0 → 1, CI = 0.67], cranial end of HEART shifted upward.

These seven synapomorphies with CI = 1.0 and four with CI = 0.67 appear to be good shared–derived characters for Hominini. Hominini is supported weakly by a BSV of 42% (cf. Fig. 3). In addition, there are two or possibly three characters which were not spelled out above, but may have been incorporated in the total complex of characters for the tribe Hominini. These features may be considered shared–derived characters for *Pan* and *Homo.* They are the ability of these two genera to make and use tools (van Lawick-Goodall, 1967, p. 32; Wrangham, 1984, p. 424; Lee, 1992, p. 342), to store tools (Boesch-Achrmann and Boesch, 1994, pp. 12–14), to engage in face-to-face or ventroventral sexual intercourse (known only in humans and pygmy chimpanzee, or bonobo, *Pan paniscus;* Thompson-Handler *et al.,* 1984, p. 352; Wrangham, 1984, p. 425; Groves, 1986, p. 204), and possibly the ability to walk in bipedal mode for considerable distances (other primates, e.g., *Hylobates* can also walk on their hind legs, in which case this character evolved independently in Hylobatidae and Hominini (parallelism; cf. Alexander, 1992, p. 80)).

Problems Encountered, Possible Considerations

Defining characters.   In the process of studying certain characters, it became evident that it is possible that descriptions of some characters encountered in the literature are either incomplete or ambiguous. A case in point, the external auditory meatus in its primitive condition [character state (0)] is nonexistent in Primates—as is the case in early mammals and some insectivores. Three possible derived conditions were incorporated in the character descriptions (character 42, Appendix 2). Apparently, fossil early anthropoids or catarrhines, e.g., *Aegyptopithecus* and *Catopithecus,* lacked long extended auditory tubes (Simons, 1992b, 1995), CS (1). More advanced catarrhines possessed the long auditory tubes, CS (3). Some omomyids, an earlier group than catarrhines, possessed a tube (see discussion under the section on fossil primates). Detailed examination of the crania of archaic primates, omomyids, and adapids should be conducted to determine precisely which character states prevail in these taxa. Szalay (1972, p. 66) noted that some lemuriforms (e.g., *Megaladapis, Palaeopropithecus,* and *Archaeoindris*) possessed elongated external auditory tube of the petrosal, not ectotympanic, suggesting yet another character state.

The tarsier controversy.   To summarize the issues concerning tarsiers and/or Tarsiiformes systematics in this paper is to do injustice to the topic, for it exemplifies a much bigger problem—that of "living fossils." Being sole representatives of groups which were extensively represented in the fossil record and had a wider distribution than the living forms do usually implies that the living fossils have evolved and acquired autapomorphic characters, setting them apart from their ancestors. The living fossils generally retain some plesiomorphic characters, making them truly mosaic taxa, and making it extremely difficult to assess their phylogenetic relationships (cf. Eldredge and Stanley, 1984). The literature on the taxonomic position of tarsiers within Primates based on morphology is prolific; following are some examples: Gregory (1910), Simpson (1945), Simons (1964, 1972, 1992b, 1995), Le Gros Clark (1965), Hill (1972), Cartmill and Kay (1978), Schwartz (1978), Tattersall *et al.* (1988), Thorington and Anderson (1984), and Groves (1991). Representatives of works for tarsier's affinities based on molecules are Goodman (1976), Goodman *et al.* (1982, 1987, 1994), Sarich and Cronin (1976), Czelusniak *et al.* (1990), and Miyamoto and Goodman (1990).

The crux of the problem with regard to the systematics of tarsier rests on whether to classify the living genus *Tarsius* with early primates (Prosimii or Strepsirhini) or with late, more advanced primates (Anthropoidea, in Haplorhini). Some morphologists, including neontologists and paleontologists, classify the lineage of *Tarsius,* i.e., Tarsiiformes, with Prosimii (e.g., Simons, 1992b; Gingerich, 1992). On the other hand, molecular biologists classify the living *Tarsius* with Anthropoidea in Haplorhini (e.g., Goodman, 1992; Miyamoto and Goodman, 1990; Table 2). A third alternative states that "*Tarsius* is intermediate between strepsirhines and Anthropoidea" (Schwartz, 1978, p. 200; cf. Appendix 1).

It is not the purpose of this paper to resolve this perplexing situation, but rather to point out some of the problems encountered. The living genus *Tarsius* is one of 46 genera of supposed Tarsiiformes whose geological range extends from the Eocene to the present (Appendix 1). It would be impractical to assume that all tarsiiform characters are embodied in *Tarsius.* Based on the characters employed for the living genus, and the computer analysis conducted in this study, *Tarsius* is grouped with Anthropoidea. If we join *Tarsius* with Strepsirhini instead of with Anthropoidea, the length of the most parsimonious tree will increase by nine steps; scores of alternative hypotheses for *Tarsius* are shown in Table 1. The union of *Tarsius* with Anthropoidea in Haplorhini is supported by 18 characters, approximately 10 are considered good characters (details under Synapomorphies for Haplorhini).

Synapomorphies in support of Tarsiiformes being a sister group of lemurs and lorises (i.e., *Tarsius* would be a member of Prosimii) are very difficult to find in

the literature. The list below (for Tarsius and omomyi-forms, Appendix 1) is after Szalay (1975, 1976), Gingerich (1981), and Rose (1995):

(1) shortened face,
(2) very large orbits (not true for *Necrolemur*),
(3) enlarged promontory arterial canal,
(4) tubular ectotympanic (not true for *Shoshonius*),
(5) very narrow and ridged choanae (maybe as a result of the enlarged orbits),
(6) enhanced elongation of tarsal elements,
(7) very anteroposteriorly deep distal femur with very high medial and lateral patellar ridges,
(8) distal tibia/fibula tightly joined (fused in some taxa, for example, *Necrolemur*).

Close scrutiny of this list may reveal why and how the results of traditional and modern techniques clash, forcing a choice between unfavorable alternatives. This statement is made because none of these characters can be substantiated as synapomorphies for Prosimii (lemurs, lorises, and tarsiers) since there is a lack of evidence for most fossil tarsiiforms. Most of these eight characters have been suggested as possible synapomorphies in the past, but many are now considered primitive retentions by some authors, while other characters do not typify all fossil tarsiiforms. Beard and MacPhee (1994) proposed some characters for *Shoshonius* and *Tarsius* only, not for the rest of tarsiiforms (see also Beard *et al.,* 1991).

The problem of finding synapomorphies is not limited to osteological characters (e.g., in fossil tarsiiforms), but also to corroborating the presence or absence of soft tissue characters in extinct taxa. For example, characters of biochemical similarities, characters typical of nocturnal primates [such as presence of retinal fovea (fovea centralis) with the yellow spot (macula lutea) and the loss of tapetum lucidum], and characters related to fetal membrane and placentation (see characters 95, 96, and 97 in Appendix 2) are shared–derived characters for tarsiers and anthropoids (Haplorhini) but cannot be confirmed for the extinct Omomyidae and Adapidae. It is possible that these characters, like other suggested synapomorphies for Haplorhini, evolved independently in Tarsiidae and Anthropoidea (cf. discussion in Schwartz (1978), Szalay *et al.* (1987), and Culotta (1992 and 1995)).

In conclusion, we have depicted four possibilities with our final cladogram (Fig. 3) for the living Primates. Tattersall *et al.* (1988, p. 566) noted that ". . . no other primate, except for humans and australopiths, has stimulated as much controversy [as *Tarsius*]"— this quandary is likely to continue.

Classification and cladograms. Staunch cladists would argue that every node on the cladogram requires a categorical name to define that taxon. This may create some problems, especially if a data set contains a large number of operational taxonomic units (OTU) (discussion in Martin (1990) and McKenna *et al.* (1995)). In this paper, since we are dealing with relatively few living primates, we tried to correlate names of categories between morphological and molecular classifications [cf. Table 2 to tables in Goodman (1962, 1963, 1976), Miyamoto and Goodman (1990), Bailey *et al.* (1992), and Schneider *et al.* (1993), and cf. Gingerich (1984)].

For comparison of material in the literature, we have included, in Appendix 1, all known primate genera, extinct and extant, authorships and years of publication, and geological ranges for families. The classification also includes synonymies and annotations on taxonomy of certain taxa. This classification is an update to that of Szalay and Delson (1979); references since 1979 are included here.

Fossil records, phylogeny, and classification. Emergence of mammalian ordinal characters probably date to the beginning of the Cretaceous to Eocene, familial characters to the Eocene through the Oligocene, subfamilial to the Miocene, and generic characters to about the Pliocene epoch (Romer, 1971). A character which is a synapomorphy on an earlier node on a cladogram (e.g., for Catarrhini of early Miocene or before) becomes a symplesiomorphy for an ingroup, particularly for closely related genera or species (e.g., *Homo* and *Pan,* whose common ancestor dates to about late Miocene or early Pliocene). A morphological synapomorphy for the last example is usually difficult to find because there has not been enough time for such characters to evolve. It is thus not surprising that there have been many studies attempting to find shared–derived characters for *Homo* and *Pan,* even though they are clearly united based on molecular data. In this study, the synapomorphies for *Homo* and *Pan* are not as strong as other clades; nevertheless, they are united in the tribe Hominini (*Homo* and *Pan,* Table 2, details below).

One of the major problems in evolutionary biology is deciding whether or not the branching pattern on a cladogram should correspond with the classification for that cladogram (see discussions in Gingerich (1979), Ridley (1986), and Forey *et al.* (1992)). Pure cladists advocate that classification and cladogram should correspond. The other extreme is to retain previously used names whenever available and not "invent" new names. Somewhere between are synchretists who name every node, and whenever names are not available, may use "unnamed taxon" and also employ "plesion" for extinct forms. In this context Martin (1990, p. 98) stressed that ". . . classifications must change over time to maintain broad compatibility with accumulated knowledge, but it is vital to keep such changes to the absolute minimum in the interests of clear communication between biologists." In this paper, we named all the clades up to the subfamily level; terminal taxa, or OTU, are generic names (Fig. 3 and Table 2).

Morphological vs Molecular Results: Congruency or Disagreement?

Interordinal relationships. There are some disagreements as to which mammalian order is the closest living relative of Primates. Based on molecular studies, there are a few candidates such as Dermoptera, Lagomorpha, Rodentia, and Scandentia; nonetheless, the relationships among the orders are not clear (details in Czelusniak *et al.* (1990), Stanhope *et al.* (1993), Allard *et al.* (1996)). Stanhope *et al.* (1993, p. 276) noted "that the closest primate relative is probably not Chiroptera." Menotyphla (including Tupaiidae and Macroscelididae), Dermoptera, Chiroptera, and Primates were classified in the superorder Archonta of Gregory (1910). Based on morphology (Shoshani and McKenna (1995), incorporating data from Novacek and Wyss (1986) and Novacek *et al.* (1988)), the clade containing Dermoptera and Chiroptera is the sister group of Primates and is supported by a bootstrap value (BSV) of 70%. The volumes edited by Genoways (1990), MacPhee (1993), Szalay *et al.* (1993), and the papers by Wible and Covert (1987) and Simmons and Quinn (1994) provide further discussions on intra- and inter-Archontan affinities.

Intraordinal relationships. A close examination of the results obtained from analyses of morphology (MOR) and molecular (MOL) approaches/studies reveals the following. In Fig. 3 many of the groupings are strong, with BSV of over 95; in fact Lorisoidea and Anthropoidea have a BSV of 100. Strepsirhini, Lemuroidea, and Hominini have the lowest BSVs of 45, 45, and 42, respectively. Indeed, it required only two extra steps from the most parsimonious tree to place *Daubentonia* as a sister group to all Strepsirhini and three extra steps to place it as a sister group to all other Primates (Table 1). *Daubentonia*'s close relationship to *Lemur* (MOR) is supported by MOL (Porter *et al.,* 1995, p. 52) and was also suggested by Simpson (1945, p. 62). The platyrrhine taxa are heavily represented in the Porter *et al.* (1995) work—19 of 32. In this study there are only four ceboids represented; nonetheless, in both studies, Ceboidea has high BSV (98 in MOR and 100 in MOL). Catarrhine monkeys, on the other hand, are poorly represented in MOR and MOL.

Relationships within Ceboidea from MOL (Porter *et al.* (1995), employing 19 genera) and MOR (employing 4 genera) are slightly different between them and from those of Rosenberger ((1984), employing 16 genera) and Ford ((1986), employing 16 genera). The difference is in the position of *Aotus*—in Rosenberger (1984), *Cebus* and *Saimiri* are closer to *Leontopithecus* than to *Aotus* (see also Tattersall *et al.,* 1988, p. 458). In Ford (1986), *Leontopithecus* is closer to *Aotus* than to the clade of *Cebus* and *Saimiri,* whereas in this study *Aotus* is closer to the clade of *Cebus* + *Saimiri* than to *Leontopithecus.* If we exclude taxa not included in this study, results from MOL by Schneider *et al.* (1993) and Porter

et al. (1995) show a polychotomy among these four cebid taxa. With further data (Harada *et al.,* 1995), however, *Cebus* and *Saimiri* unite in one clade, subfamily Cebinae. Yet the relationships among Cebinae, Aotinae (for *Aotus*), and Callitrichinae (including *Leontopithecus*) remained unresolved as a polychotomy within the family Cebidae. Results obtained with MacClade show that it takes three extra steps to join *Aotus* with *Leontopithecus* or to have *Aotus, Leontopithecus,* and *Cebus* + *Saimiri* join in a polytomy (Table 1).

The genealogical relationships among primates as depicted in Fig. 3 are based on osteological characters and soft tissue characters such as placentation, internal soft anatomy, and external anatomy. We feel that such combinations of characters from different origins of the taxa concerned is a stronger line of evidence than if we used only one source. In addition, data from masticatory apparatus (Jablonski, 1986, pp. 540–543) provide yet another set of characters in support of the branching pattern shown in Fig. 3 (with minor differences, however). Data from fossil taxa were not incorporated in the analysis but were used for better understanding morphoclines of the living ones.

Subfamily or subtribe relationships. For a number of decades, Morris Goodman and his colleagues (e.g., Goodman *et al.,* 1982) have observed close relationships among *Homo, Pan,* and *Gorilla; Pongo* was the sister group to these three genera. With increasing molecular data, *Homo* and *Pan* appear to be closer to each other than to any other living hominid taxa. *Gorilla* is a sister group to the *Homo–Pan* clade (tribe Hominini of Goodman *et al.* (1990)), and *Pongo* is a sister group to all of them (cf. Sibley and Ahlquist , 1984) Morphologists have lagged in providing evidence for such a grouping, but the two "camps" have become closer in their results than before (subfamily Homininae of Groves (1991), who classified *Gorilla* in the tribe Gorillini, *Pan* in Panini, and *Homo* in Hominini). In this study, we support, with weak morphological data, the *Homo–Pan* clade, although some studies prefer the trichotomy hypothesis (e.g., Andrews, 1987, 1988; Andrews and Martin, 1987a). Based on the branch swapping conducted (Table 1), a trichotomy among *Gorilla, Pan,* and *Homo* increases the score of the most parsimonious tree by 15 steps, possibly because of the large number of autapomorphies accumulated along each lineage. Results show that the number of autapomorphies for each genus as shown in Fig. 3, compared to forcing them in a trichotomy, increases as follows: from 9 to 20 for *Gorilla,* from 7 to 11 for *Pan,* and from 30 to 33 for *Homo* (these increases are explained by the fact that synapomorphies which were assigned for separate clades for Hominini in Fig. 3 are now autapomorphies in the trichotomy arrangement). The study of Barriel *et al.* (1993) also shows conflicting results obtained from morphology regarding the relationships among *Pan, Homo,* and *Gorilla.*

Strengths of clades. Strengths of grouping of primates clades for MOL were provided by Bailey *et al.* (1992), Schneider *et al.* (1993), Stanhope *et al.* (1993), Goodman *et al.* (1994), and Porter *et al.* (1995). Goodman *et al.* (1994, pp. 14–15) and Porter *et al.* (1995, p. 52) observed high strengths of grouping for Hominoidea (also from MOR), Catarrhini (not from MOR), Platyrrhini (also from MOR), Anthropoidea (also from MOR), and Strepsirhini (not from MOR). Haplorhini does not appear to be a strong clade according to Goodman *et al.* (1994, p. 14) (MOL), but it has a BSV of 99 based on MOR. Yet Porter *et al.* (1995, p. 52) (MOL) provided a BSV of 95 for Haplorhini.

A fairly strong clade from MOL is that of the subtribe Hominina (of Goodman *et al.,* 1990) containing the living genera *Pan* and *Homo.* Goodman *et al.* (1994, p. 18) observed that although this subtribe is not as strong as the clade of *Gorilla, Pan,* and *Homo,* "nevertheless 18 extra sequence changes over those in the MP solution were required to break up Hominina." The support from MOR for the union of *Pan* and *Homo* is relatively weak compared to other groupings in Fig. 3. To our knowledge, no other study provides evidence from a large set of morphological characters of living Primates for the close affinity between *Homo* and *Pan.*

Morphological and Molecular Methods and Results: A Comparison

A summary of general observations comparing morphological and molecular data, methods, and results is given in Table 3. With regard to the first two entries in this table, Goodman *et al.* (1987, p. 147) stressed the problem with morphological characters as indicators of genealogical relationships because there is no direct correspondence between the characters and heritable information encoded in genomic DNA. Subjectivism thus may enter into character evaluation. With modern and sophisticated techniques and computer programs, this subjectivism is reduced, especially with a well-defined and carefully coded large data set (a large number of characters may help mask convergencies and/or parallelisms; scrutinizing by reviewers also helps in reducing subjectivism). Goodman *et al.* (1987, p. 147) give the example of a big human brain, which is often used as a character to place *Homo* in a separate family, but it may represent only a few small genic changes in the DNA of our lineage since we last shared a common ancestor with chimpanzees. The problems of subjectivity, and differences between homologous vs analogous characters and between orthologous vs paralogous amino acid sequences are further discussed in Shoshani (1986b), Goodman *et al.* (1987), Patterson (1987), Goodman (1989), and Czelusniak *et al.* (1990).

CONCLUDING REMARKS

It appears that primates originated in the northern hemisphere from archaic terrestrial and nocturnal insectivores (shrew-like animals) during late Cretaceous time and radiated during the late Eocene or earlier, most probably in Africa. Archaic primates (about nine families) appear to be paraphyletic and their inclusion within Primates is not universally accepted. Unambiguous Primates (beginning with Notharctidae in Appendix 1) had postorbital bars, relatively large brains, opposable pollexes and halluces, nails on most digits, and were probably adapted to life in trees. Primates is one of about 20 extant mammalian orders; it includes approximately 46 families (of which about 33 are fossils), about 279 genera (of which 218 are fossils), with approximately 657 species (of which 405 are extinct). Fossils provide important character states which may not be present in extant taxa, and these, in turn, help in evaluating the polarities of the characters, and consequently the direction of evolution. Concomitantly, succinct definition of character states and their codings are imperative integrals of this process.

Results from cladistic analyses (Fig. 3 and Table 2) of Recent primate taxa using morphological characters (Appendices 2 and 3) are very similar to those from amino acid sequences and nuclear DNA characters (e.g., Czelusniak *et al.,* 1990; Schneider *et al.,* 1993; Bailey *et al.,* 1992). The morphologically based classification (Table 2) corresponds to this cladogram and also is similar, but not identical, to classifications of Miyamoto and Goodman (1990, p. 200), Schneider *et al.,* (1993, p. 235), and Bailey *et al.* (1992, p. 133), based on molecular data. This study demonstrates the need to combine large data sets, for when characters 1–100 and 101–264 were analyzed separately, the results were discordant with any currently held hypothesis; only when all characters were analyzed in one data set were we able to test published hypotheses. Morphological evidence for the clade of *Homo* and *Pan* is, to our knowledge, the first published report which is based on a rigorous maximum parsimony computer analysis of a large data matrix on living Primates (264 morphological characters of 18 primate taxa and four outgroups). A trichotomy among *Gorilla, Pan,* and *Homo* is very costly; it increases the score of the most parsimonious tree by 15 steps.

The phylogenetic affinities of *Tarsius* within Primates is far from being resolved. It has stimulated much controversy, primarily because it is a sole representative of a diverse Eocene primate radiation (the Tarsiiformes, omomyids included), and has acquired autapomorphies which may obscure its true taxonomic position. Figures 3B through 3D are attempts to depict alternative hypotheses (based on the fossil record) to those depicted in Figs. 3A and 3A' (based on Maximum Parsimony results presented here; cf. Table 1). Of the four alternative branch arrangements shown in Fig. 3 for the position of tarsier within Primates (Table 1), we noted that the scores of the trees in Figs. 3B through 3D were raised from 9 to 13 extra steps from the most parsimonious solution (Figs. 3A and 3A'); therefore, these hypotheses were rejected.

TABLE 3

A Summary of Observations between Morphological and Molecular Data, Methods, and Results (Modified after Shoshani (1986a, p. 239))

Subject	Morphological	Molecular
Distance from genetic code	Removed	Close
Investigator's input can be or is	Subjective	Objective[a]
Taxa that can be studied	Extant and extinct	Mostly extant, unless a taxon recently became extinct
Numbers of individual specimens examined per species	Few, several, or more	One, rarely two[b]
Number of characters that can be examined	Fewer	More[a]
Ability to determine polarity of a specific character	Yes[c]	No[c]
Resolving power of phylogenetic trees	Better[c]	—[c]
"Global" branch swapping[d]	By the computer program	By the computer program[d]
Results, branching patterns	For living taxa, overall, similar to molecular	Overall, similar to morphological
Testing the results, i.e., "strength" of the tree	Bootstrap and consistency Index values[e]	"Strength of grouping" or bootstraps[e]

[a] Automation enables gathering of large amounts of sequence data in a relatively short time without human input, whereas collecting morphological data can involve subjective descriptions of a process on a bone, such as "small," "medium," "large," or "absent." Subjectivity is, or may be, reduced when a character is evaluated on a higher category than an order where its polarity is better understood (see example of orbital fissure and foramen rotundum given in the Introduction; cf. character 39 in Appendix 2).

[b] Because of the lengthy process involved. In small samples variations cannot be detected.

[c] As many as 20 character states are possible for one amino acid position, this makes it close to impossible to determine the transformation series of a character. Polarity can be determined (in most cases) on morphological characters, and thus they yield more phylogenetic information and have better resolving power, especially when the ontogeny and phylogeny of a lineage is well documented.

[d] The computer programs employed by M. Goodman and his colleagues through 1982 (e.g., Goodman *et al.,* 1982) performed local branch swapping. Improved algorithms since 1990 (e.g., those employed by Czelusniak *et al.,* 1990; Schneider *et al.,* 1993; Stanhope *et al.,* 1993) are designed to perform global branch swapping, similar to that in PAUP (Swofford, 1993).

[e] Bootstrap values, or the confidence limits of a tree (Felsenstein, 1985) have been usually presented with morphological but also with molecular data when employing PAUP program of Swofford (1993). Consistency index (CI, a measure "of how well a tree describes a data set," or "how well the data fits a tree"; Forey *et al.,* 1992, p. 74) values are usually presented with morphological data. Molecular studies (e.g., Czelusniak *et al.,* 1990, pp. 560–561; Schneider *et al.,* 1993, p. 15; and Goodman *et al.,* 1994, p. 14) provided "strength of groupings" as numbers at nodes on their trees/cladograms. These numbers at each node are the number of extra steps required to break up that node, and may be compared to bootstraps values.

Overall, it appears that congruency between molecular and morphological results for primate intraordinal relationships is a general rule (minor differences in branching pattern include the position of *Aotus* within Cebidae). It has taken about 100 years, since the days of Nuttall (1901, 1904), for morphologists and molecular biologists to generate sufficient bodies of data on hominid relationships for us to realize that these are generally congruent. Disagreements are minor and are usually with regard to the precise relationships and classifications of hominid taxa. After all, there is only one true phylogeny—see quote from McKenna (1987) at the beginning of this paper.

APPENDIX 1: A CLASSIFICATION OF PRIMATES, EXTINCT AND EXTANT

Provisional classification of Order Primates and primate-like fossil taxa. Extant taxa are indicated in bold print. Primary references include author, date of publication, and page number on which taxon was initially described. Synonymies provide subjugated taxa only. Synonymies of fossil taxa recognized before 1979 are based primarily on Szalay and Delson (1979), while extant taxa synonymies primarily relied on Groves (1993) and Szalay and Delson (1979). Classification of New World Primates generally follows that of Rosenberger *et al.* (1990) and Rosenberger (1992) with alterations after Kay (1990) and Kay and Meldrum (in press). The primate classification of McKenna *et al.* (1995) was consulted extensively. This classification recognizes 218 fossil genera including approximately 405 species and 61 extant genera including approximately 238 species, plus 14 reinstated or newly described species, bringing the total to 252 (C.P.G.). References published before 1979 can be found in Szalay and Delson (1979); more recent literature is cited in the bibliography of this paper. Age ranges are provided for families (E, early; M, middle; L, late).

Ordinal status uncertain
     Family uncertain [E. through L. Paleocene]
        Decoredon Xu, 1977, p. 119
        Altiatlasius Sigé *et al.,* 1990, p. 49
Order Primates? (includes Order Proprimates Gingerich, 1989, and Mirorder Primatomorpha Beard, 1991 [in part])
     Suborder uncertain
        Family Eosimiidae Beard *et al.,* 1994, p. 607 [M. Eocene]
            Eosimias Beard *et al.,* 1994, p. 608; (Beard (1995) has argued, based on new dental evidence, that *Eosimias* should be included within Primates, specifically Anthropoidea)
        Family Purgatoriidae Van Valen and Sloan, 1965, p. 743 (E. Paleocene)
            Purgatorius Van Valen and Sloan, 1965, p. 743
Suborder Plesiadapiformes Simons and Tattersall, 1972, p. 284 (includes Paromomyiformes Szalay, 1973)

Superfamily Microsyopoidea Osborn and Wortman, 1892, p. 101

    Family Palaechthonidae Szalay, 1969, p. 315 (M. through L. Paleocene)

        Palaechthon Gidley, 1923, p. 6

        Plesiolestes Jepsen, 1930, p. 505 (includes *Talpohenach* Kay and Cartmill, 1977)

        Palenochtha Simpson, 1935, p. 231

        Torrejonia Gazin, 1968, p. 632 (includes *Plesiolestes:* Szalay, 1973 [in part]; *Plesiolestes:* Szalay and Delson, 1979 [in part])

        Premnoides Gunnell, 1986, p. 77, and 1989, p. 16

        Anasazia Van Valen, 1994, p. 20

    Family Microsyopidae Osborn and Wortman, 1892, p. 101 (L. Paleocene through M. Eocene)

        Microsyops Leidy, 1872, p. 363 (includes *Bathrodon* Marsh, 1872; *Mesacodon* Marsh, 1872; *Palaeacodon* Marsh, 1872; *Cynodontomys* Cope, 1882)

        Uintasorex Matthew, 1909, p. 545

        Navajovius Matthew and Granger, 1921, p. 5

        Craesops Stock, 1934, p. 349

        Niptomomys McKenna, 1960, p. 63

        Berruvius Russell, 1964, p. 124 (includes *Navajovius:* Szalay, 1972 [in part])

        Alveojunctus Brown, 1982, p. A47

        Arctodontomys Gunnell, 1985, p. 52 (includes *Pantolestes:* Cope, 1882 [in part]; *Cynodontomys:* Matthew, 1915 [in part]; *Diacodexis:* Gazin, 1952 [in part]; *Microsyops:* Szalay, 1969 [in part])

        Megadelphus Gunnell, 1989, p. 110 (includes *Cynodontomys:* White, 1952; *Microsyops:* Robinson, 1966; *Microsyops:* McKenna, 1966 [in part]; *Microsyops:* Szalay, 1969 [in part])

        Avenius Russell *et al.,* 1992, p. 244

Superfamily Plesiadapoidea Trouessart, 1897, p. 75

    Family Picrodontidae Simpson, 1937, p. 134 (M. through L. Paleocene)

        Picrodus Douglass, 1908, p. 17 (includes *Megopterna* Douglass, 1908)

        Zanycteris Matthew, 1917, p. 569 (includes *Palaeonycteris* Weber and Abel, 1928)

        Draconodus Tomida, 1982, p. 38

    Family Plesiadapidae Trouessart, 1897, p. 75 (includes Platychoeropidae Lydekker, 1887; Chiromyidae Teilhard de Chardin, 1922) [M. Paleocene through E. Eocene]

        Platychoerops Charlesworth, 1855, p. 80 (includes *Miolophus* Owen, 1865)

        Plesiadapis Gervais, 1877, p. 76 (includes [*Tricuspidens*] Lemoine, 1887; *Sciurus:* Launay, 1908 [in part]; *Nothodectes* Matthew, 1915; *Tetonius:* Gidley, 1923; *Sciuroides:* Piton, 1940; *Menatotherium* Piton, 1940; [*Ancepsoides*] Russell, 1964)

        Chiromyoides Stehlin, 1916, p. 1489

        Pronothodectes Gidley, 1923, p. 12

        Nannodectes Gingerich, 1975, p. 138

        Pandemonium Van Valen, 1994, p. 5

    Family Carpolestidae Simpson, 1935, p. 9 (M. Paleocene through E. Eocene)

        Carpodaptes Matthew and Granger, 1921, p. 6

        Elphidotarsius Gidley, 1923, p. 10

        Carpolestes Simpson, 1928, p. 7 (includes *Litotherium* Simpson, 1929)

        Chronolestes Beard and Wang, 1995, p. 3

        Carpocristes Beard and Wang, 1995, p. 14

    Family Saxonellidae Russell, 1964, p. 128 (L. Paleocene)

        Saxonella Russell, 1964, p. 128

Superfamily Paromomyoidea Simpson, 1940, p. 198 (includes most taxa assigned to Infraorder Eudermoptera Beard, 1993)

    Family Paromomyidae Simpson, 1940, p. 198 (M. Paleocene through M. Eocene)

        Phenacolemur Matthew, 1915, p. 479

        Ignacius Matthew and Granger, 1921, p. 5

        Paromomys Gidley, 1923, p. 3

        Elwynella Rose and Bown, 1982, p. 67

        Arcius Godinot, 1984a, p. 85

        Simpsonlemur Robinson and Ivy, 1994, p. 100

        Dillerlemur Robinson and Ivy, 1994, p. 103

        Pulverflumen Robinson and Ivy, 1994, p. 104

Suborder Micromomyiformes Beard, 1993, p. 145

    Family Micromomyidae Szalay, 1974, p. 243 (L. Paleocene through E. Eocene)

        Micromomys Szalay, 1973, p. 76

        Tinimomys Szalay, 1974, p. 244

        Chalicomomys Beard and Houde, 1989, p. 389 (includes *Micromomys:* Rose and Brown, 1982 [in part]; *Micromomys:* Fox, 1984 [in part]; *Micromomys:* Gunnell, 1989 [in part])

        Myrmekomomys Robinson, 1994, p. 86

    New Family (based on two genera) Rose and Bown (in press)

Order Primates Linnaeus, 1758, p. 20

    Suborder Prosimii Illiger, 1811, p. 72 (includes Prosimiae Haeckel, 1866) [or Suborder Strepsirhini É. Geoffroy Saint-Hilaire, 1812 if *Tarsius* is excluded; thus strepsirhines = tooth-combed prosimians, aye-ayes, and adapiforms; alternatively, adapiforms may form monophyletic clade with anthropoids = Neopithecini Wortman, 1903, with strepsirhines consisting only of extant tooth-combed prosimians and aye-ayes]

      Infraorder Adapiformes Szalay and Delson, 1979, p. 105

      Family Notharctidae Trouessart, 1879, p. 230 (E. Eocene through E. Miocene)

        Subfamily Notharctinae Trouessart, 1879, p. 230

          Notharctus Leidy, 1870, p. 114 (includes *Hipposyus* Leidy, 1872; *Thinolestes* Marsh, 1872; *Telmatolestes* Marsh, 1872; *Limnotherium* Marsh, 1872; *Tomitherium* Cope, 1877 [in part]; *Prosinopa* Trouessart, 1897)

          Pelycodus Cope, 1875, p. 13

          Smilodectes Wortman, 1903, p. 212 (includes *Aphanolemur* Granger and Gregory, 1917)

          Cantius Simons, 1962, p. 5 (includes *Tomitherium* Cope, 1877 [in part]; *Protoadapis:* Cooper, 1932)

          Copelemur Gingerich and Simons, 1977, p. 266 (includes *Tomitherium* Cope, 1877 [in part])

          Hesperolemur Gunnell, 1995a, p. 449

        Subfamily Notharctinae?

          Pondaungia Pilgrim, 1927, p. 12

        Subfamily Cercamoniinae Gingerich, 1975, p. 164

          Caenopithecus Rütimeyer, 1862, p. 88

          Protoadapis Lemoine, 1878, p. 101 (based on *Plesiadapis curvicuspidens* Lemoine, 1878)

          Pronycticebus Grandidier, 1904, p. 9

          Anchomomys Stehlin, 1916, p. 1406 (includes *Laurasia* Schwartz and Tattersall, 1983)

          Periconodon Stehlin, 1916, p. 1428 (includes *Fendantia* Schwartz and Tattersall, 1983; *Hallelemur* Schwartz *et al.,* 1983 [both *Fendantia* and *Hallelemur* are considered valid genera by McKenna *et al.,* 1995])

          Europolemur Wiegelt, 1933, p. 123 (includes *Megatarsius* Wiegelt, 1933; *Alsatia* Tattersall and Schwartz, 1983)

          Agerinia Crusafont-Pairo and Golpe-Posse, 1973, p. 852 (= *Agerina:* Crusafont-Pairo, 1967 which was preoccupied by *Agerina* Leach, 1814)

Huerzeleris Szalay, 1974, p. 125

Cercamonius Gingerich, 1975, p. 164

Donrussellia Szalay, 1976, p. 355 (includes *Teilhardina?:* Russell *et al.,* 1967)

Mahgarita Wilson and Szalay, 1977, p. 643 (not *Magarita* Leach, 1814)

Buxella Godinot, 1988, p. 391

Djebelemur Hartenberger and Marandat, 1992, p. 9

Barnesia Thalmann, 1994, p. 60

Aframonius Simons *et al.,* 1995, p. 578

Subfamily Sivaladapinae Thomas and Verma, 1979, p. 833

Indraloris Lewis, 1933, p. 135 (includes *Sivanasua* Pilgrim, 1932 [in part])

Sivaladapis Gingerich and Sahni, 1979, p. 415 (includes *Sivanasua* (Pilgrim, 1932 [in part]; *Indoadapis* Chopra and Vasishat, 1980)

Sinoadapis Wu and Pan, 1985, p. 2

Subfamily Hoanghoniinae Gingerich *et al.,* 1994, p. 166

Hoanghonius Zdansky, 1930, p. 75

Rencunius Gingerich *et al.,* 1994, p. 166 (includes *Hoanghonius:* Woo and Chow, 1957)

Wailekia Ducrocq *et al.,* 1995, p. 478

Family Adapidae Trouessart, 1879, p. 225 (M. Eocene through M. Oligocene)

Subfamily Adapinae Trouessart, 1879, p. 226

Adapis Cuvier, 1821, p. 265 (includes *Aphelotherium* Gervais, 1859; *Palaeolemur* Delfortrie, 1873; *Microadapis* Szalay, 1974; *Simonsia* Schwartz and Tattersall, 1982); *Chasselasia* Schwartz and Tattersall, 1982 [*Microadapis, Simonsia,* and *Chasselasia* are consider valid genera by McKenna *et al.,* 1995])

Leptadapis Gervais, 1876, p. 35 (includes *Paradapis* Tattersall and Schwartz, 1983; *?Arisella* Crusafont-Pairo, 1967 [*nomen nudum*])

Cryptadapis Godinot, 1984b, p. 1291

Adapoides Beard *et al.,* 1994, p. 605

Infraorder Adapiformes *incertae sedis*

Family unknown (M. through L. Eocene)

Subfamily unknown

Lushius Chow, 1961, p. 1

Azibius Sudre, 1975, p. 1539

Panobius Russell and Gingerich, 1987, p. 209

Infraorder Lemuriformes Gregory, 1915, p. 432 (includes Indriiformes Tattersall and Schwartz, 1974) [Tattersall (personal communication, 1995) suggested that Lemuriformes be a sister group to Indriiformes, which would include Daubentonioidea and Indrioidea as sister taxa, with Indrioidea including Indridae and Archaeolemuridae]

Superfamily Lemuroidea Mivart, 1864, p. 637

Family Cheirogaleidae Gray, 1873, p. 849 (Recent)

Subfamily Cheirogaleinae Gray, 1873, p. 849

Cheirogaleus E. Geoffroy Saint-Hilaire, 1812, p. 172 (includes *Myspithecus* Cuvier, 1833; *Cebugale* Lesson, 1840; *Myscebus* Lesson, 1840; *Myocebus* Wagner, 1841; *Myslemur* Blainville, 1846 [in part]; *Opolemur* Gray, 1872; *Chirogale* Forsyth-Major, 1894 [in part])

Microcebus É. Geoffroy Saint-Hilaire, 1834, p. 24 (includes *Scartes* Swainson, 1835; *Gliscebus* Lesson, 1840; *Mirza* Gray, 1870; *Azema* Gray, 1870; *Muirlemur* Gray, 1870)

Allocebus Petter-Rousseaux and Petter, 1967, p. 574 (includes *Chirogaleus:* Gunther, 1875; *Chirogale* Forsyth-Major, 1894 [in part])

Subfamily Phanerinae Rumpler, 1974, p. 867

Phaner Gray, 1870, p. 135 (includes *Lemur:* Blainville, 1839)

Family Lemuridae Gray, 1821, p. 296 (includes Lemurinae Mivart, 1864; Lepilemurina Gray, 1870 [in part]; Nesopithecidae Forsyth-Major, 1893) [Subrecent to Recent]

Lemur Linnaeus, 1758, p. 24 (includes *Prosimia* Brisson, 1762; *Procebus* Storr, 1780; *Catta* Link, 1806; *Maki* Muirhead, 1819; *Mococo* Trouessart, 1878)

Hapalemur I. Geoffroy Saint-Hilaire, 1851, p. 341 (includes *Myoxicebus* Lesson, 1840; *Prolemur* Gray, 1871; *Prohapalemur* Lamberton, 1936)

Varecia Gray, 1863, p. 135

Pachylemur (Lamberton, 1948, p. 1)

Eulemur Simons and Rumpler, 1988, p. 547 (includes *Lemur* Linnaeus, 1758 [in part]; *Petterus* Groves and Eaglen, 1988 [*Petterus* is a valid genus according to McKenna *et al.,* 1995])

Family Megaladapidae Flower and Lydekker, 1891, p. 6 (includes Lepilemurina Gray, 1870 [in part]) [Subrecent to Recent]

Lepilemur I. Geoffroy Saint-Hilaire, 1851, p. 75 (includes *Galeocebus* Wagner, 1855; *Lepidolemur* Peters, 1874; *Mixocebus* Peters, 1874)

Megaladapis Forsyth-Major, 1894, p. 178 (verbally reported to Royal Society in June of 1893) [includes *Peloriadapis* Grandidier, 1899; *Palaeolemur* Lorenz, 1900; *Mesoadapis* Lorenz, 1900; *Megalindris* Standing, 1908]

Family Indridae Burnett, 1828, p. 306 [following Jenkins, 1987] (includes Indrisina I. Geoffroy Saint-Hilaire, 1851; Indrisidae Alston, 1878) [Subrecent to Recent]

Subfamily Indrinae Burnett, 1828, p. 306 [following Jenkins, 1987]

Indri É. Geoffroy Saint-Hilaire and Cuvier, 1796, p. 46 (includes *Indris* Cuvier, 1800; *Lichanotus* Illiger, 1811; *Indrium* Rafinesque, 1815; *Sylvanus* Oken, 1816; *Pithelemur* Lesson, 1840)

Propithecus Bennett, 1832, p. 20 (includes *Macromerus* Smith, 1833)

Avahi Jourdan, 1834, p. 231 (includes *Microrhynchus* Jourdan, 1834; *Habrocebus* Wagner, 1840; *Semnocebus* Lesson, 1840; *Iropocus* Gloger, 1841)

Subfamily Archaeolemurinae Standing, 1908, p. 97 (includes Nesopithecidae Forsyth-Major, 1896; Archaeolemurinae Grandidier, 1905; Hadropithecinae Abel, 1931)

Archaeolemur Filhol, 1895, p. 13 (includes *Lophiolemur* Filhol, 1895; *Nesopithecus* Forsyth-Major, 1896; *Globilemur* Forsyth-Major, 1897; *Bradylemur:* Grandidier, 1899; *Protoindris* Lorenz von Liburnau, 1900)

Hadropithecus Lorenz von Liburnau, 1899, p. 255 (includes *Pithecodon* Lorenz von Liburnau, 1900)

Subfamily Palaeopropithecinae Tattersall, 1973, p. 98

Palaeopropithecus Grandidier, 1899, p. 345 (includes *Bradytherium* Grandidier, 1901)

Mesopropithecus Standing, 1905, p. 95 (includes *Neopropithecus* Lamberton, 1936)

Archaeoindris Standing, 1908, p. 9 (includes *Lemuridotherium* Standing, 1910)

Babakotia Godfrey *et al.,* 1990, p. 83

Family Daubentoniidae Gray, 1863, p. 151 (includes Cheiromydae Gray, 1821; Daubentoniadae Gray, 1863; Daubentonioidea Gill, 1872) [Recent]

Daubentonia É. Geoffroy Saint-Hilaire, 1795, p. 195 (includes *Scolecophagus* É. Geoffroy Saint-Hilaire, 1795; *Aye-Aye* Lacépède, 1799; *Cheiromys* Cuvier, 1800; *Chiromys* Illiger, 1811; *Psilodactylus* Owen, 1816; *Myspithecus:* Blainville, 1839; *Myslemur* Blainville, 1846 [in part])

Infraorder Lorisoformes Gregory, 1915, p. 435

Superfamily Lorisoidea Gray, 1821, p. 298

Family Lorisidae Gray, 1821, p. 150 [following article 23(b) of the International Code of Zoological Nomenclature (ICZN); see Jenkins, 1987 for alternative spelling; petition submitted to ICZN by Schwartz *et al.*] (includes Lo-

ridae Gray, 1821; Nycticebinae Mivart, 1864; Nycticebi-
dae Nicholson, 1870) [E. Miocene to Recent]

Loris É. Geoffroy Saint-Hilaire, 1796, p. 48 (includes
Tardigradus Boddaert, 1784; *Lori* Lacépède, 1799;
Stenops Illiger, 1811; *Loridium* Rafinesque, 1840)

Nycticebus É. Geoffroy Saint-Hilaire, 1812, p. 163 (in-
cludes *Bradycebus* Gervais, 1836; *Stenops:* Van der
Hoeven, 1834; *Bradylemur* Blainville, 1839)

Perodicticus Bennett, 1831, p. 109 (includes *Potto* Les-
son, 1840)

Arctocebus Gray, 1863, p. 150

Mioeuoticus Leakey, 1962, p. 6

Nycticeboides Jacobs, 1981, p. 585

Family Galagidae Mivart, 1864, p. 645 [petition submitted
to the ICZN by Schwartz *et al.*] (includes Galagonina
Gray, 1825; Galaginae: Mivart, 1864; Galaginidae Al-
ston, 1878) [E. Miocene to Recent]

Galago É. Geoffroy Saint-Hilaire, 1796, p. 49 (includes
Chirosciurus Cuvier and Geoffroy Saint-Hilaire, 1795;
Macropus Fischer, 1811; *Otolicnus* Illiger, 1811; *Callo-
tus* Gray, 1863)

Galagoides Smith, 1833, p. 32 (includes *Mioxicebus*
Lesson, 1840; *Otolicnus:* Temminck, 1853; *Hemiga-
lago* Dahlbohm, 1857)

Otolemur Coquerel, 1859, p. 458

Euoticus Gray, 1863, p. 140 (includes *Otogale* Gray,
1863)

Progalago MacInnes, 1943, p. 145

Komba Simpson, 1967, p. 49

Superfamily Plesiopithecoidea Simons and Rasmussen,
1994a, p. 9946

Family Plesiopithecidae Simons and Rasmussen, 1994a,
p. 9946 [L. Eocene]

Plesiopithecus Simons, 1992a, p. 10744

Suborder Tarsiiformes Gregory, 1915, p. 437 (includes Paleopi-
thecini Wortman, 1903 [in part]) [The exact phylogenetic re-
lationships of *Tarsius* remain unclear. Fossil evidence sug-
gests that *Tarsius* shares common ancestry with certain
omomyiforms and should be included with these taxa in the
suborder Prosimii. Molecular evidence and comparative anat-
omy based solely on *Tarsius* and other extant taxa suggests
that *Tarsius* may share common ancestry with anthropoids
and thus should be included in the suborder Haplorhini con-
sisting of *Tarsius* and anthropoids. However, the primitive
dentition and relatively primitive neural organization of liv-
ing *Tarsius* suggest a closer relationship with extant lemuri-
forms and lorisiforms. There is, as yet, little convincing evi-
dence that omomyiforms should be considered haplorhines.
As such, this classification recognizes Tarsiiformes as a dis-
tinct suborder from Prosimii and Anthropoidea pending reso-
lution of the "*Tarsius* problem," but two of us (E.L.S. and
G.F.G.) believe that omomyiforms and tarsiiforms should be
ranked in the suborder Prosimii.]

Family Tarsiidae Gray, 1825, p. 338 (includes Tarsina Gray,
1925; Tarsidae Burnett, 1828) [Recent]

Tarsius Storr, 1780, p. 33 (includes *Macrotarsus* Link,
1795; *Rabienus* Gray, 1821; *Cephalophacus* Swainson,
1835; *Hypsicebus* Lesson, 1840)

Suborder Tarsiiformes *incertae sedis*

Afrotarsius Simons and Bown, 1985, p. 476 [M. Oligo-
cene]

Tarsius? (the genus *Tarsius* has been reported from the
middle Eocene of China by Beard *et al.,* 1994 and
Beard, 1995 and from the early Miocene of Thailand
by Ginsburg and Mein, 1987)

Infraorder Omomyiformes Trouessart, 1879, p. 225 (includes
Tarsiiformes Gregory, 1915 [in part]; Paleopithecini Wort-
man, 1903 [in part])

Family Omomyidae Trouessart, 1879, p. 225 (includes Omo-
mynae Trouessart, 1879; Anaptomorphidae Cope, 1883;

Omomyinae: Wortman, 1904; Tetoniidae Abel, 1931;
Teilhardinidae Quinet, 1964) [E. Eocene through E. Mio-
cene]

Subfamily Microchoerinae Lydekker, 1887, p. 303 (in-
cludes Microchoeridae Lydekker, 1887; Necrolemuri-
nae Simpson, 1940; Pseudolorisinae Simpson, 1940)

Microchoerus Wood, 1844, p. 350 (formally proposed in
Wood, 1846, p. 5) (includes *Microchaerus* Forbes, 1894)

Necrolemur Filhol, 1873, p. 1112

Nannopithex Stehlin, 1916, p. 1392 (includes *Necro-
lemur:* Chantre and Gaillard, 1897; *Pseudoloris:*
Weigelt, 1933)

Pseudoloris Stehlin, 1916, p. 1397 (includes *Pivetonia*
Crusafont-Pairo, 1967)

Subfamily Anaptomorphinae Cope, 1883, p. 80 (includes
Anaptomorphidae Cope, 1883); Tetoniidae Abel, 1931;
Teilhardinidae Quinet, 1964)

Anaptomorphus Cope, 1872, p. 554 (includes *Euryaco-
don:* Wortman, 1903)

Trogolemur Matthew, 1909, p. 546

Tetonius Matthew, 1915, p. 457 (includes *Paratetonius*
Seton, 1940)

Absarokius Matthew, 1915, p. 463

Teilhardina Simpson, 1940, p. 190 (includes *Protomo-
mys* Teilhard de Chardin, 1927)

Anemorhysis Gazin, 1958, p. 25 (includes *Uintalacus*
Gazin, 1958); *Tetonoides* Gazin, 1962 [in part])

Chlororhysis Gazin, 1958, p. 27

Tetonoides Gazin, 1962, p. 34

Pseudotetonius Bown, 1974, p. 20 (includes *Mckenna-
morphus* Szalay, 1976)

Arapahovius Savage and Waters, 1978, p. 3

Aycrossia Bown, 1979, p. 50

Strigorhysis Bown, 1979, p. 60

Gazinius Bown, 1979, p. 67

Steinius Bown and Rose, 1984, p. 98 (includes *Omo-
mys?:* Matthew, 1915; *Loveina?:* Simpson, 1940; *Uin-
tanius:* Szalay and Delson, 1979 [in part])

Tatmanius Bown and Rose, 1991, p. 467

Sphacorhysis Gunnell, 1995b, p. 157

Subfamily Omomyinae Trouessart, 1879, p. 225 (includes
Omomynae Trouessart, 1879; Omomyidae: Gazin,
1958; Mytoniinae Robinson, 1968)

Omomys Leidy, 1869, p. 63 (includes *Euryacodon*
Marsh, 1872; *Palaeacodon* Marsh, 1872)

Hemiacodon Marsh, 1872, p. 212 (includes *Omomys:* Os-
born, 1902)

Washakius Leidy, 1873, p. 123 (includes *Yumanius*
Stock, 1938; *Shoshonius?:* Simpson, 1959)

Shoshonius Granger, 1910, p. 249

Uintanius Matthew, 1915, p. 455 (includes *Huerfanius*
Robinson, 1966)

Chumashius Stock, 1933, p. 954

Dyseolemur Stock, 1934, p. 150

Loveina Simpson, 1940, p. 188 (includes *Tetonius:* Se-
ton, 1940)

Macrotarsius Clark, 1941, p. 562 (includes *Hemiacodon:*
Robinson, 1968)

Ourayia Gazin, 1958, p. 70 (includes *Microsyops:* Os-
born, 1895; *Mytonius* Robinson, 1966)

Utahia Gazin, 1958, p. 66 (includes *Omomys:* Gazin,
1962)

Stockia Gazin, 1958, p. 68

Ekgmowechashala Macdonald, 1963, p. 171

Rooneyia Wilson, 1966, p. 228

Jemezius Beard, 1987, p. 458

Yaquius Mason, 1990, p. 2

Asiomomys Wang and Li, 1990, p. 179

Wyomomys Gunnell, 1995b, p. 172

Ageitodendron Gunnell, 1995b, p. 175

Family Omomyidae *incertae sedis* [M. Eocene]
    Kohatius Russell and Gingerich, 1980, p. 621
Family Omomyidae? [E. Eocene]
    Altanius Dashzeveg and McKenna, 1977, p. 126
Suborder Anthropoidea Mivart, 1864, p. 635 (or Suborder Haplorhini Pocock, 1918 if *Tarsius* is included) [Includes Suborder Simiiformes Hoffstetter, 1974; Anthropoidea, excluding *Tarsius,* may form a monophyletic group with Adapiformes = Neopithicini Wortman, 1903 with Tarsiiformes being the sister group to that clade]
  Infraorder uncertain
  Superfamily Parapithecoidea Schlosser, 1911, p. 58 (= Paracatarrhini Delson, 1977)
  Family Parapithecidae Schlosser, 1911, p. 58 (*sensu* Kay and Williams, 1994; see also Fleagle and Kay, 1987 [L. Eocene through M. Oligocene]
    Subfamily Parapithecinae Schlosser, 1911, p. 58
      Apidium Osborn, 1908, p. 271
      Parapithecus Schlosser, 1910, p. 507
      Simonsius Gingerich, 1978, p. 88 (ELS believes *Simonsius* to be a junior synonym of *Parapithecus*)
    Subfamily Qatraniinae Kay and Williams, 1994, p. 383
      Qatrania Simons and Kay, 1983, p. 624
      Serapia Simons, 1992a, p. 10743
      Arsinoea Simons, 1992a, p. 10744
  Superfamily uncertain
  Family uncertain [L. Eocene through E. Oligocene]
    Amphipithecus Colbert, 1937, p. 1
    Biretia De Bonis *et al.,* 1988, p. 929 (considered a possible qatraniine by Kay and Williams, 1994, p. 410)
    Proteopithecus Simons, 1989, p. 9957
    Algeripithecus Godinot and Mahboubi, 1992, p. 324
    Omanodon Gheerbrant *et al.,* 1993, p. 145
    Shizarodon Gheerbrant *et al.,* 1993, p. 182
    Tabelia Godinot and Mahboubi, 1994, p. 360
  Infraorder Platyrrhini É. Geoffroy Saint-Hilaire, 1812, p. 104 (includes Quadrumana Illiger, 1811 [in part]; Platyrrhina Hemprich, 1820; Platyonychae Gray, 1821 [in part]; Gampstonychae Gray, 1821; Simiae Burmeister, 1854; Simiadae Jardine, 1866; Platyrrhinae Weidenreich, 1943)
  Superfamily Ateloidea Gray, 1825, p. 338 (following Rosenberger *et al.,* 1990 and Rosenberger, 1992)
  Family Atelidae Gray, 1825, p. 338 (includes Atelina Gray, 1825; Lagotrichina Gray, 1870; Lagotrichinae Cabrera, 1900) [E. Miocene to Recent]
    Subfamily Atelinae Gray, 1825, p. 338 (includes Atelina Gray, 1825; Lagotrichina Gray, 1870; Lagothrichinae Cabrera, 1900)
      Alouatta Lacépède, 1799, p. 4 (includes *Mycetes* Illiger, 1811; *Stentor* É. Geoffroy Saint-Hilaire, 1811 [in Humboldt])
      Ateles É.Geoffroy Saint-Hilaire, 1806, p. 262 (includes *Sapajou* Lacépède, 1799; *Paniscus* Rafinesque, 1815; *Montaneia* Ameghino, 1911; *Ameranthropoides* Montandon, 1929)
      Lagothrix É. Geoffroy Saint-Hilaire, 1812, p. 356 (includes *Gastrimargus* Spix, 1823; *Oreonax* Thomas, 1927)
      Brachyteles Spix, 1823, p. 36 (includes *Eriodes* I. Geoffrey Saint-Hilaire, 1829)
      Protopithecus Lund, 1838, p. 14
      Stirtonia Hershkovitz, 1970, p. 6 (includes *Kondous* Setoguchi, 1985)
      Paralouatta Rivero and Arredondo, 1991, p. 1
    Subfamily Pitheciinae Mivart, 1865, p. 547
      Pithecia Desmarest, 1804, p. 8 (includes *Yarkea* Lesson, 1840)
      Chiropotes Lesson, 1840, p. 178
      Cacajao Lesson, 1840, p. 181

      Callicebus Thomas, 1903, p. 457
      Cebupithecia Stirton and Savage, 1951, p. 350
      Xenothrix Williams and Koopman, 1952, p. 12
      Tremacebus Hershkovitz, 1974, p. 3
      Mohanamico Luchterhand *et al.,* 1986, p. 1754 (After Kay, 1990)
  Family Cebidae Bonaparte, 1831, p. 6 (includes Callitrichidae Thomas, 1903; Callimiconidae Thomas, 1903; Saimirinae Miller, 1924) [L. Oligocene to Recent]
    Subfamily Cebinae Bonaparte, 1831, p. 6 (includes Crysotrichinae Cabrera, 1900)
      Cebus Erxleben, 1777, p. 44 (includes *Pseudocebus* Reichenbach, 1862; *Calyptrocebus* Reichenbach, 1862; *Otocebus* Reichenbach, 1862; *Eucebus* Reichenbach, 1862)
      Saimiri Voigt, 1831, p. 95 (includes *Chrysothrix* Kamp, 1835; *Pithesciurus* Lesson, 1840)
      Neosaimiri Stirton, 1951, p. 326 (includes *Laventiana* Rosenberger *et al.,* 1991a [*Laventiana* is considered a valid genus by Rosenberger, 1992a and McKenna *et al.,* 1995] and may include *Micodon* Setoguchi and Rosenberger, 1985 [considered *nomen dubium* by Kay and Meldrum, in press])
    Subfamily Callitrichinae Gray, 1821, p. 298 (includes Arctopitheci É. Geoffroy Saint-Hilaire, 1812; Gampstonychae Gray, 1821; Harpaladae Gray, 1821; Hapalidae Gray, 1821; Platyonychae Gray, 1821; Trichuri Spix, 1823; Callitricina Gray, 1825; Harpalina Gray, 1825; Sariguidae Gray, 1825; Ouistidae Burnett, 1828; Ouistitidae Burnett, 1828; Titidae Burnett, 1828; Hapalina Bonaparte, 1838; Hapalidae: Wagner, 1840; Hapalineae Lesson, 1840; Arctopithecina Gravenhorst, 1843; Jacchina Gray, 1849; Arctopithecae Dahlbohm, 1856; Mididae Gill, 1872; Arctopithecini Huxley, 1872; Hapalini Winge, 1895; Callitrichidae: Thomas, 1903; Leontocebinae Hill, 1959)
      Callithrix Erxleben, 1777, p. 55 (includes *Hapale* Illiger, 1811; *Sylvanus* Rafinesque, 1815; *Arctopithecus* Virey, 1819; *Ouistitis* Burnett, 1826; *Midas:* É. Geoffroy Saint-Hilaire, 1828; *Liocephalus* Wagner, 1840; *Mico* Lesson, 1840; *Micoella* Gray, 1870)
      Saguinus Hoffmannsegg, 1807, p. 101 (includes *Marikina* Lesson, 1840; *Oedipomidas* Reichenbach, 1862; *Tamarin* Gray, 1870; *Hapanella* Gray, 1870; *Seniocebus* Gray, 1870; *Tamarinus* Trouessart, 1899)
      Leontopithecus Lesson, 1840, p. 184 (includes *Midas* É. Geoffroy Saint-Hilaire, 1812; *Leontocebus* Wagner, 1840; *Marikina:* Reichenbach, 1862; *Leontideus* Cabrera, 1956)
      Cebuella Gray, 1866, p. 734
      Callimico Miranda-Ribiero, 1912, p. 21
      Lagonimico Kay, 1994, p. 334
      Patasola Kay and Meldrum, in press
    Subfamily Aotinae Elliot, 1913, Vol. 1, p. xxiv, xliii, liii (Authorship after Simpson, 1945, p. 64)
      Aotus Illiger, 1811, p. 71 [based on Humboldt, 1811 (Placement within Cebidae is after Harada *et al.,* 1995; see, however, Rosenberger *et al.,* 1990, and Kay, 1990)] (includes *Nyctipithecus* Spix, 1823)
    Subfamily Branisellinae Hershkovitz, 1977, p. 10
      Branisella Hoffstetter, 1969, p. 434 (includes *Szalatavus* Rosenberger *et al.,* 1991b)
  Family uncertain [E. Miocene]
    Homunculus Ameghino, 1891, p. 290 (includes *?Anthropops* Ameghino, 1891)
    Dolichocebus Kraglievich, 1951, p. 57 (Placement after Fleagle and Kay, 1989 and Fleagle *et al.* [in press])
    Soriacebus Fleagle *et al.,* 1987, p. 66
    Carlocebus Fleagle, 1990, p. 67

Antillothrix MacPhee *et al.,* 1995, p. 3

Chilecebus Flynn *et al.,* 1995, p. 603

Infraorder Catarrhini É. Geoffroy Saint-Hilaire, 1812, p. 86 (includes Catarrhina Hemprich, 1820; Eucatarrhini Delson, 1977)

Superfamily uncertain

Family Propliopithecidae Straus, 1961, p. 761 [L. Eocene through M. Oligocene]

Subfamily Propliopithecinae Straus, 1961, p. 761

Propliopithecus Schlosser, 1910, p. 507 (includes *Moeripithecus* Schlosser, 1910; *Aeolopithecus* Simons, 1965)

Aegyptopithecus Simons, 1965, p. 135

Subfamily Oligopithecinae Simons, 1989, p. 9956 (treated as a family by Kay and Williams, 1994)

Oligopithecus Simons, 1962, p. 2

Catopithecus Simons, 1989, p. 9957

Superfamily Cercopithecoidea Gray, 1821, p. 297 (includes Cercopithecidae Gray, 1821; Menocerca Haeckel, 1866; Cynomorpha Huxley, 1872; Hominidae: Hürzeler, 1958 [in part])

Family Victoriapithecidae G.H.R. Von Koenigswald, 1969, p. 41 [E. Miocene]

Prohylobates Fourtau, 1918, p. 93

Victoriapithecus G.H.R. Von Koenigswald, 1969, p. 41

Family Cercopithecidae Gray, 1821, p. 297 (includes Cynopithecina I. Geoffroy Saint-Hilaire, 1843; Lasiopygidae Elliot, 1913) [E. Miocene to Recent]

Subfamily Cercopithecinae Gray, 1821, p. 297 (includes Cynocephalina Gray, 1825; Macacidae Owen, 1843; Cynopithecinae Mivart, 1843)

Cercopithecus Linnaeus, 1758, p. 26 (includes *Lasiopyga* Illiger, 1811; "*Monichus*" Oken, 1816; *Cebus:* Rafinesque, 1815; *Cercocephalus* Temminck, 1853; *Callithrix:* Reichenbach, 1862; *Petaurista:* Reichenbach, 1862; *Diademia* Reichenbach, 1862; *Mona* Reichenbach, 1862; *Diana:* Trouessart, 1878; *Rhinostictus* Trouessart, 1897; *Otopithecus* Trouessart, 1897; *Pogonocebus* Trouessart, 1897; *Allochrocebus* Elliot, 1913; *Insignicebus* Elliot, 1913; *Melanocebus* Elliot, 1913; *Neocebus* Elliot, 1913; *Neopithecus* Elliot, 1913; *Rhinostigma* Elliot, 1913)

Papio Erxleben, 1777, p. 15 (includes *Simia* [*Papio*] Müller, 1773; *Cynocephalus* É. Geoffroy Saint-Hilaire and Cuvier, 1795 [not Boddaert, 1768]; *Paphio* Gray, 1821; *Simia* [*Chaeropithecus*] Gervais 1839; *Simia* [*Chaeropithecus*]: Senechal, 1839; *Choeropithecus* Blainville, 1839; *Hamadryas* Lesson, 1840; *Choiropithecus* Reichenbach, 1862; *Chaeropithecus* Gray, 1870 [not Gervais, 1839]; *Comopithecus* Allen, 1925; *Papio* [*Chaeropithecus*]: Ellerman *et al.,* 1953)

Macaca Lacépède, 1799, p. 4 (includes *Pithecus* É. Geoffroy Saint-Hilaire, 1812 [supressed]; *Inuus* É. Geoffroy Saint-Hilaire, 1812; *Macaco* Oken, 1817; *Macacus* Desmarest, 1820; *Silenus* Goldfuss, 1820; *Cynocephalus* Gray, 1821 [not Boddaert, 1768]; *Magotus* Ritgen, 1824; *Magus* Lesson, 1827; *Innuus* Berthold, 1827; *Pithes* Burnett, 1828; *Rhesus* Lesson, 1830; *Cynopithecus* I. Geoffroy Saint-Hilaire, 1836; *Maimon* Wagner, 1839; *Ouanderou* Lesson, 1840; *Salmacis* Gloger, 1841; *Pithex* Hodgson, 1841; *Lyssodes* Gistel, 1848; *Vetulus* Reichenbach, 1862; *Cynamolgus* Reichenbach, 1862; *Zati* Reichenbach, 1862; *Nemestrinus* Reichenbach, 1862; *Gymnopyga* Gray, 1866; *Aulaxinuus* Cocchi, 1872; *Mesopithecus:* Trouessart, 1878 [in part]; *Aulaxinus* Lydekker, 1889; *Cynomolgus* Trouessart, 1904; *Opthalmomegas:* Dehaut, 1914; "*Sylvanus*" Oken, 1916; *Auxalinus* Bernsen, 1930; *Cygnopithecus* Rensch, 1936; *Szechuanopithecus* Young and Liu, 1950; *Cynomacaca* Khajuria, 1953; *Dolichopi-*

thecus: Kretzoi, 1962 [in part]; *Cynomaca* Walker *et al.,* 1964; *Libypithecus:* Hill, 1970 [in part])

Cercocebus É. Geoffroy Saint-Hilaire, 1812, p. 97 (includes *Aethiops* Martin, 1841; *Leptocebus* Trouessart, 1904)

Mandrillus Ritgen, 1824, p. 33 (includes *Mandrill* Berthold, 1827; *Simia* [*Mandril*] Voigt, 1831; *Mormon* Wagner, 1839; *Sphinx* Gray, 1843; *Drill* Reichenbach, 1862; *Maimon:* Trouessart, 1904)

Miopithecus I. Geoffroy Saint-Hilaire, 1842, p. 720 (includes *Meiopithecus* Reichenbach, 1862; *Myiopithecus* Wallace, 1876)

Theropithecus I. Geoffroy Saint-Hilaire, 1843, p. 576 (includes *Macacus:* Rüppell, 1835; *Gelada* Gray, 1843; *Simopithecus* Andrews, 1916; *Theropythecus* Vram, 1922; *Dinopithecus:* Broom and Hughes, 1949 [in part]; *Brachygnathopithecus* Kitching, 1952 [in part]; *Gorgopithecus:* Kitching, 1953 [in part]; *Papio:* Buettner-Januusch, 1966; [*Omopithecus*] Delson, 1993)

Chlorocebus Gray, 1870, p. 5 (includes *Cynocebus* Gray, 1870)

Erythrocebus Trouessart, 1897, p. 19

Lophocebus (Palmer, 1903, p. 873)

Allenopithecus Lang, 1923, p. 1

Procynocephalus Schlosser, 1924, p. 8

Parapapio Jones, 1937, p. 727 (includes *Papio:* Haughton, 1925; *Cercocebus:* Hopwood, 1936; *Papio* [*Simopithecus*]: Dietrich, 1942; *Brachygnathopithecus* Kitching, 1952 [in part]; *Papio* [*Parapapio*]: Delson, 1975)

Dinopithecus Broom, 1937, p. 753 (includes *Papio:* Maier, 1971 [in part])

Gorgopithecus Broom and Robinson, 1949, p. 379 (includes *Parapapio:* Broom, 1940 [in part]; *Parapapio:* Broom, 1946 [in part]; *Simopithecus:* Oakley, 1954 [in part]; *Simopithecus:* Hopwood and Hollyfield, 1954 [in part]; *Papio:* Maier, 1971 [in part]; *Dinopithecus* [*Gorgopithecus*]: Delson, 1975)

Paradolichopithecus Necrasov *et al.,* 1961, p. 415

Subfamily Colobinae Jerdon, 1867, p. 3 (includes Presbytina Gray, 1825; Semnopithecidae Owen, 1843; Colobidae Blyth, 1875)

Colobus Illiger, 1811, p. 69 (includes *Colobolus* Gray, 1821; *Guereza* Gray, 1870; *Stachycolobus* Rochebrune, 1887; *Pterycolobus* Rochebrune, 1887; *Pterygocolobus* Trouessart, 1897)

Pygathrix É. Geoffroy Saint-Hilaire, 1812, p. 90 (includes *Daunus* Gray, 1821; *Lasiopyga* Reichenbach, 1862 [not Illiger, 1811]; *Rhinopithecus* Milne-Edwards, 1872; *Presbytiscus* Pocock, 1924; *Macaca:* Young, 1932 [in part]; *Pygathrix* [*Rhinopithecus*]: Groves, 1970)

Nasalis É. Geoffroy Saint-Hilaire, 1812, p. 89 (includes *Hanno* Gray, 1821; *Rhinolazon* Gloger, 1841; *Rhynchopithecus* Dahlbohm, 1856; *Simias* Miller, 1903; *Nasalis* [*Simias*]: Delson, 1975)

Presbytis Eschscholtz, 1821, p. 196 (includes *Presbytes* Gray, 1843; *Lophopithecus* Trouessart, 1878; *Corypithecus* Trouessart, 1879; *Presbypithecus* Trouessart, 1879)

Semnopithecus Desmarest, 1822, p. 532 (includes *Entellus* Gray, 1870)

Mesopithecus Wagner, 1839, p. 310 (includes *Anthropodus* Lapouge, 1894)

Trachypithecus Reichenbach, 1862, p. 89

Procolobus Rochebrune, 1877, p. 95 (includes *Piliocolobus* Rochebrune, 1887; *Tropicolobus* Rochebrune, 1887; *Lophocolobus* Pousargues, 1895)

Dolichopithecus Dépéret, 1889, p. 982 (includes "Adelopithecus" Gremyatskii, 1960; may include *Parapresbytis*

Kalmykov and Mashchenko, 1992 [*Parapresbytis* is a valid genus according to McKenna *et al.,* 1995])

Libypithecus Stromer, 1913, p. 356

Cercopithecoides Mollett, 1947, p. 298 (includes *Brachygnathopithecus* Kitching, 1952 [in part]; *Cercopithecoides:* Leakey, 1982)

Paracolobus Leakey, 1969, p. 54

Rhinocolobus Leakey, 1982, p. 154

Microcolobus Benefit and Pickford, 1986, p. 446

Superfamily Hominoidea Simpson, 1931, p. 272 (includes Anthropomorpha Huxley, 1872; Pongoidea Elliot, 1913; Dryopithecidae Gregory and Hellman, 1939; Ramapithecidae Simonetta, 1957; Pongoidea Kälin, 1961; Dryopithecidae: Pilbeam *et al.,* 1977; Ramapithecidae: Pilbeam *et al.,* 1977)

Family Pliopithecidae Zapfe, 1960, p. 261 (includes Plipithecinae Zapfe, 1960; placement within Hominoidea is uncertain) [E. through L. Miocene]

Pliopithecus Gervais, 1849, p. 5 (includes *Pithecus:* Blainville, 1839; *Protopithecus:* Lartet, 1851 [not Lund, 1838]; *Hylobates:* Rütimeyer, 1867; *Pliopithecus* [Epipliopithecus] Zapfe and Hürzeler, 1957)

Plesiopliopithecus Zapfe, 1961, p. 250 (includes *Pliopithecus* [*Plesiopliopithecus*] Zapfe, 1961)

Crouzelia Ginsburg, 1975, p. 883

Anapithecus Kretzoi, 1975, p. 579 (includes *Pliopithecus* [*Anapithecus*] Kretzoi, 1975)

Laccopithecus Wu and Pan, 1984, p. 185

Family Oreopithecidae Schwalbe, 1915, p. 218 [M. through L. Miocene]

Oreopithecus Gervais, 1872, p. 1217

Nyanzapithecus Harrison, 1986, p. 266

Family Hylobatidae Gray, 1877, p. 4 (includes Hylobatina Gray, 1870; Hylobatidae Blyth, 1875)

Hylobates Illiger, 1811, p. 67 (includes *Pithecus* É. Geoffroy Saint-Hilaire and Cuvier, 1795 [supressed]; *Pithecus:* Latreille, 1801; *Satyrus* Oken, 1816; *Cheiron* Burnett, 1828; *Siamanga* Gray, 1843; *Brachiopithecus:* Gray, 1870; *Methylobates* Ameghino, 1882; *Bunopithecus* Matthew and Granger, 1923; *Brachytanytes* Schultz, 1932) [M. Pleistocene to Recent]

Family Hominidae Gray, 1825, p. 338 [E. Pliocene to Recent]

Subfamily Ponginae Elliot, 1913, errata page (includes Pithecidae Gray, 1821; Simiadae Fleming, 1822; Simiidae Bonaparte, 1850)

Pongo Lacépède, 1799, p. 4 (includes *Pithecus:* Cuvier, 1800; *Lophotus* Fischer, 1813; "Faunus" Oken, 1816; *Brachiopithecus* Senechal, 1839; *Satyrus:* Mayer, 1856; "Metasimia" Ameghino, 1884)

Subfamily Homininae Gray, 1825, p. 338 (includes Hominidae Gray, 1825; Hominina Gray, 1825; Pithecanthropidae Dubois, 1894; Australopithecinae Gregory and Hellman, 1939; Paranthropidae Arambourg, 1957; Gorillinae Hürzeler, 1968; Gorillidae: Verschuren, 1972; Paninae Delson, 1977)

Homo Linnaeus, 1758, p. 20 (includes *Pithecanthropus* Dubois, 1894; *Proanthropus* Wilser, 1900; *Euranthropus* Sergi, 1909; *Heoanthropus* Sergi, 1909; *Notanthropus* Sergi, 1909; *Palaeanthropus* Bonarelli, 1909; *Homo* [*Protanthropus*] Bonarelli, 1909; *Pseudohomo* Ameghino, 1909; *Protanthropus:* Arldt, 1915; *Anthropus* Boyd-Dawkins, 1926; *Sinanthropus* Black and Zdansky, 1927; *Cyphanthropus* Pycraft, 1928; *Hemianthropus* Freudenberg, 1929; *Homo* [*Javanthropus*] Oppenoorth, 1932; *Praehomo* Eickstedt, 1932; "Metanthropus" Sollas, 1933; *Homo* [*Africanthropus*] Dreyer, 1935; *Palaeoanthropus* Reck and Kohl-Larsen, 1936; *Africanthropus* Weinert, 1938 [not Dreyer, 1935]; *Mauueranthropus* Montandon, 1943;

Meganthropus G.H.R. Von Koenigswald, 1944; *Nipponanthropus* Hasebe, 1948; "Präanthropus" Hennig, 1948; *Telanthropus* Broom and Robinson, 1949; *Europanthropus* Wust, 1950; *Atlanthropus* Arambourg, 1954; *Praeanthropus* Seyürek, 1955; "Euranthropus" Arambourg, 1955; *Homo* [*Pithecanthropus*]: Dolinar-Osole, 1956; "Homopithecus" Deraniyagala, 1960; "Tchadanthropus" Coppens, 1965)

Pan Oken, 1816, p. xi (includes *Simia* Linnaeus, 1758 [in part, supressed]; *Pithecus* É. Geoffroy Saint-Hilaire and Cuvier, 1795 [supressed]; *Troglodytes* É. Geoffroy Saint-Hilaire, 1812 [not Viellot, 1806]; *Mimetes* Leach, 1820 [not Eschscholtz, 1818; *Theranthropus* Brooks, 1828; *Chimpansee* Voigt, 1831; *Anthropopithecus* Blainville, 1839; *Hylanthropus* Gloger, 1841; *Pseudanthropus* Reichenbach, 1862; *Pseudoanthropus* Schaufuss, 1875; *Pongo:* Haeckel, 1866 [not Lacépède, 1799]; *Engeco* Haeckel, 1866; *Fsihego* De Pauw, 1905; *Boreopithecus* Friederichs, 1932; *Bonobo* Tratz and Heck, 1954)

Gorilla (I. Geoffroy Saint-Hilaire, 1852, p. 933) (includes *Pseudogorilla* Elliot, 1913; *Pan* [*Gorilla*]: Simonetta, 1957)

Australopithecus Dart, 1925, p. 198 (includes *Plesianthropus* Broom, 1938)

Paranthropus Broom, 1938, p. 379 (includes *Zinjanthropus* Leakey, 1959; *Australopithecus* [*Paranthropus*]: Leakey *et al.,* 1964; *Australopithecus* [*Zinjanthropus*]: Leakey *et al.,* 1964; *Paraustralopithecus* Arambourg and Coppens, 1967)

Ardipithecus White *et al.,* 1995, p. 88

Superfamily Hominoidea *incertae sedis*

Family uncertain [E. Miocene through M. Pleistocene]

Dryopithecus Lartet, 1856, p. 219 (includes *Hylobates:* Owen, 1861 [in Kaup]; *Semnopithecus:* Kaup, 1861; *Paidopithex* Pohlig, 1895; *Pliohylobates* Dubois, 1895; *Anthropodus:* Schlosser, 1901 [not Lapouge, 1894]; *Neopithecus* Abel, 1902; *Hispanopithecus* Villalta and Crusafont, 1944; *Sivapithecus:* Villalta and Crusafont, 1944 [in part]; *Udabnopithecus* Burtschak-Abramovitsch and Gabachvilli, 1950; *Pliopithecus?:* Hürzeler, 1954; *Rhenopithecus* G.H.R. Von Koenigswald, 1956; "Rahonapithecus" Crusafont and Hürzeler, 1961 [*nomen nudum*]; Dryopithecus [*Hispanopithecus*]: Crusafont and Hürzeler, 1961; *Dryopithecus* [*Dryopithecus*]: Simons and Pilbeam, 1977)

Sivapithecus Pilgrim, 1910, p. 63 [considered a junior synonym of *Dryopithecus* by McKenna *et al.,* 1995] (includes *Pithecus:* Falconer and Cautley, 1838 [in part]; *Palaeopithecus:* Lydekker, 1879 [not Voigt, 1835]; *Troglodytes:* Lydekker, 1886 [in part]; *Simia:* Lydekker, 1886 [in part]; *Anthropopithecus:* Trouessart, 1897 [in part]; *Griphopithecus* Abel, 1902; *Dryopithecus:* Pilgrim, 1915 [in part]; *Palaeosimia* Pilgrim, 1915; *Hylopithecus* Pilgrim, 1927; *Sugrivapithecus* Lewis, 1934)

Ramapithecus Lewis, 1934 [*Ramapithecus* is considered a valid genus by Szalay and Delson, 1979 and McKenna *et al.,* 1995]; *Bramapithecus* Lewis, 1934; *Austriacopithecus* Ehrenberg, 1938; *Indopithecus* G.H.R. Von Koenigswald, 1949 [in part]; *Pongo:* Hooijer, 1951 [in part]; *Mesopithecus:* Freyberg, 1951 [in part]; *Ankarapithecus* Ozansoy, 1957; *Rudapithecus* Kretzoi, 1969; *Bodvapithecus* Kretzoi, 1975; *Chinjipithecus* G.H.R. Von Koenigswald, 1981 [*Chinjipithecus* is considered a valid genus by McKenna *et al.,* 1995])

Proconsul Hopwood, 1933, p. 97 (includes *Dryopithecus:* Keith, 1932; *Xenopithecus* Hopwood, 1933; *Limnopithecus:* Le Gros Clark and Leakey, 1951; *Limnopithecus:* Le Gros Clark, 1952 [in part]; *Sivapithecus:*

Le Gros Clark and Leakey, 1951 [in part]; *Dryopithecus* [*Proconsul*]: Simons and Pilbeam, 1965; *Dryopithecus* [*Sivapithecus*]: Simons and Pilbeam, 1965 [in part]; *Dryopithecus* [*Proconsul*]: Szalay and Delson, 1979)

Limnopithecus Hopwood, 1933, p. 97 (includes *Pliopithecus* [*Propliopithecus*]: Simonetta, 1957 [in part]; *Pliopithecus* [*Limnopithecus*]: Simons, 1965; *Dryopithecus* [*Limnopithecus*]: Szalay and Delson, 1979)

Gigantopithecus G.H.R. Von Koenigswald, 1935, p. 874 (includes *Dryopithecus*: Pilgrim, 1915 [in part]; *Sivapithecus*: Lewis, 1937 [in part]; *Gigantanthropus* Weidenreich, 1946; *Giganthropus* Weinert, 1950; *Indopithecus* G.H.R. Von Koenigswald, 1950 [in part])

Kenyapithecus Leakey, 1962, p. 690

Graecopithecus G.H.R. Von Koenigswald, 1972, p. 390

Rangwapithecus Andrews, 1974, p. 189 (includes *Xenopithecus*: MacInnes, 1943 [in part]; *Proconsul*: Le Gros Clark and Leakey, 1951 [in part]; *Limnopithecus*: Le Gros Clark and Leakey, 1951 [in part]; *Sivapithecus*: Le Gros Clark and Leakey, 1951 [in part]; *Dryopithecus* [*Rangwapithecus*] Andrews, 1974; *Proconsul* [*Rangwapithecus*]: Andrews, 1976; *Dryopithecus* [*Rangwapithecus*]: Szalay and Delson, 1979)

Dendropithecus Andrews and Simons, 1977, p. 162 (includes *Xenopithecus*: Hopwood, 1933 [in part]; *Xenopithecus*: MacInnes, 1943 [in part]; *Limnopithecus*: MacInnes, 1943 [in part]; *Limnopithecus*: Le Gros Clark and Leakey, 1950 [in part]; *Proconsul*: Le Gros Clark and Leakey, 1951 [in part]; *Proconsul*: Le Gros Clark, 1952 [in part]; *Pliopithecus* [*Propliopithecus*]: Simonetta, 1957 [in part]; *Pliopithecus* [*Limnopithecus*]: Simons, 1963)

Ouranopithecus De Bonis and Melentis, 1977, p. 1395

Micropithecus Fleagle and Simons, 1978, p. 427 (includes *Limnopithecus* Hopwood, 1933 [in part]; *Dryopithecus* [*Limnopithecus*]: Hopwood, 1933 [in part])

Dionysopithecus Li, 1978, p. 188

Platodontopithecus Gu and Lin, 1983, p. 305

Afropithecus Leakey and Leakey, 1986a, p. 143

Turkanapithecus Leakey and Leakey, 1986b, p. 146

Simiolus Leakey and Leakey, 1987, p. 369

Lufengpithecus Wu, 1987, p. 269

Heliopithecus Andrews and Martin, 1987b, p. 384

Kalepithecus Harrison, 1988, p. 85 (includes [*Dendropithecus*]: Le Gros Clark and Leakey, 1950 [in part]; [*Micropithecus*]: Le Gros Clark and Leakey, 1950 [in part])

Otavipithecus Conroy *et al.,* 1992, p. 144

Kamoyapithecus Leakey *et al.,* 1995b, p. 520 (includes *Proconsul* [*Proconsul*]: Madden, 1972 [in part]; *Proconsul* [*Proconsul*]: Andrews, 1978 [in part]; *Proconsul* [*Xenopithecus*]: Madden, 1980)

APPENDIX 2: MORPHOLOGICAL CHARACTERS (MOSTLY NONDENTAL) EMPLOYED IN EVALUATING PRIMATE INTRAORDINAL RELATIONSHIPS[1]

General notes:

• This study considers two sets of characters: one set—characters 1–100—after Shoshani (1986b) and emended from the literature (credits are given under References and/or Notes for each character), the second set—characters 101–264—after Groves (1986, 1995).

[1] Data matrix is presented in Appendix 3.

Note that to leave all of Grove's characters intact, some characters which were also in Shoshani's list (e.g., presence vs absence of the baculum) were deleted. The sequence of presentation of characters 1–100 below and in Appendix 3 is from anterior to posterior of skull (cranium and mandible) followed by skeleton; skull foramina and dentition are presented at the end of skull characters. Soft anatomy characters are at the end of the appendix. Characters 101–264 are presented as close as possible to that in Groves (1986).

• In case of polymorphic taxa, the following guidelines were employed to make a decision on whether or not a character for a taxon is primitive or derived. When it is certain from the literature that one character state is more primitive than another, then if the majority of individuals of a genus examined exhibit this plesiomorphic condition, ergo the minority exhibit the derived condition, the coding for that genus is the primitive state. For example, most humeri of *Aotus* examined at the Mammalogy Department, American Museum of Natural History (AMNH, New York), possess entepicondylar foramen (the primitive condition; Gregory, 1910); some, however, do not (the derived condition, e.g., AMNH 201647). Thus, the coding used is the primitive state (see character 62). This approach was followed even when the majority (over 90%) of the specimens exhibited the derived condition, as long as there is sufficient evidence to support that the majority is in fact the derived, and not the primitive, condition. In this case, the primitive coding of the minority prevails.

• Each character description is composed of these parts: Title, Character states, References, and Notes.

—Title. Main subject is written in capital letters and may be followed by a subtitle.

—Character states. In all cases, for binary or multistate characters, condition (0) is considered/suggested as primitive and (1), (2), (3), (4), (5), and (6) are derived conditions for most Mammalia and/or Eutheria. A "?" was used when no data were collected (either because that structure was not available on a particular specimen, or a character could not be evaluated on a species—e.g., the lacrimal foramen cannot be examined on specimens of species which lost the lacrimal bone). In multistate characters, the sequences in which the numbers are written do not necessarily imply polarity of a character or a morphocline. All characters were analyzed as unordered and unweighted.

—References. It is very difficult, and in some cases, impossible, to trace the exact source of reference for the original observation(s). The key below includes only selected citations which themselves may include references of the original observations. In the section References, citations to sources are given—usually chronologically—followed by a page number or a character number. Examples: T+(88, p. 113) refers to Tattersall *et al.* (1988, p. 113), and No(92):ch. 37 refers to Novacek (1992, pages are given with the key below), character 37. For simplicity, we did not use quotation marks for descriptions of characters.

—Notes. Some contain brief descriptions, especially for unfamiliar features, e.g., foramina characters.

Key to authors whose works may have been consulted more than once:

An(87), Andrews (1987); An(88), Andrews (1988).

AJ(84), Anderson and Jones (1984). This is an edited volume; specific authors are not mentioned but are incorporated when citation is used.

Be(93), Beard (1993), pp. 131–142 [character matrix on p. 143, cladograms on p. 132].

Ca(78), Cartmill (1978); Ca(81), Cartmill (1981); Ca(92), Cartmill (1992).

De(92), Delson (1992).

FT(93), Fischer and Tassy (1993), pp. 219–222 [character matrix on p. 222, cladograms on p. 219].

Fo(86), Ford (1986).

G(86), Groves (1986), tables on pp. 188–193, and Appendix (pp. 209–216); G(91), Groves (1991); G(95), Groves (1995).

Ge(86), Gebo(86), Ge(88), Gebo(1988).

Gi(92), Gingerich (1992).

Gr(10), Gregory (1910), used as a general source; specific pages are sometimes given. Many of the characters used in this study were mentioned in Gregory's monograph; Gr(20), Gregory (1920).

GRC, used as a general source for Vertebrata/Mammalia extinct and extant taxa, including the works of Gregory (1910), Romer (1966, 1971), and Carroll (1988).

Hi(72), Hill (1972).

LGC(71), Le Gros Clark (1971).

Lu(80), Luckett (1980); Lu(93), Luckett (1993).

McP(81), MacPhee (1981); McP(94), MacPhee (1994), pp. 161–179 [character matrix on p. 161, cladograms on pp. 181–196].

MC(42), Midlo and Cummins (1942).

WM(93), Wible and Martin (1993).

NW(86), Novacek and Wyss (1986), pp. 260–261 [no character matrix, synapomorphies are incorporated on cladogram, p. 259].

No(86), Novacek (1986); No(92), Novacek (1992, Appendix 1, incorporating characters of Novacek and Wyss (1986), Novacek (1986), Novacek et al. (1988)), pp. 60–73 [character matrix on p. 60, cladograms on pp. 61–65, 68]; No(92x), Novacek (1992, Appendix 2), p. 73.

Po(18), Pocock (1918).

RHKW, used as a general source for comparative vertebrate zoology material of Vertebrata/Mammalia, including the works of Romer (1971), Romer and Parsons (1986), Hildebrand (1995), Walker and Liem (1994), Walker and Homberger (1992), Kent (1987), and Kardong (1995).

SD(79), Szalay and Delson (1979). Many of the osteological characters used in this study were mentioned in this book.

Sa(85), Sarmiento (1985); Sa(87), Sarmiento (1987); Sa(88), Sarmiento (1988); Sa(94), Sarmiento (1994).

Sc(84), Schwartz (1984); Sc(86), Schwartz (1986).

SM(95), Shoshani and McKenna (1995).

Sh(86b), Shoshani (1986b), pp. 225–235 [character matrix, as Appendix L on pp. 537–553, cladograms on p. 224]; Sh(93), Shoshani (1993), p. 238 [character matrix on p. 239, cladogram on p. 247]; Sh(95), Shoshani (1995, personal observations).

Si(77), Simons (1977); Si(95), Simons (1995).

T+(88), Tattersall et al. (1988).

TA(84), Thorington and Anderson (1984).

Th(94), Thewissen (1994).

WF(93), Wyss and Flynn (1993), pp. 37–46 [character matrix on p. 36, cladograms on pp. 37, 47].

Wa(74), Wahlert (1974); Wa(85), Wahlert (1985).

We(36), Weidenreich (1936).

Other abbreviations used: AMNH, American Museum of Natural History, New York; CS, character state.

SKULL: CRANIUM (CHARACTERS 1–27)

1. ROSTRUM OR MUZZLE
   Character states: (0) long, with an index of 33–51; (1) short, with an index of 10–30.
   References: Gi(92, p. 201); Sh(95).
   Notes: Index was calculated using length of the rostrum (the facial region of cranium anterior to the plane drawn through anterior margin of orbits, to tip of premaxillae) divided by the length of the cranium in dorsal view (taxa with long canine, e.g., Macaca and Papio, were measured when their tooth alveoli were leveled) and multiplied by 100. The narrow gap between the index of 30 (for Pongo) and 33 (for Macaca) may be a result of insufficient sampling; in many cases only one specimens per genus was measured. See also character 6.

2. ORBITS
   Character states: (0) facing laterally or anterolaterally; (1) facing more anteriorly.

References: Gi(92, p. 201).
Notes: None.

3. POSTORBITAL BAR
   Character states: (0) absent or incomplete; (1) complete.
   References: Sh(86b):ch. 152; cf. GRC, RHKW.
   Notes: CS (0) may include dorsal and/or ventral postorbital process(es) as seen in Pteropus.

4. POSTORBITAL PLATE behind eye
   Character states: (0) absent or incomplete; (1) present, complete.
   References: Po(18, p. 51); cf. Jones (1929), Ca(81), Sc(86):chs. 6–7, Sh(86b):ch. 150, Gi(92, p. 201), and Si(95).
   Notes: Tarsius was coded (0) because its postorbital plate is incomplete and, in addition, a portion of the plate of Tarsius may be composed of other elements than in Anthropoidea [Ca(81), Simons, personal communication to J. Shoshani, 1995, and Si(95)]. The function of the postorbital plate, according to Ca(81, p. 270), is to ". . . insulate the foveate retina from temporalis constriction, preserving visual acuity when the animal was simultaneously chewing and hunting for hard-to-find food items like insects."

5. BRAINCASE
   Character states: (0) small with postorbital constriction; (1) large and rounded.
   References: Gi(92, p. 201).
   Notes: None.

6. FACIAL ELONGATION (prognathism)
   Character states: (0) absent or small; (1) elongated and linked with several features (narrow interorbital distance, long nasal bones, lacrimal extends anteriorly, vomer forms a part of medial wall of orbit, and ethmoid expands anteriorly).
   References: T+(88, p. 123), De(92, p. 218).
   Notes: cf. this character to character 1.

7. FRONTALS
   Character states: (0) not fused in midline on dorsal of cranium; (1) fused in midline.
   References: Gi(92, p. 201).
   Notes: None.

8. FRONTAL and ALISPHENOID contact
   Character states: (0) present; (1) absent.
   References: Ashley-Montague (1933, p. 163); Fo(86, pp. 80, 86); Sc(86, p. 11); TA(84, p. 204); Sh(95).
   Notes: Contact between frontal and alisphenoid is eliminated when the parietal and the jugal (malar or zygoma) abut.

9. POSTPALATINE coronal TORUS
   Character states: (0) present; (1) absent.
   References: Gr(10); Sh(86b):ch. 17.
   Notes: CS (0) present but weak in Daubentonia (e.g., AMNH 185643).

10. POSTERIOR PALATAL SPINE
    Character states: (0) spine absent, posterior edge of palate straight (transversely), postpalatine torus may be present, vomer usually not in contact with hard palate at posterior edge; (1) small to large midline posterior spine projection present (contributed from each palatine bone), postpalatine torus may be present, vomer usually not in contact with hard palate at posterior edge; (2) large midline posterior spine slopes dorsally and is supported by the vomer which extends ventrally, postpalatine torus absent; (3) as in CS (2) except that the midline posterior spine is small or absent.
    References: Sh(95), cf. Gray, 1901, pp. 107–108.
    Notes: Gray (1901, p. 107) named it "posterior nasal spine" and on p. 108 noted that it functions for the attachment of the azygos uvule muscles. Palates of hominoids are illustrated in Gregory (1920, p. 712).

11. JUGAL (MALAR), posterior end
    Character states: (0) participates in the formation of the glenoid fossa, i.e., mandibular condyle is in contact with jugal, or the jugal is close to glenoid fossa; (1) jugal is away from glenoid fossa and/or close to center of zygomatic arch.

References: Gr(10); Sh(86b):ch. 190; NW(86):ch. 61; No(92x):ch. 5; Sh(95).

Notes: It is possible that CS (1) is the primitive condition; NW(86): ch. 61 and No(92x):ch. 5, considered CS (0) as a derived condition within Mammalia. Within Primates, e.g., in *Leontopithecus* (AMNH 185347), the jugal is removed from the glenoid fossa, but not as much as in other platyrrhines and catarrhines, yet it differs from strepsirhines and thus was coded with CS (1).

12. SUBARCUATE FOSSA

Character states: (0) deep; (1) greatly expanded, and dorsal semicircular canal clearly separated from endocranial wall of squamosal; (2) moderately deep to shallow; (3) very shallow to nonexistent.

References: NW(86):ch. 31; No(92):ch. 31, and No. 43; McP(94): ch. 15.

Notes: None.

13. TYMPANIC FLOOR

Character states: (0) largely membranous; (1) fully ossified, ectotympanic major element; (2) fully ossified (chondrified), entotympanic major element; (3) fully ossified, petrosal plate major element (forms anterior, medial, and posterior walls).

References: WM(93, pp. 139–141):ch. 1, cf. McP(81).

Notes: None.

14. ENTOTYMPANIC

Character states: (0) absent; (1) main element forms anteromedial to cochlear capsule continuous with cartilage of auditory tube; (2) main element forms posteromedial to cochlear capsule.

References: WM(93, pp. 139–141):ch. 2.

Notes: None.

15. ECTOTYMPANIC

Character states: (0) phaneric (extrabullar, i.e., in side view, the ectotympanic is easily seen); (1) aphaneric (intrabullar, i.e., ectotympanic is hidden in side view).

References: WM(93, pp. 139–141):ch. 3, after MacPhee *et al.* (1988); Cartmill and MacPhee (1980).

Notes: None.

16. ECTOTYMPANIC shape

Character states: (0) simple (annular or horseshoe shaped), not expanded greatly medially or laterally; (1) expanded significantly relative to ontogenetically early condition.

References: WM(93, pp. 139–141):ch. 4.

Notes: cf. this character to character 42.

17. CAUDAL TYMPANIC PROCESS of petrosal

Character states: (0) surrounds stapedius fossa; (1) does not surround stapedius fossa.

References: WM(93, pp. 139–141):ch. 5.

Notes: None.

18. BASIOCCIPITAL

Character states: (0) no contact with medial bullar wall; (1) contact entotympanic element in medial bullar wall.

References: WM(93, pp. 139–141):ch. 6.

Notes: None.

19. TEGMEN TYMPANI

Character states: (0) forms broad roof over mallear—incudal articulation; (1) enlarged to roof entire middle-ear ossicular chain; (2) reduced, tapered to a short, round process; (3) reduced, tapered to an elongate, round, process.

References: WM(93, pp. 139–141):ch. 7.

Notes: None.

20. EPITYMPANIC CREST (canal for stapedial artery) on TEGMEN TYMPANI

Character states: (0) absent; (1) present.

References: WM(93, pp. 139–141):ch. 8.

Notes: None.

21. TEGMEN TYMPANI, arterial foramen in

Character states: (0) absent; (1) present, for stapedial artery; (2) present, for ramus superior of stapedial artery.

References: MW(93, pp. 139–141):ch. 9.

Notes: CS (2) of WM(93, pp. 139–141):ch. 9 was coded for Ptilocercinae, a taxon, not included in the present analysis.

22. AUDITORY TUBE + ENTOTYMPANIC + TEGMINAL COMMISSURE, cartilage of

Character states: (0) absent; (1) present.

References: WM(93, pp. 139–141):ch. 10.

Notes: None.

23. EPITYMPANIC WING of petrosal

Character states: (0) present; (1) absent.

References: WM(93, pp. 139–141):ch. 11.

Notes: None.

24. EPITYMPANIC WING of alisphenoid

Character states: (0) moderately large, expanded posteriorly at least to the level of the promontorium's anterior pole; (1) small, does not reach to the level of the anterior pole.

References: WM(93, pp. 139–141):ch. 12.

Notes: None.

25. INTERNAL CAROTID ARTERY

Character states: (0) well developed and in transpromontorial course; (1) perbullar course (within petrosal); (2) perbullar course (between entotympanic and petrosal); (3) insignificant or obliterated during ontogeny (accompanying nerve in transpromontorial course).

References: WM(93, pp. 139–141):ch. 13.

Notes: None.

26. OSSEOUS CAROTID CANAL leading to carotid foramen

Character states: (0) absent; (1) in petrosal; (2) between entotympanic and petrosal.

References: WM(93, pp. 139–141):ch. 14.

Notes: None.

27. GREATER PETROSAL NERVE

Character states: (0) partial or complete canal floored by petrosal; (1) partial or complete canal floored by entotympanic and/or cartilage of the auditory tube.

References: WM(93, pp. 139–141):ch. 15.

Notes: None.

SKULL: MANDIBLE (CHARACTERS 28–34)

28. MANDIBULAR SYMPHYSIS

Character states: (0) unfused or slightly fused; (1) well fused.

References: Sh(86b):ch. 51; Gi(92); Si(95); cf.An(88, p. 160):ch. 47.

Notes: None.

29. MANDIBULAR SYMPHYSIS

Character states: (0) extremely elongated and spout-like, angle of mandibular symphysis to alveoli of teeth is about 170°–155°; (1) elongated and spout-like with an angle of 150°–145°; (2) symphysis with an angle of 137°–115°; (3) angle of mandibular symphysis (excluding the Simian Shelf) to horizontal ramus is narrow, approaching vertical when observed dorsally and laterally, with a mandibular symphysis angle of about 100°–90° or less.

References: We(36, pp. 78–83); Si(77, p. 40); Sh(86b):ch. 25; Sh(95).

Notes: The mandibular symphysis angle was measured internally on the dorsal surface from the upper end of the fossa genioglossi to the posterior side of the incisor alveoli in relation to the horizontal tooth alveoli, slightly different from the measurements taken by We(36). In character state (0) the area of contact between the two dentaries at symphysis is longer/greater than in CS (1); see drawings in We(36, p. 44) and Si(77, p. 40). This is a homoplasic character since it occurs independently within Hominoidea.

30. Base of CORONOID PROCESS at anterior end in adult individuals

Character states: (0) caudal to, or in line with the last molar;

(1) rostral to the last molar sometimes during postnatal development.

References: Sh(86b):ch. 52; SM(95); Sh(95).

Notes: Another way to view this character is to observe the mandible (leveled, or only one dentary) laterally, and if M_3 is only partly seen or abstracted entirely from view, then CS (1) is satisfied. *Homo* is coded with a "?" because most Recent specimens exhibit CS (0), yet a few extinct samples exhibit CS (1).

31. CORONOID PROCESS of mandible when teeth are fully occluded

Character states: (0) projects dorsal to margin of zygomatic arch; (1) slightly or just projecting dorsal to margin of zygomatic arch; (2) not projecting dorsal to margin of zygomatic arch.

References: Sh(86b):ch. 49; Sh(95).

Notes: None.

32. MANDIBULAR CONDYLE, orientation of long axis

Character states: (0) axis is antero-posteriorly (parasagittal) or condyle is approximately round, without clear long axis; (1) axis is latero-medially (transverse or coronal).

References: Sh(86b):ch. 46; Sh(95).

Notes: CS (0) was observed also in *Indri* (e.g., AMNH 100504).

33. ANGULAR PROCESS of mandible

Character states: (0) distinct, with posterior projection; (1) not distinct.

References: Gr(10); Sh(86b):ch. 48; Sh(95).

Notes: Within Haplorhini CS (0) is usually associated with CS (1) of character 31. Although some catarrhines, including hominoids, have somehow distinct angular process, yet it is not as large as that of earlier primates. *Hylobates,* has a larger process than other hominoids, and thus was coded CS (0).

34. MANDIBULAR GONIAL REGION

Character states: (0) nonexpanded; (1) expanded, shallow mesially.

References: T+(88, p. 139); De(92, p. 218).

Notes: Strasser and Delson (1987) and De(92, p. 218) employed other characters comparing colobine and cercopithecine monkeys.

SKULL: FORAMINA (CHARACTERS 35–44)

35. PREMAXILLARY CANAL

Character states: (0) absent; (1) present.

References: Sh(86b):ch. 119; Sh(95).

Notes: As much as can be ascertained from the literature, this canal was not described before (illustrated in Shoshani (1986b, p. 266) and presented by Shoshani at the 67th Annual Meeting of the American Society of Mammalogists in 1987). This canal, sometimes a minute opening (but visible to the naked eye), is located on the ventral side of the premaxillae between the incisive foramina and interpremaxillary foramen (if present), close to margins or midline. Possibly transmits small blood vessels and/or nerves. The homology of the premaxillary canal could not be established (dissection of specimen would be required), and determination on absence or presence was based on delimitation, clarity, and location based on experience from crania of Mammalia. For example, the large openings on the palate of hominoids on the premaxillae, lateral to the incisive foramina [e.g., see illustration in SD(79, p. 468)], were considered as the premaxillary canals. However, since the homology was not certain we ran PAUP with and without this character; the branching pattern in Fig. 3A did not change but the score of the tree was lowered by the three steps.

36. INCISIVE FORAMEN [anterior palatine], direction of

Character states: (0) opening is directed dorsoventrally as in most mammals and the observer can "see through" the fora-

men; (1) foramen is directed diagonally, from anterior-ventral to posterior-dorsal, the opening is small, leads to a tube-like structure, and one cannot "see through" the foramina.

References: Sh(86b):ch. 121, modified after Wa(74, p. 371) and Wa(85, pp. 316–319); Sh(95).

Notes: cf. this character to characters 117 and 128.

37. NASOLACRIMAL FORAMEN

Character states: (0) foramen pierces the lacrimal bone and is outside the boundary of the orbit or on the rim of the orbital opening; (1) foramen is within the boundary of the orbit.

References: Gr(10); Sh(86b):chs. 19, 136, modified after Wa(74, p. 372) and Wa(85, pp. 316–319); Sh(95).

Notes: When there are two foramina and one of them exhibits CS (0), and the other CS (1), the coding was CS (0).

38. ORBITAL OPENING

Character states: (0) maxilla does not contribute to the rim of the orbit laterally or anteriorly; (1) maxilla contributes to rim of orbit.

References: GRC; RHKW; Sh(86b):ch. 146; Sh(95).

Notes: Sutures on cranial bones of adult dermopterans are usually obliterated; AMNH 187862 juvenile exhibits CS (0), and in *Tupaia javanica occidentalis* CS (0) shows well in AMNH 106498.

39. FORAMEN ROTUNDUM

Character states: (0) foramen rotundum is confluent with or incompletely separated from the orbital fissure; (1) foramen rotundum is clearly separate.

References: Gr(10), pp. 223, 246–247; No(86, p. 85):ch. 33; Sh(86b):ch. 164, modified after Wa(74, pp. 372–373); McP(94):ch. 7; Th(94):ch. 34; SM(95); Sh(95).

Notes: In *Tarsius,* the orbital mosaic is difficult to interpret and the illustrations and text in Ca(81, pp. 245–249) have been very helpful; see also illustrations in Hi(72, p. 71) and Ca(78, pp. 90–91, 97, 100, 102). In this genus, the foramen rotundum is very small and requires correct identification of specific bones within the orbital mosaic.

40. CAROTID CANAL, viewed from ventral side of cranium

Character states: (0) canal does not perforate bulla or perforates it close to basicranium; (1) canal perforates bulla away from basicranium and is clearly within it, opening of canal is directed medially, ventrally, or ventro-medially, but the imaginary lines (one from each side) which emerge from these openings do not cross at the foramen magnum, or cross at its anterior border at the level of the occipital condyles; (2) as in CS (1), but opening of canal is directed postero-medially and the imaginary lines which emerge from these openings cross the foramen magnum posterior to the occipital condyles, or caudal to the foramen magnum itself (see under Notes).

References: Sh(86b):ch. 175, modified after Wa(74,373) and Wa(85, pp. 316–319); cf. No(92, p. 72):ch. 82; Sh(95).

Notes: To view CS (1) and CS (2) place straight wires inside the carotid canals and note the point of intersection of the imaginary lines in continuation of these wires. In CS (1), the lines cross at anterior end of the foramen magnum or in front of it, whereas in CS (2) these imaginary lines cross posterior to the occipital condyles or caudal to the foramen magnum itself.

41. POSTGLENOID FORAMEN

Character states: (0) present; (1) very small or absent.

References: Gr(10); Sh(86b):ch. 176, modified after Wa(74, p. 374); Th(94, p. 163); McP(94, p. 25):ch. 7; McP(94, p. 20):ch. 14; Sh(95).

Notes: In some primates (e.g., *Tarsius* and *Cebus*) this foramen is large, whereas in catarrhines it is usually absent, or very small in adults although may be larger in juveniles (e.g., *Papio* AMNH 187368). McP(94, p. 25):ch. 7, used "Temporal sinus (postglenoid foramen) (0) present, (1) absent," and No(92, p. 72):ch. 52, used "Postglenoid foramen, shifted, opens in lateral eminence of squamosal."

42. EXTERNAL AUDITORY MEATUS or CANAL
Character states: (0) auditory bulla and auditory tube absent; (1) auditory tube incomplete (ectotympanic is "horseshoe shaped" and the rest of the tube margin is formed by the squamosal), may be formed anteriorly by the postglenoid process and posteriorly as part of the ectotympanic, opening of external acoustic meatus or the tube is short, and does not reach the lateral margins of the zygoma, margin of tube opening faces laterally; (2) opening of external acoustic meatus is large, round with thickened margins forming a rim of ectotympanic all around the opening except on the dorsal posterior edge ("horseshoe shaped"), margin of tube opening is medial to the zygoma, opening faces diagonally from the ventral of bulla dorsally and laterally; (3) auditory tube complete, formed entirely by ectotympanic, tube is long, and almost reaches the lateral margins of the zygoma, margin of tube opening faces laterally.
References: Turner (1848, p. 78); Gray (1901, p. 68); Gr(10); LGC(71, pp. 138–139); Szalay (1972, p. 66); Packer and Sarmiento (1984, pp. 12–19); Sh(86b):ch. 196; Sh(95).
Notes: There may be another character state as suggested by Szalay (1972, p. 66). See also character 16.

43. FOSSA GENIOGLOSSI FORAMINA
Character states: (0) fossa genioglossi and foramina absent; (1) fossa present but foramina, if present, only as minute openings (visible to the naked eye) on the posterior end of the mandibular symphysis, inside the fossa genioglossi, just above the spina mentalis and the Simian Shelf; (2) fossa and relatively large foramina clearly delineated and visible to the naked eye in the same location as in CS (1).
References: We(36, pp. 36, 43, 45, 46); Hillmann (1975, p. 1247); Sh(86b):ch. 207; Sh(95).
Notes: These foramina were described by We(36, pp. 36, 43, 45, 46) for hominoids. On page 43, We(36), described two "small foramina" which may be the same "foramina of the fossa genioglossi" [We(36, p. 45)]. Also described for *Sus scrofa* by Hillmann (1975, p. 1247). In some forms (e.g., *Sus*), where the symphysis is well fused, the foramina, one on each side, are present close to the ventral border of symphysis, while in other species (e.g., *Castor*), where symphysis is not fused, foramina appear to be located close to dorsal end or in the middle of symphysis. It is possible that these foramina are present, but not clearly delineated, in early primates where the dentaries are not fused. Sh(86b) called these structures MEDIAL MENTAL FORAMINA; We(36), although not naming them FOSSA GENIOGLOSSI FORAMINA, is credited for excellent description. In many specimens the fossae and the foramina from both sides coalesce into one fossa and one foramen.

44. FORAMINA SUPERSPINOSA
Character states: (0) absent; (1) present, see details under Notes.
References: We(36, p. 46); Sh(95).
Notes: These foramina were described by We(36, p. 46) for *Sinanthropus* (now junior synonym of *Homo,* see Appendix 1) as "two small foramina superspinosa of unequal size." They are located inside the mandible, on the posterior side of the symphysis, above (dorsal) to the fossa genioglossi, and just ventral to the incisor alveoli; they are clearly delineated and centrally located, one on each side of the symphysis. In fact, each one of these foramina superspinosa is located just below (about 0.5 cm) the middle incisor of a mandible of *Pan* at the collection of Wayne State University Museum of Natural History (WSUMNH 4560). These foramina, centrally located, are clearly delineated from the minute nutrient foramina which are found close to the alveolar border. All in all, there are two pairs of foramina on the posterior border of the symphysis—one close to the ventral end of the mandibular symphysis, inside the fossa genioglossi (character 43), and the other pair

close to the dorsal end of the symphysis (this character). The foramina superspinosa are best seen in hominids, less delineated in *Hylobates,* and occasionally found in other primates (e.g., *Presbytis, Papio,* and questionably in adult *Lemur*). Following the guidelines in this appendix (see notes at the beginning), *Presbytis, Papio,* and *Lemur* are coded with CS (0), and hominoid taxa with CS (1).

SKULL: DENTITION (CHARACTERS 45–51)

45. INCISORS
Character states: (0) non spatulate; (1) spatulate.
References: Gi(92, p. 201).
Notes: None.

46. LOWER INCISORS, enamel on lingual side of
Character states: (0) present; (1) absent.
References: T+(88, p. 123).
Notes: None.

47. I^1, size of
Character states: (0) of about the same size of I^2; (1) enlarged relative to I^2; (2) much enlarged relative to I^2.
References: G(86, p. 191):Table 4a, ch. 1; G(95); An(87, p. 34): 9th appearing in table 2.1; T+(88, p. 123).
Notes: None.

48. HONING in males (back of upper canine sharpens against third lower premolar)
Character states: (0) absent, i.e., P_3 not modified for honing on C^1; (1) present, i.e., P_3 bilaterally compressed (sectorial) and modified for honing on C^1, P_3 is larger than P_4 especially mesiodistally, also may involve honing C^1 on C_1; (2) honing reduced, P_3 slightly bucco-laterally compressed, P_3 is larger than P_4 especially mesiodistally; (3) honing further reduced, P_3 about the same size as P_4 in length in occlusal view.
References: SD(79, p. 304); T+(88, p. 113), see also Gr(20, pp. 704–705); Sh(95).
Notes: SD(79, p. 304) considered this character as one of a number of changes from the postulated ancestral catarrhine morphotypes to the inferred latest common ancestor of Pliopithecidae, Hominidae, Cercopithecidae, and Oreopithecidae. J. H. Schwartz (personal communication, 1995) believes that, if female specimens were to be examined, then *Pongo* and *Gorilla* should be coded CS (3).

49. PREMOLARS
Character states: (0) three upper and lower premolars present; (1) two upper and lower premolars present.
References: SD(79, p. 303); Sc(86, pp. 10–11); T+(88, p. 113).
Notes: SD(79, pp. 303–304) noted that ancestral catarrhine would have had three upper and lower premolars; latest common ancestor of catarrhine, however, lost the P^2 and P_2.

50. MOLARS
Character states: (0) not bilophodont; (1) bilophodont, i.e., cusps are linked by transverse ridges (lophs or lophids).
References: Swindler (1976, p. 119); SD(79, p. 321); Sc(86, p. 18).
Notes: In upper molars, anterior loph is formed by joining the protocone and paracone cusps, and posterior loph by the hypocone and metacone; in lower molars, anterior lophid is formed by protocone and metaconid, and posterior lophid by the hypoconid and entoconid. Sa(87, p. 10) noted that bilophodonty was acquired independently in suids, perissodactyls, artiodactyls, and it is also known to occur in proboscideans (Osborn, 1936).

51. DENTITION
Character states: (0) primitive conditions of five characters, see Notes; (1) derived conditions of five characters, see Notes.
References: Sc(86, p. 9).
Notes: Derived characters in support of the living lorises include, after Sc(86, p. 9): (1) a prehypocone crista on M^{1-2}, (2)

a lower molar paracristid that courses down the face of the protoconid, "kinks" severely at the cusp's base, and then proceeds up the face of the metaconid, (3) at least the M$_1$ protoconid and metaconid broadly melded at their bases and forming a steep wall that faces upon the talonid, (4) an angular hypoconid that is distended buccally, and (5) the alveolar margin of the premaxilla distinctly distended downward. An error was made and *Lemur* was coded with "1" instead of "0"; it was corrected after the PAUP analysis was conducted, and thus the length of the tree in Fig. 3A is 603 instead of 604— all other details remain the same.

HEAD: SOFT CHARACTERS (CHARACTERS 52–57)

52. RHINARIUM and UPPER LIP
    Character states: (0) rhinarium moist, upper lip split; (1) rhinarium dry, upper lip partially, or not, split.
    References: Po(18); Hi(72, p. 23); Lu(80, p. 352); T+(88, p. 570); Ca(92, p. 28).
    Notes: None.
53. CHEEK POUCHES
    Character states: (0) absent or small; (1) large.
    References: T+(88, p. 123), De(92, p. 218).
    Notes: None.
54. RETINA, central foveal spot on
    Character states: (0) absent, (1) present.
    References: Walls [1942, and other sources earlier than Lu(80) and T+(88), cited in Ca(81, p. 255)]; T+(88, p. 567); cf. Lu(80, p. 352):ch. 5.
    Notes: Lu(80, pp. 352–353) employed five characters uniting Haplorhini; some are used here. The retinal fovea (functions to improve visual acuity) is found in *Tarsius* and anthropoids and apparently not in any other mammals. Primates with fovea have postorbital plate or septum (character 4) except for *Aotus* which lost its fovea secondarily, perhaps because it is nocturnal [details in Ca(81, p. 255)].
55. TAPETUM LUCIDUM, on the choroid
    Character states: (0) present; (1) absent.
    References: Wolin and Massopust (1970); Ca(81, pp. 262–270); T+(88, p. 567); Ca(92, p. 26).
    Notes: Ca(81, p. 264) noted that "The absence of the tapetum appears to be a synapomorphy of *Tarsius*–anthropoid clade, not of the Haplorhini as a whole" [comparison was made to the following omomyids: *Tetonius, Necrolemur,* and *Rooneyia*].
56. BRAIN, sylvian and superior temporal sulci
    Character states: (0) parallel; (1) merge caudally.
    References: Fo(86, pp. 110–112):B10:1.
    Notes: Fo(86) cited Falk (1979) as the source for this character.
57. CAROTID ARTERIES
    Character states: (0) small; (1) large.
    References: Gi(92, p. 201).
    Notes: None.

BODY: VERTEBRAL COLUMN AND APPENDAGES (CHARACTERS 58–89)

58. THORACIC VERTEBRAE
    Character states: (0) 15 or more; (1) fewer than 15.
    References: Sh(86b):ch. 54; Schultz (1961); Straus and Wislocki (1932); AJ(84); FT(93):ch. 74; Sh(95).
    Notes: FT(93):ch. 74 noted that character state (1) ". . . is allied to strongly inclined diaphragm."
59. RIBS
    Character states: (0) oval or roundish in a cross section; (1) flattened latero-medially.
    References: NW(86):ch. 37; No(92):ch. 37; Sh(95).

Notes: In *Pteropus* (AMNH 249992) all ribs are flattened latero-medially, and in *Cynocephalus,* rib 1 is flattened antero-posteriorly, ribs 2–4 are partly flattened, and ribs 5–13 are completely flattened latero-medially. In addition, both *Pteropus* and *Cynocephalus* lack or have short spinous processes (which are of the same length) on their thoracic vertebrae.
60. SCAPULA
    Character states: (0) infraspinous fossa approximately equal to or larger than supraspinous fossa; (1) infraspinous fossa is larger than supraspinous fossa.
    References: Sh(86b):ch. 62; SM(95); Sh(95).
    Notes: Homoplasy within Primates and on the interordinal level has been observed; here all Primates are coded with CS (1) since this character is employed for interordinal relationships.
61. HUMERAL SUPRATROCHLEAR, or supracondylar FORAMEN (septal aperture)
    Character states: (0) absent; (1) present.
    References: Gr(10, p. 249); Sh(86b):ch. 71; Sh(95).
    Notes: This is not a true foramen partly because there are no blood vessels or nerves which pass through it; instead, there is an opening above the trochlea to accommodate the olecranon process of the ulna. The term "septal aperture" is after White Folkens (1991, p. 174). Among hominoids, this foramen/aperture is common in *Hylobates, Pongo,* and *Gorilla.* In *Pan,* of the 40 specimens studied, only 8 possessed this foramen, and of the approximately 50 specimens of *Homo,* 9 have this foramen. G. J. Sawyer and E. E. Sarmiento (personal communications, independently, 1995) noted that females more than males exhibit CS (1). Sa(85) observed that skeletons of captive *Pongo* lack this foramen whereas humeri of wild-caught individuals have it.
62. HUMERAL ENTEPICONDYLAR FORAMEN
    Character states: (0) present; (1) absent.
    References: Gr(10); Sh(86b):ch. 72; Sh(95).
    Notes: None.
63. ENTEPICONDYLAR FORAMEN, position of
    Character states: (0) located over medial epicondyle, or lost; (1) located further laterad, over trochlea on ventral surface only; (2) located even more laterad, over trochlea on ventral surface and partially on dorsal surface.
    References: Fo(86, pp. 77, 106–107):PC105:2.
    Notes: Character states are as given in Fo(86), even though all states are not used here. This character is depicted on the cladogram of Fo(86, Fig. 2).
64. HUMERAL EPITROCHLEAR NOTCH or groove on MEDIAL EPICONDYLE distally and anteriorly
    Character states: (0) notch or groove absent; (1) shallow open notch or groove; (2) some or all with medium deep notch or groove; (3) split distribution; some individuals with a deep notch or groove; (4) deep, closed U-shaped notch or groove.
    References: Fo(86, pp. 86, 106–107):PC111:2.
    Notes: Character states are as given in Fo(86), even though all states are not used here. Shoshani's (1986b) characters 69 and 70 concern the lateral and medial epicondyles of the humerus in relation to their relative surface area of articulation with the radius and ulna.
65. ULNAR STYLOID PROCESS
    Character states: (0) long and contacts carpal bones; (1) shortened; (2) very short, fails to contact carpal bones.
    References: G(95); An(87, p. 34):8th appearing in table 2.1; T+(88, p. 251); cf. Cartmill and Milton (1977), Sa(88), and Sa(94).
    Notes: SD(79, p. 323) noted that the styloid process of the ulna articulates with the wrist in Old World monkeys (Cercopithecidae). J. H. Schwartz (personal communication, 1995) noted that *Hylobates* and *Pongo* should be coded CS (2).
66. SCAPHOID and LUNAR
    Character states: (0) separate; (1) fused.

References: Gr(10); Sh(86b):ch. 76; WF(93):ch. 55.
Notes: None.

67. POLLEX
Character states: (0) of normal size, i.e., distal end of pollex (digit I) reaches about the level of middle or distal end of proximal phalanx of digit II; (1) reduced (i.e., distal end of pollex reaches to about the level of distal end of metacarpal II) or lost, e.g., *Presbytis aygula* (AMNH 200836).
References: SD(79, p. 383); T+(88, pp. 129, 139); De(92, p. 218); Sh(95).
Notes: None.

68. PELVIS, shape of acetabulum
Character states: (0) roughly circular in lateral view; (1) elliptical in outline, elongated in the cranial–caudal dimension.
References: Be(93):ch. 20.
Notes: Homoplasy within Primates has been observed; here all are coded with CS (1) since this character is employed for interordinal relationships.

69. PELVIS, size of acetabular fossa
Character states: (0) acetabular fossa smaller than obturator foramen; (1) acetabular fossa approximate size of obturator foramen.
References: Sh(86b):ch. 88; Sh(95).
Notes: None.

70. PELVIS, obturator groove or notch
Character states: (0) absent or indistinct; (1) shallow, present within the proximal end of the obturator foramen; (2) deep, and well delineated.
References: Sh(86b):ch. 87; Sh(95).
Notes: This groove or notch is on the medial surface of the ilio-pubis junction at the proximal or dorsal area of the obturator foramen; it transmits obturator vessels and nerve. Among Hominoidea specimens examined, although many pelves of *Pongo* and *Gorilla* have clearly defined notches in an "8-shape," the groove is shallow compared to that of *Pan* and *Homo.*

71. FEMORAL HEAD: FOVEA (pit, or small fossa) for LIGAMENTUM TERES
Character states: (0) does not interrupt margin of articular surface of femoral head; (1) interrupts margin.
References: Be(93):ch. 22; McP(94):ch. 27.
Notes: Be(93, p. 143) coded CS (1) for *Cynocephalus,* yet AMNH 14021 exhibits CS (0), also for *Pteropus* AMNH 249992. Within primate taxa studied, only strepsirhines and *Tarsius* exhibit CS (1). CS (1) is homoplasic since it is randomly found independently in other mammalian orders, and not in all taxa examined.

72. FEMUR, relative thickness of neck
Character states: (0) mean of 102–120; (1) 93–101; (2) less than 93.
References: Fo(86, pp. 100, 103):PC89:2.
Notes: Relative thickness of neck of femur was obtained by comparing diameter of neck to transverse diameter of proximal shaft. A high value indicates wide neck, and a lower value indicates a narrower more constricted neck.

73. FEMORAL THIRD TROCHANTER
Character states: (0) present; (1) absent.
References: Gr(10); Sh(86b):ch. 91; Pr+(88):ch. 28; Sh(95).
Notes: In *Loris* and *Nycticebus,* this trochanter is small to non-existent, and in *Tarsius,* it is very close to the proximal end.

74. FEMORAL CONDYLES
Character states: (0) symmetrical; (1) markedly asymmetrical, i.e., the medial condyle is larger.
References: T+(88, p. 249); Sh(95).
Notes: T+(88, pp. 248–249) employed other characters for Hominoidea; cf. SD(79, pp. 434–435). Some specimens of lemurs (e.g., AMNH 48192) and daubentonids (e.g., AMNH 185643) exhibit slight asymmetry in the size of these condyles.

75. TIBIA, length of fibular facet
Character states: (0) short, tiny, absent, or fused facet; (1) moderately long facet or split distribution; (2) long facet.
References: Fo(86, pp. 86, 95, 96):PC43:1.
Notes: Character states are as given in Fo(86), even though all states are not used here.

76. TIBIA, fibular facet location
Character states: (0) anterior location (or facet absent, or tibia/fibula fused); (1) central location; (2) central or posterior location; (3) posterior location.
References: Fo(86, pp. 86, 95–97):PC46:2.
Notes: Character states are as given in Fo(86), even though all states are not used here.

77. TIBIA, presence of horizontal posterior malleolar groove
Character states: (0) absent; (1) split distribution, some individuals have slight horizontal groove; (2) slight horizontal groove present; (3) marked horizontal groove present.
References: Fo(86, pp. 77, 95, 98):PC54:1.
Notes: Character states are as given in Fo(86), even though all states are not used here. This character is depicted on the cladogram of Fo(86, Fig. 2).

78. FIBULA–CALCANEUM contact
Character states: (0) present; (1) absent.
References: Gr(10); Sh(86b):ch. 98.
Notes: None.

79. ASTRAGALUS–CUBOID contact
Character states: (0) present; (1) absent.
References: Gr(10); Sh(86b):ch. 109; FT(93):ch. 27.
Notes: A slight contact was occasionally observed in some primates, but the vast majority of specimens exhibited CS (1).

80. ASTRAGALUS (TALUS) FIBULAR FACET, viewed posteriorly
Character states: (0) steep, or vertical in relation to trochlear facet; (1) oblique.
References: Ge(86, pp. 423–425):ch. 1 on p. 423; Ge(88, pp. 31–33, 36–37).
Notes: None.

81. ASTRAGALUS (TALUS) TIBIAL FACET on medial side
Character states: (0) extensive, reaches ventral (plantar) side of astragalus; (1) restricted, does not reach plantar side of astragalus.
References: Ge(86, pp. 423–425):ch. 2 on p. 423; Ge(88, pp. 31–33, 36–37).
Notes: Ge(88, p. 36), Table x compares this character for Primates and Tupaia.

82. ASTRAGALUS (TALUS): FLEXOR HALLUCIS LONGUS GROOVE, position on posterior trochlea
Character states: (0) midline; (1) lateral.
References: Ge(86, pp. 423–425):ch. 3 on p. 423; Ge(88, pp. 31–33, 36–37).
Notes: None.

83. NAVICULAR DISTAL FACET
Character states: (0) prominent and clearly defined; (1) poorly defined.
References: Ge(86, pp. 423–425):ch. 4 on p. 423; Ge(88, pp. 31–33, 36–37).
Notes: None.

84. ENTOCUNEIFORM, lateral distal facet on
Character states: (0) extends to a proximal position; (1) no antero-posterior extension.
References: Ge(86, pp. 423–425):ch. 10 on p. 423; Ge(88, pp. 31–33, 36–37).
Notes: None.

85. METATARSALS
Character states: (0) short, ends are narrow; (1) long, distal ends are broad; (2) long, proximal ends are broad.
References: Ge(86, pp. 423–425):ch. 14 on p. 423; Ge(88, pp. 31–33, 36–37).
Notes: None.

86. FIRST METATARSAL PERONEAL TUBERCLE

Character states: (0) very large; (1) large; (2) small.
References: Ge(86, pp. 423–425):ch. 11 on p. 423; Ge(88, pp. 31–33, 36–37).
Notes: None.

87. HALLUX
Character states: (0) long, robust; (1) very long, less robust; (2) short, less robust.
References: Ge(86, pp. 423–425):ch. 12 on p. 423; Ge(88, pp. 31–33, 36–37).
Notes: None.

88. THIRD (III) DIGIT, size of, in pes
Character states: (0) largest; (1) not largest, i.e., digit IV is larger.
References: Ge(86, pp. 423–425):ch. 13 on p. 423; Sh(86b):ch. 84; see also Mivart (1867), Gr(10), and Midlo (1934).
Notes: Articulated pedes are useful but need to verify accuracy of articulation. See also character 89.

89. DIGITS III and IV, relative sizes in pes
Character states: (0) digit III is larger than IV; (1) about equal size.
References: T+(88, p. 139).
Notes: cf. this character to character 88.

BODY: SOFT TISSUE CHARACTERS (CHARACTERS 90–100)

90. CLAWS
Character states: (0) present on all digits; (1) present on all digits except hallux; (2) present on one or two digits only; (3) absent.
References: Modified after Gi(92, p. 201);cf. An(88, p. 159):ch. 41.
Notes: See notes under character 260 about the falcula.

91. STOMACH
Character states: (0) simple, nonsacculated; (1) sacculated.
References: T+(88, p. 139); De(92, p. 218).
Notes: None.

92. UTERUS
Character states: (0) bicornuate; (1) simplex.
References: Lu(80, pp. 352–353):ch. 10.
Notes: None.

93. EMBRYONIC NASAL CAPSULE
Character states: (0) small; (1) enlarged.
References: TA(84, p. 204) who cited sources for this character.
Notes: None.

94. EMBRYONIC DISC
Character states: (0) antimesometrial; (1) orthomesometrial.
References: Lu(93, p. 170):ch. 1.
Notes: None.

95. CHORIOVITELLINE PLACENTA
Character states: (0) present; (1) absent.
References: Lu(93, p. 170):ch. 3; cf. Lu(80, p. 352):ch. 2.
Notes: None.

96. ALLANTOIC DIVERTICULUM
Character states: (0) large; (1) partially vestigial; (2) vestigial.
References: Lu(93, p. 170):ch. 4, slightly modified.
Notes: None.

97. PLACENTA
Character states: (0) epitheliochorial; (1) intermediate stage between epitheliochorial and hemochorial; (2) hemochorial.
References: Lu(93, p. 170):ch. 5; cf. Lu(80, p. 352):ch. 7.
Notes: CS (1) also occurs in Rodentia and Lagomorpha.

98. INTRAPLACENTAL MATERNAL VESSELS
Character states: (0) absent; (1) present.
References: Lu(80, p. 352):ch. 16, also used by Fo(86, p. 86) and TA(84, p. 204).
Notes: None.

99. PLACENTAL HEMATOPOIESIS
Character states: (0) absent; (1) present.
References: Lu(80, p. 352):ch. 17; Fo(86, p. 86); TA(84, p. 204).
Notes: None.

100. OVARIAN INTERSTITIAL GLAND TISSUE DEVELOPMENT
Character states: (0) little or moderate; (1) abundant.
References: Lu(80, p. 352):ch. 18; TA(84, p. 204).
Notes: None.

CHARACTERS 101 THROUGH 264 ARE FROM GROVES (1986, 1995)

101. INTERORBITAL PILLAR
Character states: (0) wide; (1) narrow.
References: G(86, p. 193):Table 5a, ch. 3; G(86, p. 209); G(95); An(87, p. 34):2nd appearing in Table 2.1.
Notes: For this and all other characters of G(86)—most of characters 101–264—the Appendix on pp. 209–216 of Groves (1986) provides details and statistics which may not be available in the tables cited.

102. MIDDLE EAR
Character states: (0) shallow; (1) deepened, more than 8.5 mm.
References: G(86, p. 189):Table 2a, ch. 24; G(86, p. 209); G(95); An(87, p. 39):4th appearing in Table 2.2.
Notes: None.

103. EAR BONES, axis of
Character states: (0) acute angle; (1) right angle or more.
References: G(86, p. 191):Table 4a, ch. 23; G(86, p. 209); G(95).
Notes: None.

104. INNER EAR, area of
Character states: (0) low, <50 mm^2; (1) increased, >50 mm^2.
References: G(86, p. 189:Table 2a, ch. 26; G(95).
Notes: None.

105. MANUBRIUM MALLEI, angle of
Character states: (0) high, above $45°$; (1) more acute.
References: G(86, cf. p. 209); G(95).
Notes: None.

106. KLINORHYNCHY
Character states: (0) airorhynch or straight; (1) more klinorhynch; (2) strongly klinorhynch.
References: G(95), modified after Shea (1988).
Notes: Klinorhynchy is a condition in which there is a deep foreshortened facial skeleton which bends downward with respect to cranial base.

107. FRONTOZYGOMATIC SUTURE
Character states: (0) vertical; (1) medially directed.
References: G(95).
Notes: The bone, zygoma, is also known as jugal or malar.

108. UPPER FACE HEIGHT, relative
Character states: (0) high, index about 70; (1) reduced.
References: G(86, p. 189):Table 2a, ch. 34; G(95).
Notes: None.

109. FACIAL INDEX
Character states: (0) low, about 50; (1) increased.
References: G(86, cf. p. 209); G(95).
Notes: Facial Index is the upper face height as percentage of face breadth.

110. MANDIBULAR SYMPHYSIS
Character states: (0) low, its height about 60% of toothrow length; (1) deepened, at least 75% of toothrow length.
References: G(86, p. 188):Table 1, ch. 15; G(95).
Notes: None.

111. FRONTAL SINUS
Character states: (0) absent; (1) present.
References: G(86, p. 189):Table 2a, ch. 31; G(95), An(87, p. 39): 1st appearing in Table 2.2.
Notes: None.

112. PYRIFORM APERTURE (external naris)
Character states: (0) narrow; (1) widened; (2) very wide.
References: G(86, p. 189):Table 2a, ch. 32; G(95).
Notes: None.

113. INFRAORBITAL FORAMEN
Character states: (0) close to zygomaxillar suture; (1) further
from zygomaxillar suture.
References: G(86, p. 189):Table 2a, ch. 33; G(95); Sc(84, p. 503):
4th appearing in Table 2.
Notes: None.

114. ZYGOMATIC BONE, orientation of
Character states: (0) more frontally; (1) more superolaterally;
(2) still further superolaterally.
References: G(95).
Notes: None.

115. FRONTAL BONE
Character states: (0) flat; (1) more convex; (2) strongly convex.
References: G(95).
Notes: None.

116. GLABELLA PROMINENCE
Character states: (0) strong; (1) reduced; (2) absent.
References: G(86, p. 193):ch. 8 in Table 5a; G(95); An(87, p. 34):
3rd appearing in Table 2.1.
Notes: None.

117. INCISIVE FORAMEN
Character states: (0) double, i.e., one on each side of the midline;
(1) single, confluency of two foramina, at least close to the
surface.
References: G(86, 95); cf. Sc(84, p. 503):14th appearing in Table 2.
Notes: cf. this character to characters 36 and 128.

118. MAXILLARY SINUS
Character states: (0) small; (1) expanded.
References: G(95).
Notes: None.

119. SUPRAORBITAL development
Character states: (0) weak; (1) more marked; (2) torus-like.
References: G(95).
Notes: According to J. H. Schwartz (personal communication,
1995), as described, this character is too simplified; it needs
to be studied in detail.

120. SUPRAORBITAL contour
Character states: (0) arched; (1) less arched.
References: G(95).
Notes: None.

121. ORBITS
Character states: (0) as wide as high; (1) oval dorso-ventrally;
(2) high-oval.
References: G(86, p. 193):ch. 11 in Table 5a; G(95); An(87, p.
34):1st appearing in Table 2.1.
Notes: None.

122. SUPRAORBITAL TRIGON
Character states: (0) not developed; (1) developed.
References: G(95).
Notes: Supraorbital trigon is the triangular area enclosed by
the torus and the backwardly converging temporal lines.

123. NASAL width
Character states: (0) broad; (1) reduced.
References: G(95).
Notes: None.

124. NASALS
Character states: (0) long; (1) shortened.
References: G(95).
Notes: None.

125. NASALS
Character states: (0) taper inferiorly; (1) less tapered.
References: G(95).
Notes: None.

126. ZYGOMATIC FORAMINA
Character states: (0) very small; (1) enlarged.
References: G(86, p. 193):ch. 6 in Table 5a; G(95).
Notes: None.

127. ZYGOMATIC FORAMINA
Character states: (0) at or below plane of orbital rim; (1) above
plane of orbital rim.
References: G(86, p. 193):ch. 7 in Table 5a; G(95).
Notes: None.

128. INCISIVE FORAMINA, size of
Character states: (0) large; (1) reduced in size; (2) tiny.
References: G(86, p. 193):ch. 9 in Table 5a; G(95).
Notes: cf. this character to characters 36 and 117; see notes
there.

129. PALATINE FORAMINA
Character states: (0) large and wide; (1) small and narrow.
References: G(86, p. 193):ch. 10 in Table 5a; G(95); An(87, p.
34):5th appearing in Table 2.1.
Notes: None.

130. PREMAXILLARY SUTURE
Character states: (0) patent in adult; (1) obliterated in adult.
References: G(86, p. 191):Table 4a, ch. 21; G(95).
Notes: None.

131. FORAMEN LACERUM MEDIUM
Character states: (0) absent; (1) present.
References: G(95); cf. Sc(84, p. 503):15th appearing in Table 2.
Notes: This is a small space, bilateral to the anterior edge of the
basioccipital, just behind the suture with the basisphenoid;
bordered laterally by the anterior end of the petrosal. In hu-
mans it is covered over with cartilage but pierced by the as-
cending pharyngeal artery. It is large in *Homo,* small in
Pongo, and absent in *Pan* in which the medial side of the ante-
rior petrosal fills up the gap.

132. TEMPORAL LINES
Character states: (0) converge posteriorly; (1) do not converge.
References: G(95).
Notes: None.

133. LUMBAR VERTEBRAE, NUMBER OF
Character states: (0) high, about 7; (1) reduced in number; (2)
further reduced.
References: G(86, p. 209); G(95).
Notes: None.

134. LUMBAR REGION
Character states: (0) long, 40% length of trunk; (1) shortened,
less than 30% of trunk.
References: G(86, p. 189):Table 2b, ch. 1; G(95).
Notes: None.

135. SACRUM
Character states: (0) short, under 15% of total spine; (1) en-
larged.
References: G(86, p. 209); G(95).
Notes: None.

136. CHEST GIRTH, relative
Character states: (0) narrow, about 150%; (1) increased; (2) very
wide, above 180%.
References: G(86, p. 190):Table 3b, ch. 1; G(95).
Notes: Relative chest girth is an index of chest circumference
as percentage of trunk length.

137. CARPUS
Character states: (0) no conjunct rotation; (1) conjunct rotation.
References: G(86, p. 189):Table 2a, ch. 29; G(86, p. 210); G(95).
Notes: Conjunct rotation is the locking mechanism on the car-
pus in knuckle-walkers. A spiral groove on the hamate (unci-
form) and constriction on the capitate (magnum) guides the
distal carpals into a stable lock.

138. OS CENTRALE
Character states: (0) free; (1) fused with scaphoid in advanced
age; (2) always fused with scaphoid.
References: G(86, p. 189):Table 2a, ch. 30; G(95); An(87, p.39):
5th appearing in Table 2.2.
Notes: None.

139. METACARPAL HEADS, dorsal transverse ridges on
Character states: (0) absent; (1) present.
References: G(95); cf. An(87, p. 42):7th appearing in Table 2.3.
Notes: These ridges define the articular surfaces from the shafts and contribute to the locking mechanism.

140. METACARPAL HEADS, of articular surfaces
Character states: (0) restricted; (1) expanded.
References: G(95); cf. An(87, p. 42):8th appearing in Table 2.3.
Notes: In knuckle-walkers the articular surfaces are extended dorsally on the metacarpals, permitting hyperextension at this joint.

141. HUMERUS robusticity
Character states: (0) high, about 100 Robusticity Index; (1) reduced; (2) humerus slender.
References: G(86, p. 211); G(95).
Notes: None.

142. HUMERAL TORSION
Character states: (0) low; (1) increased; (2) strong.
References: G(86, p. 191):Table 4b, cf. ch. 1; G(86, cf. p. 211); G(95).
Notes: None.

143. HUMERUS, deltoid plane of
Character states: (0) flat; (1) round.
References: G(95).
Notes: None.

144. RADIAL NECK
Character states: (0) narrow; (1) widened compared to head.
References: G(86, p. 211); G(95).
Notes: None.

145. FEMUR–HUMERUS
Character states: (0) index high; (1) index reduced; (2) index low, <100.
References: G(86, p. 189):Table 2b, ch. 4; G(95).
Notes: Index refers to humerus length as percentage of femur length.

146. TALUS (ASTRAGALUS)
Character states: (0) narrow; (1) widened.
References: G(86, p. 189):Table 2a, ch. 4; G(95).
Notes: "Breadth/length index of talus above 80" from G(86, p. 189):Table 2a, ch. 4.

147. HALLUCIAL TARSOMETATARSAL JOINT
Character states: (0) absent; (1) present.
References: G(95), after Conroy (1976).
Notes: None.

148. LOWER LIMB, relative length to trunk length
Character states: (0) low, <120; (1) increased slightly; (2) extremely elongated.
References: G(86, p. 211); G(95).
Notes: None.

149. UPPER LIMB, relative length to lower limbs
Character states: (0) low, <140; (1) increased slightly; (2) extremely elongated; (3) increased even further, i.e., upper limbs are relatively very long compared to the lower limbs.
References: G(86, p. 189):Table 2b, cf. ch. 5; G(95).
Notes: None.

150. FOOT length, relative to trunk length
Character states: (0) low, <50; (1) increased.
References: G(86, p. 211); G(95).
Notes: None.

151. HAND length, relative, as percentage of body height
Character states: (0) low, about 35; (1) increased; (2) further lengthened.
References: G(86, p. 189):Table 2b, ch. 6; G(95).
Notes: "35" refers to relative hand length (i.e., hand length as percentage of body height).

152. FOOT, power arm of
Character states: (0) low, <20% of lever; (1) increased relative to lever; (2) further increased, more than 35% length of lower arm.
References: G(86, p. 191):Table 4c, ch. 2; G(95).
Notes: None.

153. DENTAL DEVELOPMENT
Character states: (0) early relative to epiphyseal fusion; (1) delayed relative to epiphyseal fusion.
References: G(86, p. 189):Table 2a, ch. 7; G(95).
Notes: None.

154. ANKLE (TARSUS) EPIPHYSES
Character states: (0) delayed; (1) not delayed relative to elbow and hip.
References: G(86, p. 191):Table 4a, ch. 5; G(95).
Notes: None.

155. TROCHLEAR KEEL
Character states: (0) poor; (1) more prominent.
References: G(95).
Notes: "Trochlear" refers to the articular surface of humerus with ulna.

156. TROCHLEA
Character states: (0) narrow, not spool-shaped; (1) broad, and spool-shaped.
References: G(95).
Notes: "Trochlea" refers to the articular surface of humerus with ulna.

157. Second CERVICAL SPINE
Character states: (0) short; (1) lengthened; (2) greatly lengthened.
References: G(86, p. 191):Table 4a, cf. ch. 24; G(95).
Notes: None.

158. Fifth CERVICAL SPINE
Character states: (0) short; (1) lengthened; (2) greatly lengthened.
References: G(86, p. 189):Table 2b, ch. 3; G(95).
Notes: None.

159. CANINE, mesial groove of male's
Character states: (0) present; (1) extends onto root; (2) absent.
References: G(86, p. 215); G(95).
Notes: None.

160. CANINE, male's
Character states: (0) high relative to mesiodistal length; (1) lower relative to mesiodistal length.
References: G(86, cf. p. 215); G(95).
Notes: None.

161. I^2 occlusal edge
Character states: (0) slopes distally; (1) does not slope distally.
References: G(86, p. 215); G(95).
Notes: None.

162. CANINES
Character states: (0) slender; (1) more robust.
References: G(86, cf. p. 215); G(95).
Notes: None.

163. MANDIBULAR CANINE, basal keel of
Character states: (0) present; (1) absent.
References: G(86, p. 191):Table 4a, ch. 2; G(95).
Notes: None.

164. PARACONE of upper premolars, basal area
Character states: (0) subequal to protocone; (1) smaller than protocone.
References: G(86, cf. p. 215); G(95).
Notes: None.

165. MOLAR CINGULUM
Character states: (0) prominent, shelf-like; (1) reduced, incomplete; (2) fragmented or absent.
References: G(95), after Swindler and Olshan (1988); cf. Sc(84, p. 503):12th appearing in Table 2.
Notes: None.

166. PROTOCONID APEX on dP_3
Character states: (0) more lingual from the median axis; (1) located bucally from the median axis.
References: G(95), after Swarts (1988).
Notes: None.

167. METACONID of dP_3
Character states: (0) present; (1) absent.

References: G(95), after Swarts (1988).
Notes: None.

168. PROTOCRISTID of dP$_3$
Character states: (0) aligned with tooth mesiodistal axis; (1) angled.
References: G(95), after Swarts (1988).
Notes: None.

169. TALONID BASIN of dP$_3$
Character states: (0) open distally; (1) closed.
References: G(95), after Swarts (1988).
Notes: None.

170. METACONID of dP$_4$
Character states: (0) subequal to protoconid; (1) increased relative to protoconid on dP$_4$.
References: G(95), after Swindler and Olshan (1988).
Notes: None.

171. CRISTA OBLIQUA on dP$_4$
Character states: (0) does not reach protoconid apex; (1) reaches protoconid apex.
References: G(95), after Swarts (1988).
Notes: None.

172. TALONID BASIN on dP$_4$
Character states: (0) open distally; (1) closed.
References: G(95), after Swarts (1988).
Notes: None.

173. PROTOCONE of dP^3, in crown view
Character states: (0) larger than paracone; (1) smaller than paracone.
References: G(95), after Swarts (1988).
Notes: None.

174. PREPROTOCRISTA of dP^4
Character states: (0) weak; (1) more developed.
References: G(95), after Swarts (1988).
Notes: None.

175. POSTPROTOCRISTA of dP^4
Character states: (0) poor; (1) more developed; (2) still more developed.
References: G(95), after Swarts (1988).
Notes: None.

176. MOLARS, protocristid grooves of
Character states: (0) prominent; (1) barely visible.
References: G(86, p. 191):Table 4a, ch. 22; G(95), after Swindler and Olshan (1988).
Notes: None.

177. MOLARS, lingual marginal ridges of
Character states: (0) hardly appreciable; (1) more prominent; (2) very prominent.
References: G(86, p. 216, 5th character from top); G(95).
Notes: None.

178. ENAMEL thickness on molar
Character states: (0) thin; (1) increased thickness; (2) very thick.
References: G(95); An(87, p. 42):4th appearing in Table 2.3; cf. Sc(84, p. 503):11th appearing in Table 2.
Notes: In addition to citations under References, Martin, L. B. (1983), "The Relationships of the Later Miocene Hominoidea," Ph.D. thesis, London Univ., may be consulted.

179. PATTERN 3 ENAMEL, proportion of
Character states: (0) high; (1) reduced; (2) very reduced.
References: G(95); An(87, p. 34):11th appearing in Table 2.1, also An(87, p. 42):5th appearing in Table 3.2.
Notes: Martin (1983, cited in notes for character 178) devised elaborate methods of estimating thickness and proportion of enamel types. According to J. H. Schwartz (personal communication, 1995), this character is no longer valid.

180. HAMSTRINGS, relative mass of
Character states: (0) great; (1) reduced.
References: G(95).
Notes: None.

181. LONG FIBULAR FLEXOR
Character states: (0) extends to toe of digit IV; (1) withdrawn from digit IV.
References: G(86, p. 210); G(95).
Notes: None.

182. LONG TIBIAL FLEXOR
Character states: (0) extends to toe of digit I; (1) withdrawn from digit I.
References: G(86, p. 210); G(95).
Notes: None.

183. FLEXOR POLLICIS BREVIS, deep head of
Character states: (0) large; (1) reduced.
References: G(86, p. 191):Table 4b, ch. 2; G(95).
Notes: None.

184. FLEXOR POLLICIS LONGUS
Character states: (0) present, of normal size; (1) reduced; (2) absent.
References: G(86, p. 210); G(95).
Notes: According to J. H. Schwartz (personal communication, 1995), *Pongo* should be coded CS (2).

185. GENIOGLOSSAL insertion
Character states: (0) above inferior transverse torus of internal (or posterior) of mandibular symphysis; (1) shifted to inferior transverse torus.
References: G(86, p. 210); G(95).
Notes: None.

186. GENIOHYOIDEUS insertion
Character states: (0) basally on inferior transverse torus; (1) higher on inferior transverse torus; (2) above inferior transverse torus.
References: G(86, p. 210); G(95).
Notes: None.

187. DIGASTRIC, insertion of
Character states: (0) posterior to inferior transverse torus; (1) inferior transverse torus; (2) not on symphysis.
References: G(86, p. 210);G(95).
Notes: None.

188. EXTRINSIC PEDAL FLEXORS
Character states: (0) small; (1) increased; (2) enlarged.
References: G(95).
Notes: None.

189. VASTI, relative mass of
Character states: (0) small; (1) increased; (2) further increased.
References: G(95).
Notes: None.

190. RIGHT LUNG
Character states: (0) 4 lobes; (1) fewer than 4 lobes.
References: G(86, p. 191):Table 4a, ch. 18; G(86, p. 193):Table 5a, ch. 21; G(95).
Notes: None.

191. LARYNGEAL AIR SAC
Character states: (0) small or absent; (1) enlarged.
References: G(86, p. 212); G(95).
Notes: None.

192. TUBERCULUM CUNEIFORME
Character states: (0) large; (1) reduced.
References: G(86, p. 212); G(95); An(87, p. 39):11th appearing in Table 2.2.
Notes: Tuberculum cuneiforme (or Wrisberg's tubercle) is a cartilaginous nodule on the posterior end of the plica aryepiglottica of the larynx.

193. CAECUM
Character states: (0) long; (1) shortened relative to small intestine.
References: G(86, p. 212); G(95).
Notes: None.

194. APPENDIX, VERMIFORM
Character states: (0) absent or short; (1) lengthened relative to caecum; (2) very long.
References: G(86, p. 212); G(95).
Notes: None.

195. APPENDIX, VERMIFORM
Character states: (0) spiral; (1) straightened, less spiraled; (2) straight.
References: G(86, p. 212); G(95).
Notes: None.

196. KIDNEY type
Character states: (0) type C; (1) type B; (2) type E.
References: G(86, p. 212); G(95).
Notes: Kidney type C, refers to a kidney with one primary pyramid, ending in an undivided papilla; type B, as in C, but ending in a ledge divided by one or more grooves; type E, as in C, but with two or more primary pyramids, each ending in a primary papilla.

197. SMALL INTESTINE
Character states: (0) short; (1) lengthened relative to head + body.
References: G(86, p. 212); G(95).
Notes: None.

198. VALVULAE CONNIVENTES
Character states: (0) absent, or develop early; (1) found in adults only.
References: G(86, p. 188):Table 1, ch. 13; G(86, p. 191):Table 4c, ch. 8; G(86, p. 193):Table 5a, ch. 22; G(86, p. 212); G(95).
Notes: Valvulae conniventes are large (nonmuscular) folds or flaps projecting into the intestinal lumen. "develop early" means that they develop before the adult stage.

199. RECTUM FLEXURE
Character states: (0) absent; (1) present.
References: G(86, p. 191):Table 4c, ch. 2; G(86, p. 212); G(95).
Notes: None.

200. PAROTID GLAND
Character states: (0) postero-ventral to ear; (1) shifted forward relative to ear; (2) shifted well forward.
References: G(86, p. 212); G(95).
Notes: None.

201. PAROTID GLAND, accessory lobes of
Character states: (0) none; (1) developed.
References: G(86, p. 190):Table 3c, ch. 7; G(86, p. 212); G(95).
Notes: None.

202. PAROTID GLAND
Character states: (0) overlies sternomastoid muscle; (1) freed from sternomastoid muscle.
References: G(86, p. 191):Table 4a, ch. 20; G(86, p. 212); G(95).
Notes: None.

203. PAROTID GLAND, orifice of
Character states: (0) level with molars; (1) shifted forward.
References: G(86, p. 189):Table 2b, ch. 8; G(95).
Notes: None.

204. SUBMANDIBULAR and SUBLINGUAL GLANDS, orifices of
Character states: (0) separate; (1) confluent.
References: G(86, p. 189):Table 2a, ch. 25; G(86, p. 212); G(95).
Notes: None.

205. FUNGIFORM PAPILLAE, of tongue
Character states: (0) on sides and apex; (1) concentrated on apex; (2) fully concentrated on apex.
References: G(86, p. 189):Table 2a, ch. 8; G(86, p.193):Table 5a, ch. 18; G(86, p. 213); G(95); An(87, p. 34):19th appearing in Table 2.1; cf. Kardong (1995, p. 677).
Notes: None.

206. FOLIATE PAPILLAE
Character states: (0) on lateral of tongue; (1) shifted to dorsum of tongue.
References: G(86, p. 190):Table 3b, ch. 4; G(86, p. 213); G(95); An(87, p. 34):18th appearing in Table 2.1.
Notes: None.

207. FRENULUM
Character states: (0) absent or poorly developed; (1) developed.
References: G(86, p. 193):ch. 16 in Table 5a; G(86, p. 213); G(95).
Notes: None.

208. PALATINE ridges
Character states: (0) regular; (1) irregular; (2) asymmetrical.
References: G(86, p. 188):Table 1, ch. 7; G(86, p. 213); G(95).
Notes: "Irregular" refers to when palatine ridges are short, not continuous ridges.

209. PALATINE ridges
Character states: (0) on whole palate; (1) restricted in extent; (2) very reduced.
References: G(86, p. 189):Table 2a, ch. 9; G(86, p. 213); G(95).
Notes: None.

210. ILEO-CAECAL VALVE
Character states: (0) slit-like; (1) widened; (2) wide.
References: G(86, p. 189):Table 2a, cf. ch. 10; G(86, p. 213); G(95).
Notes: "wide" means "oval," and "widened" is more compressed than this, but not slit-like.

211. ILEO-CAECAL VALVE, number of folds of
Character states: (0) one; (1) more than one.
References: G(86, p. 213); G(95).
Notes: None.

212. LIVER, number of lobes of
Character states: (0) four; (1) less than four.
References: G(86, p. 191):Table 4a, ch. 6; G(86, p. 213); G(95).
Notes: None.

213. TUBERCULUM INTERVENOSUM in heart
Character states: (0) large, i.e., well-marked; (1) reduced, i.e., poorly marked.
References: G(86, p. 213); G(95).
Notes: None.

214. ANTERIOR PAPILLARY MUSCLE of heart
Character states: (0) multiple; (1) reduced.
References: G(86, p. 189):Table 2a, ch. 14; G(86, p. 213); G(95).
Notes: None.

215. HEART, cranial end of
Character states: (0) level with ribs 2–3; (1) shifted upward; (2) shifted further upward.
References: G(86, p. 191):Table 4a, cf. ch. 14; G(86, p. 213); G(95).
Notes: The level of heart in this and the next character relate partly to heart size and partly to its positioning in the thorax.

216. HEART, caudal end of
Character states: (0) level with rib 6; (1) shifted downward.
References: G(86, p. 191):Table 4a, cf. ch. 15; G(86, p. 213); G(95).
Notes: See under character 215.

217. THORACICALIS SUPREMA ARTERY
Character states: (0) present; (1) absent.
References: G(86, p. 191):Table 4a, ch. 16; G(86, p. 214); G(95).
Notes: None.

218. RECURRENS RADIALIS ARTERY origin
Character states: (0) from radialis artery; (1) shifted to brachialis artery.
References: G(86, p. 214); G(95).
Notes: None.

219. RECURRENS ULNARIS ARTERY
Character states: (0) split to communis and interossea; (1) split to anterior and posterior branches.
References: G(86, p. 189):Table 2a, ch. 15; G(95).
Notes: None.

220. ENCEPHALIZATION
Character states: (0) low, <10; (1) increased, 10–11; (2) high, >11.
References: G(95), after Ziller and Rehlkämper (1988).
Notes: None.

221. PALAEOCORTEX INDEX
Character states: (0) small, <0.5; (1) relatively enlarged, 0.5–0.8; (2) much enlarged, >0.8.
References: G(95), after Ziller and Rehlkämper (1988).
Notes: None.

222. CEREBRUM, frontal pole of
Character states: (0) narrow; (1) broadened.
References: G(95), after Ziller and Rehlkämper (1988).
Notes: None.

223. RECEPTIVITY, female's
Character states: (0) restricted; (1) less restricted; (2) unrestricted.
References: G(86, p. 214); G(95).
Notes: None.

224. PUBERTY
Character states: (0) reached at <3 years; (1) slightly delayed, reached at 3–5 years; (2) delayed, reached at 6–7 years; (3) further delayed, reached at >7 years.
References: G(86, p. 191):Table 4a, ch. 7; G(95).
Notes: None.

225. OVUM
Character states: (0) small, about 100 µm; (1) enlarged.
References: G(86, p. 214); G(95).
Notes: None.

226. MITOCHONDRIAL COILS
Character states: (0) many, 30–50; (1) reduced in number.
References: G(86, p. 214); G(95).
Notes: None.

227. TESTES
Character states: (0) >0.5% of body weight; (1) from 0.1 to 0.5% relative to body weight; (2) very small 0.05–0.1% of body weight; (3) even smaller, <0.05% of body weight.
References: G(86, p. 190):Table 3b, ch. 7; G(86, p. 191):Table 4c, cf. ch. 10; G(95).
Notes: None.

228. SCROTUM
Character states: (0) less pendulous; (1) pendulous.
References: G(86, p. 191):Table 4a, ch. 8; G(95).
Notes: None.

229. PROCESSUS VAGINALIS
Character states: (0) persists in adult; (1) obliterated in adult.
References: G(86, p. 189):Table 2a, ch. 11; G(95); An(87, p. 34): 13th appearing in Table 2.1.
Notes: None.

230. OVARIES
Character states: (0) small; (1) enlarged, more than 20 mm long; (2) very large, more than 40 mm long.
References: G(86, p. 188):Table 1, ch. 8; G(86, p. 191):Table 4c, ch. 11; G(95).
Notes: None.

231. UTERUS
Character states: (0) small; (1) enlarged, above 37 mm.
References: G(86, p. 189):Table 2a, ch. 12; G(95); An(87, p. 39): 7th appearing in Table 2.2.
Notes: None.

232. UTERINE FUNDUS
Character states: (0) globular; (1) flattened.
References: G(86, p. 191):Table 4a, ch. 9; G(95).
Notes: None.

233. GLANS PENIS, corona of
Character states: (0) present; (1) reduced.
References: G(86, p. 214); G(95).
Notes: See also Po(18).

234. BACULUM
Character states: (0) long, over 20 mm; (1) reduced; (2) tiny or absent.
References: G(86, p. 191):Table 4a, ch. 10; G(86, p. 193):Table 5d, ch. 14; G(95).
Notes: See also Po(18).

235. PENIS, when erect
Character states: (0) short; (1) lengthened, over 80 mm.
References: G(86, p. 191):Table 4a, ch. 11; G(95).
Notes: See also Po(18).

236. LABIA MINORA
Character states: (0) small or absent; (1) developed.
References: G(86, p. 191):Table 4a, ch. 12; G(86, p. 214); G(95).
Notes: See also Po(18).

237. OESTRIOL concentration in pregnancy
Character states: (0) low level; (1) raised concentration.
References: G(95), after Czekala et al. (1988); cf. Sc(84, p. 503): 25th appearing in Table 2.
Notes: None.

238. PREGNANEDIOL concentration in pregnancy
Character states: (0) low level; (1) raised.
References: G(95), after Czekala et al. (1988).
Notes: None.

239. FLUORESCENT F BODY
Character states: (0) none; (1) present in sperm.
References: G(86, p. 191):Table 4c, ch. 3; G(95).
Notes: None.

240. MAMMARY DEVELOPMENT IN FEMALE
Character states: (0) none; (1) present, at least from first pregnancy.
References: G(86, p. 188):Table 1, ch. 9; G(95).
Notes: None.

241. OESTRUS SWELLING in female
Character states: (0) large and prominent; (1) reduced.
References: G(86, p. 215); G(95).
Notes: None.

242. PLANTAR pattern intensity
Character states: (0) less than palmar; (1) predominates over palmar.
References: G(86, p. 189):Table 2a, ch. 2; G(95).
Notes: None.

243. THENAR pattern intensity
Character states: (0) less than hypothenar on sole; (1) predominates over hypothenar on sole; (2) greatly predominates over hypothenar on sole.
References: G(86, p. 211); G(95); MC(42).
Notes: None.

244. HYPOTHENAR pattern intensity
Character states: (0) less than thenar on palm; (1) predominates over thenar on palm.
References: G(86, p. 211); G(95); MC(42).
Notes: None.

245. PALMAR AND PLANTAR, development of transverse pattern groups
Character states: (0) distal group expressed less than proximal; (1) distal group predominate over proximal.
References: G(86, p. 211); G(95); MC(42).
Notes: None.

246. EAR breadth
Character states: (0) >75% of height; (1) breadth less relative to height.
References: G(86, p. 191):Table 4c, ch. 6; G(95).
Notes: None.

247. EAR LOBE
Character states: (0) absent; (1) present.
References: G(86, p. 189):Table 2a, ch. 27; G(95).
Notes: None.

248. UPPER EAR height
Character states: (0) high; (1) reduced; (2) very reduced, less than 40% of ear length.
References: G(86, p. 190):Table 3c, ch. 2; G(95).
Notes: None.

249. APOCRINE GLANDS
Character states: (0) many; (1) reduced over body surface.
References: G(86, p. 189):Table 2a, ch. 16; G(95); An(87, p. 39): 8th appearing in Table 2.2.
Notes: None.

250. ECCRINE GLANDS
Character states: (0) few over body surface; (1) increased over body surface; (2) predominate over body surface.

References: G(86, p. 189):Table 2a, ch. 16; G(95); An(87, p. 39): 9th appearing in Table 2.2.
Notes: None.

251. AXILLARY ORGAN
Character states: (0) absent; (1) small; (2) developed, elaborate, and specialized.
References: G(86, p. 188):Table 1, ch.10; G(86, p. 189):Table 2a, ch. 17; G(95); An(87, p. 34):16th appearing in Table 2.1, and An(87, p. 39):10th appearing in Table 2.2.
Notes: None.

252. APOCRINE GLANDS, orifices of
Character states: (0) well inside follicles; (1) nearer to body surface.
References: G(86, p. 216); G(95).
Notes: None.

253. SEBACEOUS GLANDS
Character states: (0) large; (1) reduced in size.
References: G(86, p. 216); G(95).
Notes: None.

254. HAIR DENSITY on scalp
Character states: (0) $>650/cm^2$; (1) reduced; (2) further reduced.
References: G(86, p. 189):Table 2a, cf. ch. 19; G(95); An(87, p. 34):17th appearing in Table 2.1.
Notes: None.

255. HAIR DENSITY on back
Character states: (0) $>450/cm^2$; (1) reduced, under $200/cm^2$; (2) further reduced.
References: G(86, p. 188):Table 1, ch. 11; G(86, p. 191):Table 4a, cf. ch. 17; G(95).
Notes: None.

256. HAIR DENSITY on chest
Character states: (0) more than $100/cm^2$; (1) reduced, under $100/cm^2$; (2) very sparse, $5/cm^2$ or less.
References: G(86, p. 188):Table 1, ch. 11; G(86, p. 191):Table 4c, ch. 2; G(95).
Notes: None.

257. SEXUAL DIMORPHISM expressed in body size
Character states: (0) expressed as male larger than female; (1) reduced sexual dimorphism in body size.

References: G(95).
Notes: None.

258. MEISSNER'S CORPUSCLES
Character states: (0) absent; (1) present.
References: G(95), after Zollman and Winkelmann (1965).
Notes: May be present in other mammalian orders, not only primates.

259. INCISORS and MIDDLE CANINES
Character states: (0) nontoothcomb; (1) toothcomb.
References: G(91, p. 201); cf. TA(84, pp. 191–202); cf. An(88, p. 159):ch. 43.
Notes: None.

260. FALCULA
Character states: (0) deep stratum about 60% or more of claw; (1) deep stratum <60% of claw; (2) deep stratum absent.
References: G(91, pp. 75–76).
Notes: The falcula, which is in essence a mammalian claw, contains deep stratum and superficial stratum. A nail may have a deep stratum, and a claw may lack one; cf. this character to character 90 [see also LGC(71, p. 172)].

261. Concentration of PNEUMATIZATION in central and posterior parts of TYMPANIC ROOF rather than in TYMPANIC FLOOR
Character states: (0) absent; (1) present.
References: McP(81), cited in G(91, p. 78).
Notes: None.

262. ANTERIOR CAROTID ARTERY (anastomosis) between the ascending pharyngeal and promontory arteries
Character states: (0) absent; (1) present.
References: G(91, p. 79); Sc(86):chs. 9, 14.
Notes: None.

263. STAPEDIAL ARTERY
Character states: (0) present; (1) absent in adult.
References: G(91, p. 79).
Notes: None.

264. FACIAL SKELETON
Character states: (0) hafted wholly in front of braincase; (1) hafted partly below braincase.
References: Groves, personal observation, 1995.
Notes: None.

APPENDIX 3: DATA MATRIX FOR MORPHOLOGICAL CHARACTERS 1 THROUGH 264[2]

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
1 Solenodon	0	0	0	0	0	0	0	0	0	1	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
2 Tupaia	0	0	1	0	0	0	0	0	0	0	0	0	2	1	0	1	1	1	1	1	1	1	1	0	0	2	1	0	0	0	0	1	0
3 Cynocephalus	0	0	0	0	0	0	0	0	0	1	0	1	2	1	0	1	0	1	2	0	0	0	1	0	3	2	1	0	0	0	0	1	0
4 Pteropus	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	0	3	0	0	1	1	0	2	1	1	1	0	0	0	1	0
5 Lemur	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	1	1	0	0	1	0	1	0	0	1	0	0	1	0
6 Daubentonia	1	0	1	0	0	0	0	0	0	1	0	0	3	0	0	1	0	1	1	1	0	0	0	1	0	1	0	0	2	1	2	0	1
7 Loris	1	0	1	0	0	0	0	0	0	1	0	0	3	0	0	0	0	1	0	1	0	0	0	1	3	1	0	0	1	1	0	0	0
8 Nycticebus	1	0	1	0	0	0	0	0	0	1	0	0	3	0	0	1	0	1	1	0	0	0	0	1	3	1	0	0	1	0	2	1	0
9 Tarsius	1	0	1	0	0	0	0	0	0	1	0	0	3	0	0	1	1	1	1	0	0	0	?	1	1	1	0	1	2	1	0	0	0
10 Leontopithecus	1	1	1	1	1	0	1	1	1	1	1	0	3	0	0	1	?	1	1	0	0	0	?	1	1	1	0	1	1	1	1	1	0
11 Aotus	1	1	1	1	1	0	1	1	1	1	1	0	3	0	0	1	?	1	1	0	0	0	?	1	1	1	0	1	1	1	1	1	0
12 Cebus	1	1	1	1	1	0	1	1	1	1	1	0	3	0	0	1	?	1	1	0	0	0	?	1	1	1	0	1	0	0	2	1	0
13 Saimiri	1	1	1	1	1	0	1	1	1	1	1	0	3	0	0	1	?	1	1	0	0	0	?	1	1	1	0	1	1	0	2	1	0
14 Macaca	0	1	1	1	1	1	1	1	0	2	1	0	3	0	0	0	?	1	1	0	0	0	?	1	1	1	0	1	1	0	2	1	1
15 Papio	0	1	1	1	1	1	1	0	0	2	1	0	3	0	0	1	?	1	1	0	0	0	?	1	3	1	0	1	1	0	2	1	1
16 Colobus	1	1	1	1	1	0	1	1	1	2	1	0	3	0	0	1	?	1	0	0	0	0	?	1	1	1	0	1	1	0	2	1	1
17 Presbytis	1	1	1	1	1	0	1	1	1	2	1	0	3	0	0	1	?	1	1	0	0	0	?	1	1	1	0	1	1	0	2	1	1
18 Hylobates	1	1	1	1	1	0	1	0	1	3	1	2	3	0	0	1	?	0	1	0	0	0	?	1	1	1	0	1	2	1	2	1	0
19 Pongo	1	1	1	1	1	1	1	1	1	3	1	3	3	0	0	0	?	1	1	0	0	0	?	1	1	1	0	1	2	1	2	1	0
20 Gorilla	1	1	1	1	1	0	1	0	1	1	1	3	3	0	0	1	?	1	1	0	0	0	?	1	1	1	0	1	1	1	2	1	0
21 Pan	1	1	1	1	1	0	1	1	1	3	1	3	3	0	0	0	?	1	0	0	0	0	?	1	1	1	0	1	2	1	2	1	1
22 Homo	1	1	1	1	1	0	1	0	1	3	1	3	3	0	0	1	?	1	1	0	0	0	?	1	1	1	0	1	3	?	2	1	1

	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66
1 Solenodon	0	?	0	1	1	1	0	0	0	0	?	0	0	2	0	0	0	0	0	0	0	0	?	0	0	0	0	1	0	?	?	0	1
2 Tupaia	0	0	0	1	0	1	2	?	1	0	?	0	0	0	0	0	0	0	0	0	0	0	?	0	1	0	0	1	0	?	?	0	1
3 Cynocephalus	0	1	0	1	0	1	0	1	0	0	?	0	0	?	0	1	0	0	0	0	0	0	?	0	1	1	1	1	0	?	?	0	1
4 Pteropus	0	0	1	0	1	1	0	0	1	0	?	0	0	0	0	0	0	0	0	0	0	0	?	0	1	1	0	0	1	0	0	0	1
5 Lemur	0	?	0	0	0	1	0	0	1	0	?	0	0	0	0	0	0	0	0	0	0	0	?	0	1	0	1	0	0	0	0	0	0
6 Daubentonia	0	1	0	0	0	1	0	0	1	0	?	0	0	1	0	0	0	0	0	0	0	0	?	0	0	1	1	0	0	?	0	0	0
7 Loris	0	0	0	1	0	1	0	0	1	0	?	0	0	0	0	0	1	1	0	0	0	0	?	0	0	0	1	1	0	?	0	0	0
8 Nycticebus	0	0	0	0	1	1	0	0	1	0	?	0	0	0	0	0	1	1	0	1	0	0	?	0	0	1	0	0	0	?	0	0	0
9 Tarsius	0	0	0	0	1	1	1	0	3	0	?	0	0	2	0	0	1	0	0	1	1	1	0	1	1	1	1	0	0	1	1	0	0
10 Leontopithecus	0	?	0	1	1	1	1	2	2	1	?	1	0	2	0	0	1	0	1	0	1	1	0	1	0	1	1	0	1	2	3	0	0
11 Aotus	0	1	0	1	1	1	2	0	2	1	?	1	0	0	0	0	1	0	1	0	0	1	0	1	1	0	1	0	0	2	2	0	0
12 Cebus	0	1	0	1	1	1	2	0	2	1	?	1	0	0	0	0	1	0	1	0	1	1	1	1	1	1	0	0	0	2	2	0	0
13 Saimiri	0	1	0	1	1	1	2	0	2	1	?	1	0	1	0	0	1	0	1	0	0	1	1	1	1	0	1	0	0	0	0	0	0
14 Macaca	0	1	0	1	1	1	1	1	3	2	?	1	1	1	1	1	1	0	1	1	1	1	?	1	1	0	1	0	0	0	0	0	0
15 Papio	0	0	0	1	1	1	1	1	3	2	?	1	0	0	1	1	1	1	1	0	1	1	?	0	0	0	1	1	0	0	0	0	0
16 Colobus	1	1	0	1	1	1	1	1	3	2	?	1	0	0	1	1	1	1	1	0	1	1	?	1	1	1	1	0	1	0	0	0	0
17 Presbytis	1	1	0	1	1	1	2	0	3	2	1	1	0	0	1	1	1	0	1	0	1	1	?	1	1	0	1	0	1	0	0	0	0
18 Hylobates	0	1	1	1	1	1	1	1	3	2	1	1	0	0	2	1	0	0	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
19 Pongo	0	1	1	1	1	1	1	1	3	2	1	1	1	2	2	1	0	0	1	0	1	1	?	1	1	0	1	1	1	0	0	1	0
20 Gorilla	0	1	1	1	1	1	1	1	3	2	1	1	0	2	1	1	1	1	1	0	1	1	?	1	1	0	1	1	1	0	0	2	0
21 Pan	0	1	1	1	1	1	1	1	3	2	1	1	1	1	3	1	0	0	1	0	1	1	?	1	1	0	1	0	1	0	0	2	0
22 Homo	0	?	1	1	1	1	1	1	3	2	1	1	0	1	3	1	0	0	1	0	1	1	?	1	1	0	1	0	1	0	0	2	0

[2] Definitions of these characters are given in Appendix 2.

		67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99
1	*Solenodon*	0	0	0	0	0	?	0	0	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0
2	*Tupaia*	0	0	0	0	0	?	0	0	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0
3	*Cynocephalus*	0	1	0	0	0	?	0	0	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	1	1	2	0	0
4	*Pteropus*	0	1	0	0	0	?	1	0	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	1	1	0	0
5	*Lemur*	0	1	0	0	0	?	0	0	0	0	?	1	1	1	0	1	0	0	0	0	0	1	0	2	0	0	?	1	0	0	0	0	0
6	*Daubentonia*	0	1	0	0	1	?	0	0	0	0	?	1	1	1	0	1	0	0	0	0	0	1	0	1	0	0	?	1	0	0	0	0	0
7	*Loris*	0	1	0	0	1	?	0	0	0	0	?	1	1	1	0	1	0	0	0	0	0	1	0	2	0	0	?	1	0	0	0	0	0
8	*Nycticebus*	0	1	0	0	1	?	0	0	0	0	?	1	1	1	0	1	0	0	0	0	0	1	0	2	0	0	?	1	0	0	0	0	0
9	*Tarsius*	0	1	0	0	1	?	0	0	0	0	?	1	1	0	0	0	0	0	1	1	1	1	0	2	0	0	?	1	1	2	2	0	0
10	*Leontopithecus*	0	1	0	0	0	1	0	0	1	2	3	1	1	0	1	0	1	1	2	2	2	0	0	1	0	1	1	1	1	2	2	1	1
11	*Aotus*	0	1	0	0	0	0	0	0	2	2	1	1	1	0	1	0	1	1	2	2	2	0	0	3	0	1	1	1	1	2	2	1	1
12	*Cebus*	0	1	0	0	0	2	1	0	1	3	1	1	1	0	1	0	1	1	2	2	2	0	0	3	0	1	1	1	1	2	2	1	1
13	*Saimiri*	0	1	0	0	0	2	1	0	1	2	1	1	1	0	1	0	1	1	2	2	2	0	0	3	0	1	1	1	1	2	2	1	1
14	*Macaca*	0	1	0	0	0	?	1	0	0	0	?	1	1	0	1	0	1	1	2	2	2	0	0	3	0	1	?	1	1	2	2	0	0
15	*Papio*	0	1	0	0	0	?	1	0	0	0	?	1	1	0	1	0	1	1	2	2	2	0	0	3	0	1	?	1	1	2	2	0	0
16	*Colobus*	1	1	0	1	0	?	1	0	0	0	?	1	1	0	1	0	1	1	2	2	2	0	1	3	1	1	?	1	1	2	2	0	0
17	*Presbytis*	1	1	0	1	0	?	1	0	0	0	?	1	1	0	1	0	1	1	2	2	2	0	1	3	1	1	?	1	1	2	2	0	0
18	*Hylobates*	0	1	0	0	0	?	1	1	0	0	?	1	1	0	1	0	1	1	2	2	2	0	0	3	0	1	?	1	1	2	2	0	0
19	*Pongo*	0	1	1	1	0	?	1	1	0	0	?	1	1	0	1	0	1	1	2	2	2	0	0	3	0	1	?	1	1	2	2	0	0
20	*Gorilla*	0	1	1	1	0	?	1	1	0	0	?	1	1	0	1	0	1	1	2	2	2	0	0	3	0	1	?	1	1	2	2	0	0
21	*Pan*	0	1	1	2	0	?	1	1	0	0	?	1	1	0	1	0	1	1	2	2	2	0	0	3	0	1	?	1	1	2	2	0	0
22	*Homo*	0	1	1	2	0	?	1	1	0	0	?	1	1	0	1	0	1	1	2	2	2	0	0	3	0	1	?	1	1	2	2	0	0

		100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132
1	*Solenodon*	0	0	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	?	?	?	1	?	1	?
2	*Tupaia*	0	0	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	?	?	?	1	?	0	?
3	*Cynocephalus*	0	0	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	1	?	?	?	1	?	1	?
4	*Pteropus*	0	0	?	?	?	?	0	0	0	1	0	0	0	0	0	0	2	?	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0
5	*Lemur*	0	0	?	?	?	?	0	1	0	0	1	0	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1
6	*Daubentonia*	0	0	?	?	?	?	0	0	0	0	0	0	0	1	0	1	2	0	1	0	0	0	0	?	1	1	0	1	0	1	0	0	1
7	*Loris*	0	1	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	1	?	?	0	1	?	?	?
8	*Nycticebus*	0	1	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	1	?	?	0	1	?	?	?
9	*Tarsius*	0	1	?	?	?	?	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	1
10	*Leontopithecus*	1	0	?	?	?	?	0	1	1	0	1	0	0	1	1	2	1	0	0	1	1	0	0	0	1	1	1	0	0	0	0	1	1
11	*Aotus*	1	1	?	?	?	?	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	0	?	?	?	?
12	*Cebus*	1	1	?	?	?	?	0	0	1	0	1	0	0	1	0	2	1	1	0	0	0	1	0	0	1	1	0	0	0	0	0	1	1
13	*Saimiri*	1	1	?	?	?	?	0	0	1	0	?	0	0	1	0	2	1	1	0	0	0	1	0	1	0	0	0	1	0	0	0	1	1
14	*Macaca*	0	1	?	?	?	?	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0
15	*Papio*	0	1	?	?	?	?	0	0	0	1	1	0	0	0	1	0	0	1	0	2	1	0	1	0	0	0	0	0	0	0	0	1	0
16	*Colobus*	0	0	?	?	?	?	0	0	0	0	1	0	0	1	1	2	0	0	0	1	1	0	1	0	1	1	0	1	0	0	0	1	1
17	*Presbytis*	0	0	?	?	?	?	0	0	0	0	1	0	0	0	1	2	0	0	0	1	1	0	1	0	1	1	0	1	0	0	0	1	1
18	*Hylobates*	0	0	0	1	0	1	1	0	1	0	0	0	2	0	0	1	2	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1
19	*Pongo*	0	1	0	1	0	1	0	1	0	1	1	0	1	1	1	2	1	1	1	0	0	2	1	1	0	0	1	1	2	1	0	1	0
20	*Gorilla*	0	0	1	1	1	0	2	0	0	1	1	1	2	0	2	0	0	0	0	2	1	0	1	0	0	0	0	0	1	0	0	0	0
21	*Pan*	0	0	1	0	1	1	2	0	0	1	1	1	2	0	2	0	0	0	0	2	0	0	1	0	0	0	0	0	1	0	1	0	0
22	*Homo*	0	0	1	0	1	0	2	0	1	0	0	1	2	0	2	2	0	1	0	2	0	0	0	0	1	0	0	0	1	0	1	1	1

		133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165
1	Solenodon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	?	?	0	0	0	0	0	0	0	?	?	?	?	?	?	?
2	Tupaia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	?	?	0	0	0	0	0	0	0	?	?	?	?	?	?	?
3	Cynocephalus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	?	?	0	0	0	0	0	0	0	2	0	?	?	1	1	1
4	Pteropus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	?	?	0	0	0	0	0	0	0	2	0	0	1	1	1	1
5	Lemur	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	2	2	0	0	0	1	0
6	Daubentonia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	1	1	0	0	0	0	0	0	0	2	?	?	0	1	1	1
7	Loris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	2	0	?	?	?	1	?
8	Nycticebus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	2	?	0	?	1	1
9	Tarsius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	2	1	2	2	0	0	0	0	0	0	0	2	1	0	0	1	1	1
10	Leontopithecus	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	1	2	0	0	0	0	0	0	0	0	1	0	?	0	1	0
11	Aotus	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	?	0	1	0	?	?	?
12	Cebus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1
13	Saimiri	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	2	1	1	1	?	0	1
14	Macaca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1
15	Papio	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1
16	Colobus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	1	0	0	1	1
17	Presbytis	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	1
18	Hylobates	1	0	0	1	1	0	2	1	1	1	1	1	2	0	?	2	3	2	2	0	0	0	1	0	1	1	0	0	0	0	1	0	1
19	Pongo	2	0	1	1	0	0	1	0	1	1	1	0	2	0	?	1	3	1	2	0	0	0	1	1	2	2	2	1	0	0	1	0	1
20	Gorilla	2	1	1	2	1	1	0	1	2	1	1	0	1	1	?	2	1	1	2	1	1	1	1	1	2	2	0	1	1	0	1	0	1
21	Pan	2	1	1	1	1	1	1	0	1	1	1	1	1	0	?	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	2
22	Homo	1	0	0	1	2	2	1	2	0	1	1	0	0	1	?	2	1	0	2	1	1	1	1	1	0	0	0	1	1	1	0	0	2

		166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198
1	Solenodon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
2	Tupaia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	?	?
3	Cynocephalus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	?	?
4	Pteropus	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0
5	Lemur	?	?	?	?	?	?	?	?	?	?	0	1	?	?	?	?	?	?	?	?	?	?	1	?	?	0	0	0	0	0	0	0	0
6	Daubentonia	?	?	?	?	?	?	?	1	?	?	1	?	?	?	?	?	?	?	?	?	?	?	1	?	?	0	0	0	0	0	0	0	0
7	Loris	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	0	0	0	0	0	0	0
8	Nycticebus	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	0	0	0	0	0	0	0
9	Tarsius	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?	0	?	?	0	0	0	0	0	0	0	0
10	Leontopithecus	?	?	?	?	?	1	1	0	0	?	0	0	?	?	?	?	?	?	?	0	0	0	1	0	1	0	0	0	0	0	0	0	0
11	Aotus	?	?	?	?	?	1	1	1	?	?	0	0	?	?	?	?	?	?	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
12	Cebus	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
13	Saimiri	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	0	0	0	0	0	?	0	0	0	1	2	1	0	0	0	0	0	0
14	Macaca	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	0	0	0	0	0	?	1	1	0	0	0	0	0	0	0	0	0	0
15	Papio	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	0	0	0	0	0	?	1	1	0	0	0	0	0	0	0	0	0	0
16	Colobus	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0
17	Presbytis	?	?	?	?	1	1	1	?	?	?	0	0	?	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0
18	Hylobates	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	1	0	1	0	2	2	0	0	1	0	1	1	0	1	1	1	0	0
19	Pongo	1	0	1	0	1	1	1	0	1	1	2	2	1	1	0	0	1	1	2	2	0	1	1	0	1	0	1	1	2	1	1	1	0
20	Gorilla	0	1	0	0	0	0	1	1	1	2	2	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1	2	1	1	2	1	0	1
21	Pan	0	1	0	0	1	0	0	1	?	1	2	1	0	0	1	0	1	1	2	1	1	1	1	1	0	2	1	1	2	1	0	1	0
22	Homo	1	0	1	1	0	1	1	1	1	2	1	0	0	1	1	1	0	2	1	1	2	1	1	1	1	1	2	2	1	2	1	1	1

		199	200	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220	221	222	223	224	225	226	227	228	229	230	231
1	Solenodon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?
2	Tupaia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?
3	Cynocephalus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?
4	Pteropus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?
5	Lemur	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?
6	Daubentonia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	0	?	?	?	?
7	Loris	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	0	?	?	?	?
8	Nycticebus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	0	?	?	?	?
9	Tarsius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	?	0	0	?	?	?
10	Leontopithecus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	1	1	?	?	0	1	?	?	?
11	Aotus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	1	0	?	?	0	?	?	?	?
12	Cebus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	1	0	?	?	0	?	?	?	?
13	Saimiri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	1	0	?	?	0	?	?	?	?
14	Macaca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	1	0	?	?	0	?	?	?	?
15	Papio	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	0	0	?	?	0	?	?	?	?
16	Colobus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	1	0	?	?	0	?	?	?	?
17	Presbytis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	1	0	?	?	0	?	?	?	?
18	Hylobates	0	1	?	?	0	1	1	0	1	1	1	1	1	1	1	1	2	0	1	1	1	1	2	1	2	2	0	0	0	1	1	0	0
19	Pongo	0	2	1	1	0	0	2	1	0	2	2	2	0	1	0	0	2	0	1	1	0	0	0	0	0	2	?	?	3	0	0	1	0
20	Gorilla	1	2	0	1	1	1	2	1	1	2	0	0	1	0	1	1	1	1	0	0	1	0	1	0	1	2	?	?	3	0	1	2	1
21	Pan	0	1	0	1	1	1	2	0	1	2	2	1	1	0	0	1	1	1	1	0	1	2	1	1	1	3	?	1	1	1	1	2	1
22	Homo	1	2	1	1	0	1	2	0	1	2	2	1	1	0	1	1	1	1	0	1	1	2	2	1	2	3	1	1	2	1	2	2	1

		232	233	234	235	236	237	238	239	240	241	242	243	244	245	246	247	248	249	250	251	252	253	254	255	256	257	258	259	260	261	262	263	264
1	Solenodon	?	?	0	?	?	?	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Tupaia	?	?	0	?	?	?	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Cynocephalus	?	?	0	?	?	?	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	Pteropus	?	?	0	?	?	?	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
5	Lemur	?	?	0	?	?	?	?	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	1
6	Daubentonia	?	?	0	?	?	?	?	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1
7	Loris	?	?	0	?	?	?	?	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	0	0	0
8	Nycticebus	?	?	0	?	?	?	?	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	0	0	1
9	Tarsius	?	?	2	?	?	?	?	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0
10	Leontopithecus	?	?	0	?	?	?	?	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1
11	Aotus	?	?	0	?	?	?	?	0	0	0	0	?	0	1	?	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1
12	Cebus	?	?	0	?	?	?	?	0	0	0	0	1	0	1	?	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1
13	Saimiri	?	?	0	?	?	?	?	0	0	0	0	1	0	1	?	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1
14	Macaca	?	?	0	?	?	?	?	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	1
15	Papio	?	?	0	?	?	?	?	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	1
16	Colobus	?	?	0	?	?	?	?	0	0	0	0	?	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	1
17	Presbytis	?	?	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	1
18	Hylobates	1	0	1	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	1	1	0	0	0	0	1	1	0	0	1	0	0	0	1
19	Pongo	1	1	0	1	0	1	0	1	1	1	0	2	0	2	0	1	2	1	2	1	1	1	2	1	2	0	1	1	1	1	0	0	1
20	Gorilla	0	1	1	0	0	0	1	1	1	1	1	0	1	1	0	0	1	1	2	1	1	1	1	2	2	1	1	0	2	0	0	0	1
21	Pan	1	1	2	1	1	0	1	1	1	1	1	1	1	2	0	1	2	1	2	1	1	1	2	2	1	1	1	0	2	0	0	0	1
22	Homo	1	0	2	1	1	1	0	1	1	0	1	2	1	2	1	1	2	1	2	2	1	1	0	2	2	1	1	0	2	0	0	0	1

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