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Phylogenetic analysis of anthropoid relationships

The relationships of anthropoids to other primates are currently debated, as are the relationships among early fossil anthropoids and crown anthropoids. To resolve these issues, data on 291 morphological characters were collected for 57 taxa of living and fossil primates and analyzed using PAUP and MacClade. The dental evidence provides weak support for the notion of an adapid origin for anthropoids, the cranial evidence supports the tarsier-anthropoid hypothesis, and the postcranial evidence supports a monophyletic Prosimii and a monophyletic Anthropoidea. Combining these data into a single data set produces almost universal support for a tarsier-anthropoid clade nested within omomyids. *Eosimias* and *Afrotarsius* are certainly members of this clade, and probably basal anthropoids, although the Shanghuang petrosal may not belong to *Eosimias*. The tree derived from the combined data set resembles the tree derived from the cranial data set rather than the larger dental data set. This may be attributable to relatively slower evolution in the cranial characters. The combined data set shows Anthropoidea to be monophyletic but the features traditionally held to be anthropoid synapomorphies are found to have evolved mosaically. Parapithecines are the sister taxon to crown anthropoids; qatraniines and oligopithecids are more distantly related sister taxa. There is support for a relationship of a *Tarsius*+Anthropoidea clade with either washakiines or *Uintanius*. These elements of tree topology remain fairly stable under different assumptions sets, but overall, tree topology is not robust. Previously divergent hypotheses regarding anthropoid relationships are attributable to the use of restricted data sets. This large data set enables the adapid-anthropoid hypothesis to be rejected, and unites *Tarsius*, Anthropoidea and Omomyiformes within a clade, Haplorhini. However, relationships among these three taxa cannot be convincingly resolved at present.

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Introduction

Anthropoidea—the group that includes monkeys, apes and humans—has long been recognized as a “natural” group among primates, united by a suite of features of the skull, dentition and postcranium. Anthropoidea is also generally—although not universally (Cachel, 1979)—thought to be

monophyletic, descended from a common ancestor not shared with any other primates.

However, the relationships of anthropoids to other primates are not yet resolved. Advocates of several competing hypotheses continue to debate the merits of their respective models. This lack of consensus reflects a broader uncertainty of the relationships among primate higher taxa and the fossil groups thought to have given origin to them. Why does this debate persist? Is it because key fossils are yet to be discovered? It is well established that fossils are vital for

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deciphering relationships among living taxa because they contain novel combinations of primitive and derived characters and because they preserve morphologies more closely approximating ancestral conditions (Gauthier *et al.*, 1988; Huelsenbeck, 1991; Novacek, 1992). In the case of anthropoid origins however, most workers agree on the relationships between living taxa (tarsiers and anthropoids are more closely related to each other than to strepsirrhines); it is the relationships of certain fossil taxa to the living groups that are debated.

Clearly, more fossils would help resolve these issues. However, before our lack of clarity about anthropoid relationships can be attributed to a paucity of appropriate fossils, another question needs to be addressed: have the data accumulated to date been appropriately and exhaustively analyzed using the best methods available? We believe that the answer to this question is "no", and set out here to resolve this problem.

Currently the most widely accepted method for reconstructing evolutionary relationships is phylogenetic analysis using parsimony aided by algorithms utilized by computer programs such as PAUP (Swofford, 1991) and MacClade (Maddison & Maddison, 1992). To date, these methods have been applied to the question of anthropoid relationships haphazardly. Separate analyses have been performed on data derived from the dentition (Kay & Williams, 1994a), the skull (Ross, 1994) and the post-cranium (Dagosto & Gebo, 1994), but these data have not yet been combined into a "total evidence" analysis. Moreover, the individual analyses were restricted to limited numbers of taxa. This limitation is attributable, in part, to the nature of the material. For example, those fossil taxa for which dental data are available are not always the same as those for which cranial or postcranial data are known.

In this paper we gather together data on a large number of living and fossil primates, as

well as several outgroups, and analyze them using PAUP and MacClade. One of the aims of this work is to evaluate the various competing hypotheses of anthropoid relationships using parsimony as the criterion for choosing among them. The most salient aspects of our findings have been published recently (Kay *et al.*, 1997). We present here a more extensive data set on primate morphology that includes explicit descriptions of character states and their assignments among taxa.

Questions surrounding anthropoid origins

Debates concerning the origins and early diversification of the Anthropeida have centered around several related questions:

- (1) Is Anthropeida a monophyletic group, and if so what are its synapomorphic features?
- (2) To which group of fossil or extant primates is Anthropeida most closely related?
- (3) How do Eocene and Oligocene anthropoids of Africa (Parapithecoidea, Propliopithecidae, Oligopithecidae) relate to the Platyrrhini and Catarrhini?

With respect to anthropoid monophyly, older views such as those of W. K. Gregory (1922) that catarrhines and platyrrhines evolved from separate and not very closely related Eocene "tarsioids" have been largely abandoned. More recent discussions of anthropoid origins recognize shared-derived features that support anthropoid monophyly (Delson & Rosenberger, 1980; Hoffstetter, 1980; Rosenberger, 1986; Szalay, 1976; Szalay & Delson, 1979). However, there remains a debate as to whether some or all "monkey-like" traits evolved independently in the New and Old Worlds, or just once in a stem anthropoid (see Rosenberger, 1986, for a review). Recent evidence suggests that the suite of features long thought to unite anthropoids (spatulate and erect incisors; molars with reduced trigonids lacking

paraconids; postorbital closure; fusion of the mandibular symphysis; and specializations of the ear region) evolved in a mosaic fashion (Simons, 1989, 1992; Kay & Williams, 1994a; Ross, 1994; Beard *et al.*, 1996). Adaptive scenarios for anthropoid origins (Ross, 1996; Kay *et al.*, 1997) must take into account this mosaicism.

In addressing the second question, regarding the group from which anthropoids arose, proponents of three positions can be identified (Figure 1). Some workers advocate separate origins for *Tarsius* and Anthropoidea among different groups of omomyids (Szalay, 1975; Szalay & Delson, 1979; Rosenberger, 1986; Szalay *et al.*, 1987; Beard *et al.*, 1988). Various omomyids have been advanced as anthropoid ancestors, including *Teilhardina*, *Omomys* or *Chumashius* (Cartmill & Kay, 1978; Hoffstetter, 1980; Kay, 1980; Rose *et al.*, 1994; Rosenberger, 1986; Szalay, 1976; Szalay & Delson, 1979). Recently, discovery of several skulls of the washakiine omomyid, *Shoshonius cooperi*, from late early Eocene (50.5 Ma) localities in Wyoming led Beard *et al.* (1991) to hypothesize that *Tarsius* is more closely related to *Shoshonius* than to other omomyids or anthropoids.

Another group of workers hypothesizes that a lineage of omomyids gave rise to a clade consisting of *Tarsius* and Anthropoidea (Cartmill & Kay, 1978; Cartmill *et al.*, 1981; MacPhee & Cartmill, 1986; Kay & Williams, 1994a; Ross, 1994, 1996). Under this hypothesis, tarsiers and anthropoids are more closely related to each other than to omomyids.

The third position suggests that anthropoids arose from a lineage of fossil adapids. The acknowledged grandfather of the adapid-anthropoid hypothesis is Jacob L. Wortman (Rasmussen, 1994; Simons & Rasmussen, 1996). In a series of papers on Eocene mammals from the Marsh Collection in the Yale Peabody Museum, Wortman divided the order Primates into

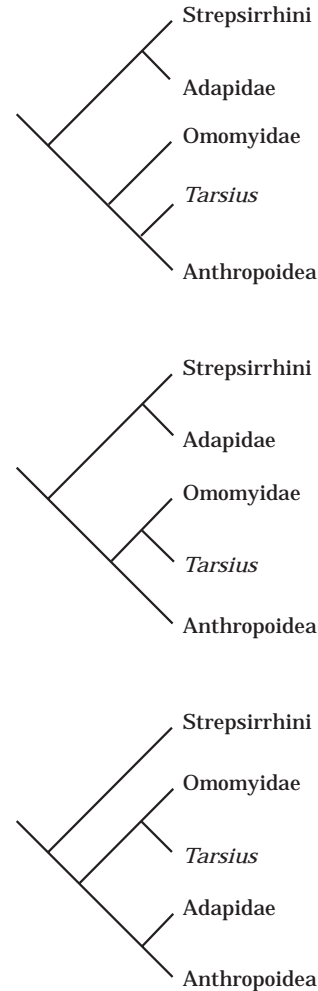


Figure 1. Three mutually exclusive hypotheses of anthropoid relationships. Top: Tarsiers and anthropoids are sister-taxa and this clade arose from a common ancestor which was either shared with omomyids, or was an omomyid (Cartmill & Kay, 1978; Cartmill *et al.*, 1981; MacPhee & Cartmill, 1986; Kay & Williams, 1994a; Ross, 1994, 1996). Center: Tarsiers and anthropoids arose separately from different omomyid ancestors (Szalay, 1975; Szalay & Delson, 1979; Rosenberger, 1986; Szalay *et al.*, 1987; Beard *et al.*, 1988). The most recent and best supported of these hypotheses is that of Beard *et al.* (1988) that *Tarsius* is closely related to washakiines. Bottom: Anthropoids arose from adapids. Most recently cercamoniine adapids have been advanced as the most likely candidate for anthropoid ancestry (Gingerich, 1980; Rasmussen, 1990; Franzen, 1987, 1994; Simons & Rasmussen, 1996). Rasmussen (1986) pointed out that an adapid origin for anthropoids does not rule out a tarsier-anthropoid clade among living primates.

three suborders: the Cheiromyoidea, containing *Daubentonia*, *Smilodectes* and an assortment of North American microsyopids; the Lemuroidea, consisting of lemurs, indriids and subfossil lemurs; and the Anthroipoidea (Wortman, 1903–1904). Wortman's Anthroipoidea consisted of three superfamilies: Arctopithecini, or callitrichids; the Paleopithecini, consisting of anaptomorphine omomyids and *Tarsius*; and the Neopithecini, consisting of adapids and non-callitrichid anthropoids. Gingerich (1980), Rasmussen (1990), Franzen (1987, 1994) and Shoshani *et al.* (1996) have championed various versions of the adapid–anthropoid hypothesis. Simons & Rasmussen have even gone so far as to resurrect Wortman's classification (Simons & Rasmussen, 1996:285; see also Shoshani *et al.*, 1996: Appendix 1).

Several workers at the 1992 Anthropoid Origins Conference and Workshop at Duke University (Fleagle & Kay, 1994) voiced the possibility of a nonadapid, nonomomyid, and nontarsier origin for anthropoids (Culotta, 1992). At that time, a likely candidate for this unknown group had appeared in the form of *Eosimias* (Eosimiidae), a diminutive fossil primate from the late middle Eocene (approx. 45 Ma) of China with several features linking it to anthropoids (Beard *et al.*, 1994, 1996). Also in the early 1990s, older, Eocene (ca. 37 m.y.a.) fossil anthropoids were being recovered from North Africa (Godinot, 1994; Godinot & Mahboubi, 1992; Simons, 1992). This suggested that the anthropoid clade might be as old, or older, than the earliest omomyids and adapids and that a fundamental dichotomy might exist between omomyids and adapids of the Northern continents and Anthroipoidea of Africa and South America.

The third area of disagreement and debate concerns cladogenesis within early anthropoids and centers around the phyletic positions of the Oligopithecidae and Parapithecoidae relative to platyrrhines and

catarrhines (Figure 2). Oligopithecids (*Oligopithecus*, *Catopithecus* and possibly *Protopithecus*, of the Fayum late Eocene/early Oligocene) are assigned by Rasmussen and Simons (Rasmussen & Simons, 1988; Simons, 1989, 1990) to Propliopithecidae, "true catarrhines that are plausibly ancestral to later hominoids and cercopithecoids" (Simons & Rasmussen, 1994). Others have also argued that *Oligopithecus* is a stem catarrhine (Kay, 1977; Szalay & Delson, 1979), or a stem anthropoid (Hoffstetter, 1980). At the opposite extreme, Gingerich (1980) argued that *Oligopithecus* is very similar dentally to some Adapidae and may even be an adapid. The Parapithecoidae have been argued to be near the ancestry of Old World monkeys (Cercopithecidae) (Simons, 1974) or the sister group of all other living and fossil anthropoids (Fleagle & Kay, 1987; Hoffstetter, 1977, 1980; Harrison, 1987; Simons & Rasmussen, 1994).

Here we review the evidence for the phylogenetic relationships of eosimiids, omomyids and adapids to the living haplorhines and strepsirrhines. As part of our analysis, the phyletic positions of parapithecoids, oligopithecids and propliopithecids are also evaluated.

Materials and methods

Characters

Data on 291 morphological characters were collected. These characters included 182 dental characters, 49 cranial characters, 56 postcranial characters and four soft tissue characters. Descriptions and discussions of most of these have been published previously, the dental characters by Kay & Williams (1994a), and Williams (1994), the cranial characters by Ross (1994), the postcranial characters by Covert (1988), Szalay & Dagosto (1988), Dagosto (1988, 1990), Dagosto & Gebo (1994), Ford (1994) and Dagosto & Schmid (1996), and the soft tissue characters by Martin (1990). New

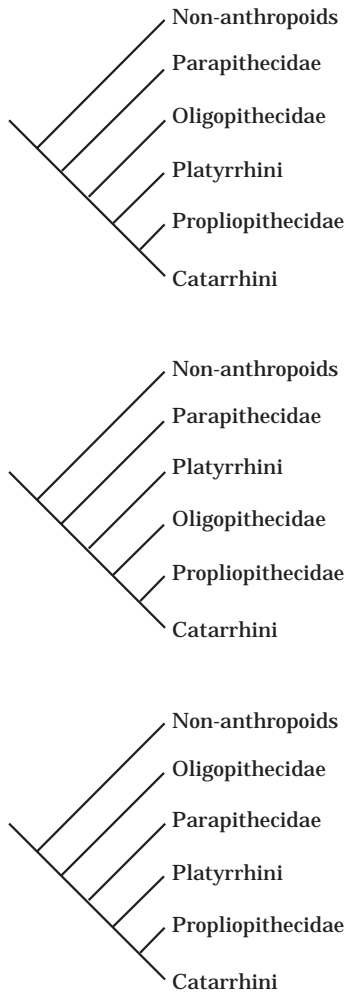


Figure 2. Three hypotheses of relationships among early anthropoids. Harrison (1987), Fleagle & Kay (1987) and Simons & Rasmussen (1994) argued for a placement of parapithecids outside crown anthropoids; i.e., as the sister taxon of platyrrhines and catarrhines. In this context, and assuming monophyly of both oligopithecids and parapithecids, hypotheses regarding the phylogenetic position of Oligopithecidae can be divided into three groups. Top: Oligopithecids are the sister taxon to crown anthropoids. Center: Oligopithecids are the sister taxon to catarrhines (Kay, 1977; Szalay & Delson, 1979). Simons & Rasmussen classify oligopithecines as Propliopithecidae, Hominoidea (Rasmussen & Simons, 1988; Simons, 1989, 1990), but appear to consider them basal catarrhines as well (Simons & Rasmussen, 1994). Bottom: Oligopithecids are the sister taxon to all other living or fossil anthropoids (Hoffstetter, 1980).

characters have been added to these lists to incorporate features emphasized in recent studies of early anthropoids (e.g. Simons & Rasmussen, 1996). All characters and character states are listed in Appendix A. The character-taxon matrix is given in Appendix B.*

Taxa

Data were initially gathered on over 100 species of extant and fossil primates plus several nonprimate outgroups. However, this data set proved too unwieldy to analyze, in part due to large amounts of missing data for many taxa, and it was necessary to reduce the number of taxa. Taxa were included to achieve the following objectives: (a) to represent all the major groups of living and fossil primates; (b) to include as many fossil taxa for which it was possible to score characters from the dentition, skull and postcranium; (c) to include all the taxa that have figured prominently in hypotheses of anthropoid relationships (e.g. *Eosimias*).

Recently discovered forms, such as *Asiopithecus* and *Xanthorhysis*, are excluded from our analysis because we have not had a chance to examine the original material.

Some taxa included in the analysis are genera—compilations of data from more than one species in the same genus, or from unassociated specimens representing several areas of the body. Such combining of taxa to create operational taxonomic units (OTUs) was done to minimize the number of taxa with large amounts of missing data. Missing data can negatively impact on the outcome of an analysis by affecting resolution, making determination of polarity uncertain, and under-representing homoplasy (Nixon & Davis, 1991; Simmons, 1993; Kay & Williams, 1994a). Taxa with missing data also significantly lengthen the search process using PAUP, often resulting in multiple

*A complete character-taxon matrix and character list can be downloaded from the web at <http://www.informatics.sunysb.edu/anatomy/cross.html>

equally parsimonious trees that differ in only trivial ways (Swofford, 1990; Huelsenbeck, 1991). For example, *Tetonius* sp. is a compilation of data from the *T. homunculus* cranium (AMNH 4194, described by Cope [1882]) recovered from a locality in the Bighorn Basin for which the precise provenance is now unknown, upper and lower jaws of *Tetonius matthewi* recovered from multiple localities in the Bighorn and Washakie Basins, and unassociated calcanei recovered from Bighorn and Washakie Basin localities that have also produced dental material of *Tetonius matthewi* and can be reasonably assigned to that taxon.

A more crucial example of such a compilation is *Eosimias* spp. *E. centennicus* is represented by a well-preserved lower mandible with complete dentition from Shanxi Province, China (Beard *et al.*, 1996). Postcranial remains of eosimiids have also been reported from the fissure fillings at Shanghuang (Dagosto *et al.*, 1996; Gebo *et al.*, 1996), as has a small petrosal bone (MacPhee *et al.*, 1995). This petrosal is important because it lacks features of the middle ear region that have been used to link anthropoids to tarsiers in a clade excluding other primates (Cartmill & Kay, 1978; MacPhee & Cartmill, 1986; Ross, 1994). However, the assignment of the Shanghuang petrosal to the Eosimiidae is not without difficulty. Not only is the petrosal fragmentary, but it is only associated with eosimiids in so far as it comes from the same fissure—Fissure D—a fissure which has also yielded teeth of adapiforms and omomyids (MacPhee *et al.*, 1995). The nature of the association between the Shanghuang petrosal and eosimiids and the importance of eosimiids as potential primitive anthropoids requires that their phylogenetic position be evaluated both with the petrosal and the dentition in the same taxon and in separate taxa.

Four outgroups were included in the analyses discussed below. Simultaneous use of more than one outgroup provides a more

accurate estimate of character polarity than use of a single outgroup (Maddison *et al.*, 1984, but see Nixon & Carpenter, 1993). It also enables the monophyly of the ingroup to be tested in the context of putative close relatives. There is little agreement on exactly which mammals, living or fossil, are the closest relatives of primates. In recent years, many workers have supported the close affinities of Primates with Chiroptera (bats), Scandentia (tree shrews), Dermoptera (flying lemurs) and the Paleocene to Eocene Plesiadapiformes, leading some workers to resurrect Gregory's supraordinal category Archonta to nominalize this concept (Wible & Covert, 1987; Novacek & Wyss, 1986; Pettigrew *et al.*, 1989; Novacek, 1992; Kay *et al.*, 1994; Beard, 1993a,b). However, recent analyses of DNA sequences suggest the extant taxa included in "Archonta" may not represent a monophyletic group. Also, even if the group proves to be a clade, some archontans such as bats and flying lemurs are known only from extremely derived taxa and reveal little about their ancestry. Thus, it remains to be determined exactly which "archontan", if any, is the closest relative of primates.

In this state of uncertainty, we decided to select as our outgroups several taxa from within the archontan cluster that we regard as least derived: representatives of Scandentia (a compilation of the skull and postcranium of *Tupaia glis* and the dentition of *Ptilocercus lowii*), and the extinct Plesiadapiformes (*Purgatorius unio*, *Plesiolestes problematicus*, and a compilation of cranial characters of *Plesiadapis tricuspidens*, and dental features of *Pronothodectes jepi*). These taxa were designated as outgroups and the analyses run. If primate monophyly was not supported (i.e., if it was not possible to root the resulting network such that these outgroup taxa were all excluded from Primates), then constrained analyses were run. In principle, we concur with Nixon & Carpenter (1993) that outgroup and

ingroup taxa should be included in the same unconstrained analysis as a test of ingroup monophyly. However, some of our outgroup taxa have large proportions of missing data, especially *Purgatorius* and *Plesiolestes* (56% and 57% missing respectively), suggesting that constrained analyses are justified to determine the ingroup branching pattern resulting from the assumption that these taxa are indeed true outgroups to Primates.

Analyses

Analyses were performed using MacClade 3.07 (Maddison & Maddison, 1992) and PAUP 3.0s+1 (Swofford, 1991). Data were entered in MacClade, analyses were performed in PAUP, and the resulting trees transferred back to MacClade for assessment of character evolution.

The large size of our data set precludes the use of the “branch-and-bound” analysis in PAUP which guarantees that the shortest trees will be discovered. Instead the “heuristic” search program option was selected. Although there is no guarantee that a heuristic search will find all of the most parsimonious trees, the amount of error introduced is unlikely to be significant (Sanderson & Donoghue, 1989). This is particularly the case if care is taken to randomly vary the topology of the starting tree in the heuristic searches and to perform a high number of replications (Maddison, 1991; Page, 1993). Furthermore, we were never able to find more parsimonious arrangements of the data via manual manipulations of the branching pattern using MacClade. We are therefore confident that the branching patterns revealed by the heuristic searches are close to, if not absolutely, the most parsimonious arrangements of our data set. In particular, we are certain that more parsimonious arrangements of the most important taxa under consideration here (anthropoids, eosimiids, tarsiers, cercamoniines, washakiins) are not to be found.

Heuristic analyses were performed using the following options: stepwise addition, random addition sequence, mulpars in effect, tree-bisection-reconnection branch swapping, branches with zero length collapsed to form polytomies. When necessary, primate monophyly constraints were enforced by inserting “dummy characters”. A minimum of 1000 replications was performed on each analysis.

Assumptions and data combinations

Multistate characters unduly influence tree topologies more than binary characters because they contribute more to tree lengths. One way of avoiding this effect is to scale all characters to the same weight regardless of the number of character states. To determine the effect of multistate characters on our data, we ran our analyses both with the multistate characters scaled and with all the characters of equal weight.

Controversy surrounds the issue of whether multistate characters should be ordered or unordered (Mickevich, 1982; Mabee, 1989; Mickevich & Weller, 1990; Hauser & Presch, 1991; Slowinski, 1993). It seems reasonable to think that multistate characters should be designated as “ordered” if changes from one state to another require passing through intermediate states also represented in the data set (e.g. “absent”–“small”–“large”) (Slowinski, 1993). However, this assumes a gradualistic model of evolutionary change and excludes the possibility that characters can change from, for example, “absent” to “large” without a “small” stage (Hauser & Presch, 1991). Hauser & Presch suggest comparisons between trees based on ordered and unordered data to determine the effects of ordering on tree topology (see also Simmons, 1993). To evaluate the effect of character ordering on tree topologies derived from our data set, we ran our analyses both with all multistate characters unordered and with some multistate

Table 1 Classification followed in the text and taxa included in analyses. Genera shown are only those used in the cladistic analyses. All genera are represented by dental data; # indicates postcranial data; @ indicates cranial data

Order Primates
Semioorder <i>incertae sedis</i>
<i>Rooneyia</i> @
Semioorder Strepsirrhini
Suborder Lemuriformes
<i>Galagoides</i> ##@, <i>Nycticebus</i> ##@, <i>Microcebus</i> ##@, <i>Lemur</i> ##@
Suborder Adapiformes
Family Adapidae: <i>Adapis</i> ##@, <i>Leptadapis</i> ##@, <i>Aframonius</i> , <i>Mahgarita</i> @, <i>Protoadapis</i> , <i>Cantius</i> (includes some cranial and postcranial data from <i>Notharctus</i> ##@), <i>Pronycticebus</i> , <i>Donrussellia</i>
Semioorder Haplorhini
Suborder Omomyiformes
Family Omomyidae: <i>Omomys</i> #, <i>Uintanius</i> , <i>Absarokius</i> #, <i>Tetonius</i> @, <i>Anaptomorphus</i> , <i>Aycrossia</i> , <i>Strigorhysis</i> , <i>Anemorhysis</i> , <i>Microchoerus</i> , <i>Necrolemur</i> ##@, <i>Pseudoloris</i> , <i>Trogolemur</i> , <i>Arapahovius</i> , <i>Tetonoides</i> , <i>Dyseolemur</i> , <i>Loveina</i> , <i>Shoshonius</i> @, <i>Hemiaecodon</i> #, <i>Macrotarsius</i> , <i>Teilhardina americana</i> , <i>Teilhardina belgicus</i> , <i>Steinius</i> , <i>Nannopithec</i> @, <i>Washakius</i>
Suborder Tarsiiformes
Family Tarsiidae: <i>Tarsius</i> ##@
Suborder Anthropoidea
Infraorder Platyrrhini
Family Cebidae: <i>Dolichocebus</i> , <i>Saimiri</i> ##@, <i>Aotus</i> ##@, <i>Callicebus</i> ##@
Infraorder Catarrhini
Family Propliopithecidae: <i>Aegyptopithecus</i> ##@
Infraorder Parapithecoidae
Family Parapithecidae: <i>Apidium</i> ##@, <i>Parapithecus</i> , <i>Simonsius</i>
Infraorder <i>incertae sedis</i>
Family Oligopithecidae: <i>Catopithecus</i> ##@, <i>Proteopithecus</i> #
Family Qatraniidae: <i>Qatrania</i> , <i>Serapia</i> , <i>Arsinoea</i>
Family Eosimiidae: <i>Eosimias</i> ##@
Family Afrotarsiidae: <i>Afrotarsius</i>

characters ordered (ordered characters indicated in Appendix A).

For reasons discussed above, we performed one set of analyses of the complete data set in which we assumed that all these fossils assigned to *Eosimias* do actually belong to the same OTU (Analysis Group 1), and one set of analyses of the complete data set in which the Shanghuang petrosal was either omitted entirely from the data set, or was included as a taxon separate from *Eosimias* (Analysis Group 2). All possible combinations of constrained (when necessary), unconstrained, ordered and unordered analyses were run.

The use of many different anatomical systems for phylogeny estimation is advocated by many investigators (e.g., Luckett & Hartenberger, 1985; Wible & Novacek,

1988; Kay *et al.*, 1997). However, whether characters from multiple systems should automatically be combined in a “total evidence” approach (Kluge, 1989; Chippendale & Wiens, 1994) or examined first for differing phylogenetic signals (Bull *et al.*, 1993; Huelsenbeck *et al.*, 1994) is debatable (see De Queiroz *et al.*, 1995 for a review). In this study, in addition to running all the characters together, separate analyses were performed on the data from the skull (Analysis Group 3), the dentition (Analysis Group 4) and the postcranium (Analysis Group 5). As with the complete data set, constrained, unconstrained, ordered and unordered analyses were run. (A summary of all analyses run is included in Table 2 with the summary of the results).

Taxonomic terminology

For clarity of terminology, we use a higher-rank classification of primates similar to that presented in Kay & Williams (1994a) and Kay *et al.* (1997) (see Table 1). The term “omomyids” is used to refer to all members of the Omomyidae *sensu* Fleagle (1988) except *Rooneyia*, which does not consistently fall among the other omomyids. We use “adapids” to refer to the Adapidae *sensu* Fleagle (1988), despite the fact that the last common ancestor of all adapids appears to have been shared with living strepsirrhines. We follow Kay & Williams (1994a) in using Anthropeida to refer to platyrrhines, catarrhines, Oligopithecidae, and Parapithecoidea. The (platyrrhine+catarrhine) clade is referred to as “crown anthropoids”. *Aegyptopithecus* is the only catarrhine included in this study, and the term “catarrhines” is used synonymously with *Aegyptopithecus* at times. Parapithecinae includes *Parapithecus*, *Apidium* and *Simonsius*, and Qatraniinae refers to *Qatrania*, *Serapia*, and *Arsinoea*. The valid spelling of Strepsirrhini is the original one (Geoffroy, 1812) and is followed here (see Jenkins, 1987).

A data set with the characters scaled to be of equal weight regardless of the number of character states is referred to as “scaled”; a data set with all characters of equal weight is referred to as “equally weighted”. When some multistate characters are ordered the data set is referred to as “ordered”. “Constrained” refers to an analysis in which dummy characters were included to force primate monophyly.

Results

Table 3 gives the percentage of data recorded for each taxon. These data are given for the complete data set as well as for the three data partitions. Only 57% of the cells in this matrix are filled. The dental data set is the most complete, followed by the cranial and postcranial data sets. The taxa

range from nearly 95% completeness in two extant animals (*Galagoides* and *Callicebus*) to 28% completeness in *Rooneyia*. *Rooneyia* is less complete than *Afrotarsius*, due to the large number of characters describing the lower molars.

Table 2 lists the analyses performed and various tree statistics and summarizes the most important results of the analyses. Both the rescaled consistency indices (RCIs) and the retention indices (RIs) for the complete data set are low, ranging from 0.18 to 0.27, and from 0.53 to 0.65 respectively. Low values for these indices indicate a high degree of homoplasy in the data set. Similarly high levels of homoplasy are evident in the dental data set. The cranial data set shows slightly less homoplasy, with the RCI ranging from 0.37 to 0.45, and the postcranial data set shows the least homoplasy, with RCIs of 0.73 and 0.76. The dental data set is the most homoplastic, with an RCI of only 0.17. These results are not attributable to varying amounts of missing data: the postcranial, cranial and dental data sets have 27%, 24% and 26% missing data respectively.

Analysis Group 1: all characters; Shanghuang petrosal assumed to be Eosimias

All trees produced by the complete data set share common features, whether constrained or unconstrained, ordered or unordered, and whether scaled or equally weighted. To illustrate these common features, a strict consensus tree was generated of the trees produced by the seven analyses in Analysis Group 1 (Figure 3). A majority-rule consensus tree was also generated to indicate those groups found by the majority of the Group 1 analyses (Figure 4). (1) Extant strepsirrhines form a monophyletic group (Figure 3) and are usually more closely related to adapids than to omomyids, anthropoids or tasiars (Figure 4). (2) Among strepsirrhines, *Galagoides* and *Nycticebus* are most closely related, with

Table 2 Summary of results

Data	Chara. n	Taxa n	Constraint	Wt.	Order	Tree n	Tree length	CI	RCI	RI	Primates	T,An	T,An,Om	E,An	T,Om	An,Ad	S,Ad
1	291	57	U	S	O	1	115,604	0.35	0.20	0.56	Y	Y	Y	Y	N	N	Y
1	291	57	U	E	O	30	1834+	0.39	0.24	0.63	N	N/Y	N	N	N	N	Y
1	291	57	U	S	U	2	108,570+	0.37	0.21	0.55	N	Y	Y	Y	N	N	Y
1	291	57	U	E	U	10	1658+	0.43	0.27	0.62	N	N/Y	Y	N	N	N	Y
1	291	57	C	S	U	3	108,620+	0.37	0.21	0.55	Y	Y	Y	Y	N	N	Y
1	291	57	C	E	U	5	1903+	0.37	0.20	0.53	Y	Y	Y	Y	N	N	Y
1	291	57	C	E	O	3	2094	0.34	0.18	0.54	Y	N	Y	Y	Y	N	Y
2	291	58	U	S	U	39	97,748+	0.42	0.26	0.62	Y	N	Y	Y	N	N	Y
2	291	58	U	S	O	39	103,117+	0.39	0.25	0.63	Y	Y	Y	Y	N	N	Y
2	291	58	C	S	U	123	96,211+	0.42	0.27	0.63	Y	Y	Y	Y	N	N	Y
2	291	57	U	E	U	13	1771+	0.40	0.26	0.65	N/Y	N	N	Y	N	N	Y
2	291	57	U	E	O	26	2026+	0.35	0.20	0.57	N	Y	Y	Y	N	N	Y
2	291	57	C	E	U	5	1900+	0.37	0.20	0.53	Y	Y	Y	Y	N	N	Y
2	291	57	C	E	O	50	1786+	0.40	0.26	0.64	Y	N/Y	Y	Y	N	N	N/Y
3	52	23	U	S	O	69	9625+	0.58	0.45	0.79	N	Y	Y	N	N	N	N
3	52	23	C	S	O	3	10,650+	0.52	0.38	0.73	Y	Y	Y	N	N	N	N
3	52	23	U	S	U	3	10,650+	0.52	0.37	0.73	Y	Y	Y	N	N	N	N

Table 2 Continued

Data	Chara. n	Taxa n	Constraint	Wt.	Order	Tree n	Tree length	CI	RCI	RI	Primates	T,An	T,An,Om	E,An	T,Om	An,Ad	S,Ad
4	182	58	U	S	U	3	86,232+	0.34	0.17	0.52	N	N	N	N	N	Y	N
4	182	58	U	S	O	3	91,526+	0.32	0.17	0.54	N	N	N	N	Y	Y	N
4	182	58	C	S	U	3	86,617+	0.34	0.17	0.51	Y	N	N	N	N	N	N
4	182	58	C	S	O	3	91,869+	0.32	0.17	0.53	Y	N	N	N	Y	Y	N
5	56	22	U	S	O	3	11,256+	0.54	0.73	0.40	Y	N	N	N	Y	N	Y
5	56	22	U	S	U	1	10,108	0.61	0.76	0.46	Y	N	N	N	Y	N	Y

Data: Analysis Group: Group 1, all taxa, all characters, Shanguang petrosal belongs to Eosimias; Group 2, all taxa, all characters, Shanguang petrosal either excluded or included as a separate taxon; Group 3, cranial data only; Group 4, dental data only; Group 5, postcranial data only.

Chara. n: number of characters.

Taxa n: number of taxa.

Constraint: U=unconstrained, C=constrained to ensure primate monophyly.

Wt: S=scaled so that multistate characters do not bias analysis (base weight=100); E=all characters equal weights (=1).

Order: O=some multistate characters ordered (see Appendix A); U=all multistate characters unordered.

Tree n: number of equally parsimonious trees obtained.

Tree length: length of most parsimonious tree in MacClade (excludes dummy characters). +, tree lengths for trees with polychotomies. These are minimum tree lengths that increase when polychotomies are resolved.

CI: Consistency Index (MacClade).

RCI: Rescaled Consistency Index (MacClade).

RI: Retention Index (MacClade).

Primates: Y, primate monophyly obtained; N, primate monophyly not obtained.

T,An: Y, tarsier-anthropoid clade found; N, tarsier-anthropoid clade not found.

T,An,Om: Y, tarsier-anthropoid-omomyid clade found; N, tarsier-anthropoid-omomyid clade not found.

E,An: Y, Eosimias-anthropoid (-Tarsius) clade found; N, Eosimias-anthropoid (-Tarsius) clade not found.

T,Om: Y, tarsier-omomyid clade found; N, tarsier-omomyid clade not found.

An,Ad: Y, anthropoid-adapid clade found; N, anthropoid-adapid clade not found.

S,Ad: Y, strepsirrhine-adapid clade found; N, strepsirrhine-adapid clade not found.

Clades are reported as obtained if present in strict consensus tree/majority rule consensus tree. All statistics given are for strict consensus trees.

Table 3 Percentage completeness of data set, by taxon and data partitions

Taxon	% Complete, all data	% Complete cranial data	% Complete postcranial data	% Complete dental data
All taxa	57.1	36.4	29.1	73.42
Scandentia	76.6	93.9	98.0	64.8
“ <i>P. tricuspidens</i> / <i>P. jepf</i> ”	77.0	69.4	84.0	76.9
<i>Purgatorius unio</i>	44.0	2.0	0.0	69.8
<i>Plesiolestes problematicus</i>	43.0	2.0	0.0	68.1
<i>Adapis parisiensis</i>	88.0	85.7	89.0	88.5
“ <i>Cantius</i> / <i>Notharctus</i> ”	75.3	34.7	57.0	91.8
<i>Donrussellia</i> sp.	36.4	4.1	0.0	57.1
<i>Leptadapis magnus</i>	62.9	8.2	41.0	85.7
<i>Mahgarita stevensi</i>	63.6	79.6	0.0	78.6
<i>Aframomius dieides</i>	33.0	2.0	0.0	52.2
<i>Pronycticebus gaudryi</i>	59.8	59.2	0.0	78.0
<i>Protoadapis curvicaudatus</i>	44.7	2.0	0.0	70.3
<i>Galagoidea demidoff</i>	94.5	89.8	98.0	94.5
<i>Lemur catta</i>	91.8	95.9	98.0	88.5
<i>Microcebus murinus</i>	93.1	93.9	98.0	91.2
<i>Nycticebus coucang</i>	93.1	85.7	98.0	93.4
<i>Absarokius</i> sp.	55.0	2.0	27.0	79.1
<i>Anaptomorphus</i> sp.	44.3	2.0	0.0	70.3
<i>Anemorhysis savagei</i>	32.6	2.0	0.0	51.6
<i>Arapahovius gazini</i>	59.5	2.0	14.0	90.1
<i>Aycrossia lovei</i>	50.9	2.0	0.0	80.8
<i>Dyseolemur pacificus</i>	58.1	2.0	0.0	92.3
<i>Hemiacodon gracilis</i>	68.4	2.0	79.0	84.6
<i>Loveina zephyri</i>	46.0	2.0	0.0	73.1
<i>Macrotarsius montanus</i>	30.9	2.0	0.0	48.9
<i>Microchoerus erinaceus</i>	66.3	6.1	36.0	93.4
<i>Nannopithecus</i> sp.	60.8	2.0	12.0	92.9
<i>Necrolemur antiquus</i>	80.8	87.8	48.0	89.0
<i>Omomys</i> sp.	70.4	28.6	41.0	90.7
<i>Pseudoloris parvulus</i>	54.3	2.0	0.0	86.3
<i>Rooneyia viejaensis</i>	32.3	79.6	0.0	28.6
<i>Shoshonius cooperi</i>	66.0	71.4	4.0	83.5
<i>Steinius vespertinus</i>	48.8	2.0	0.0	77.5
<i>Teilhardina americana</i>	54.0	2.0	12.0	81.9
<i>Teilhardina belgica</i>	48.8	2.0	0.0	77.5
<i>Tetonius</i> sp.	67.4	42.9	2.0	94.0
<i>Tetonoides n. sp.</i>	47.8	2.0	0.0	75.8
<i>Trogolemur myodes</i>	47.4	2.0	0.0	75.3
<i>Washakius insignis</i>	56.7	2.0	2.0	89.6
<i>Eosimias</i> sp.	56.0	18.4	32.0	73.1
<i>Tarsius</i> sp.	95.9	98.0	100.0	94.0
<i>Aegyptopithecus zeuxis</i>	80.1	85.7	57.0	85.7
<i>Apidium phiomense</i>	82.5	53.1	88.0	89.0
<i>Arsinoea kallamos</i>	36.1	2.0	0.0	57.1
<i>Catopithecus browni</i>	75.3	59.2	38.0	91.2
<i>Parapithecus fraasi</i>	36.8	0.0	0.0	58.8
<i>Qatrania wingi</i>	33.3	0.0	0.0	53.3
<i>Serapia eocaena</i>	32.3	0.0	0.0	51.6
<i>Simonsius grangeri</i>	49.8	2.0	0.0	79.1
<i>Aotus trivirgatus</i>	94.8	95.9	98.0	93.4
<i>Callicebus moloch</i>	95.5	95.9	98.0	94.5
<i>Dolichocebus gaimanensis</i>	45.7	4.1	9.0	69.2
<i>Saimiri sciureus</i>	94.2	95.9	98.0	92.3
<i>Proteopithecus sylviae</i>	21.0	2.0	0.0	54.4
<i>Afrotarsius chatrathi</i>	18.6	0.0	0.0	29.7
<i>Strigorhysis</i> sp.	45.7	0.0	0.0	73.1
<i>Uintanius ameghini</i>	46.4	0.0	0.0	74.2

Bold numbers indicate taxa included in each data set.

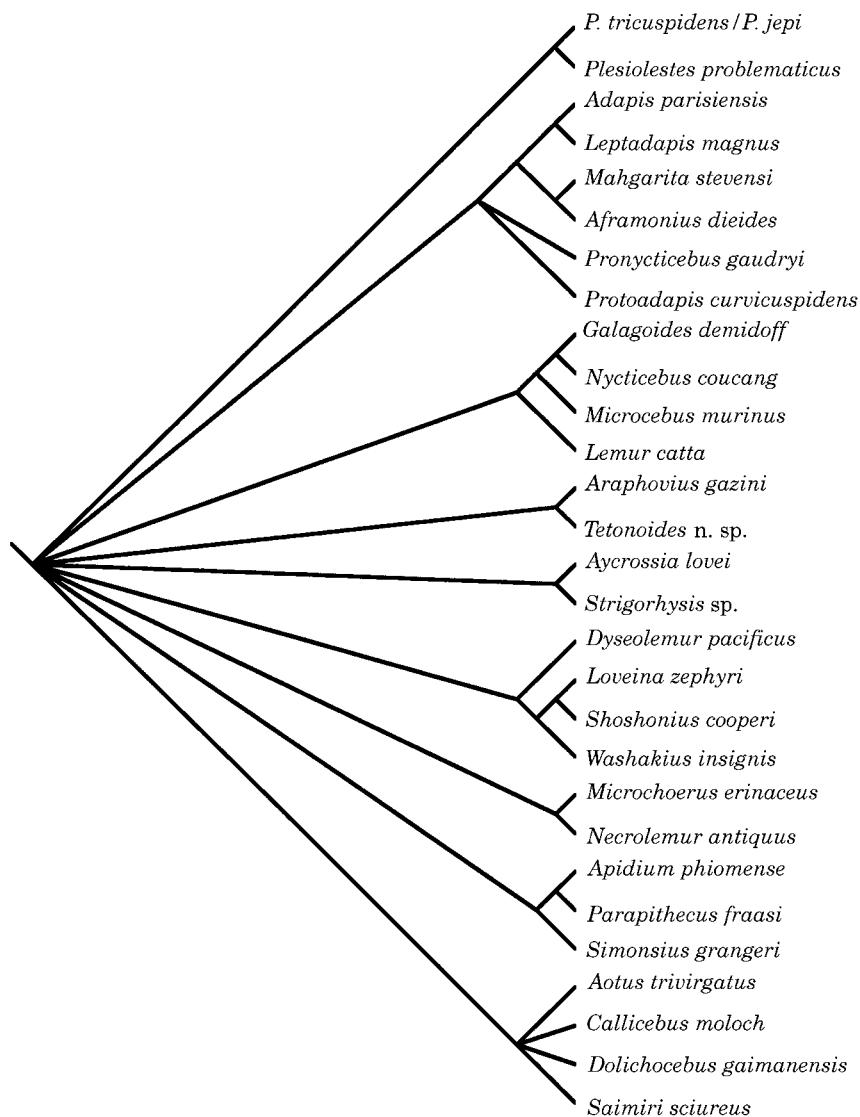


Figure 3. Strict consensus of all Analysis Group 1 consensus trees. This network illustrates the groups found by all Group 1 analyses, regardless of the assumptions made. Taxa not united with other taxa are omitted for clarity but would join the polytomy at the base of the tree.

Microcebus the sister-group to this lorid clade and *Lemur catta* as the outgroup to all living strepsirrhines. Thus, Malagasy primates are not found to be monophyletic (Figure 3). (3) *Adapis* and *Leptadapis* form a clade, as do *Maharita* and *Aframoni*, and these two clades form a monophyletic group with *Protoadapis* and *Pronycticebus* as outgroups

(Figure 3). (4) The clade of adapids described in (3) usually forms a monophyletic group with extant strepsirrhines and the *Cantius/Notharctus* taxon falls as the outgroup to this clade (Figure 4).

Within omomyids, four clades consistently appear (Figures 3 and 4): (1) an “anaptomorphine” clade, consisting of

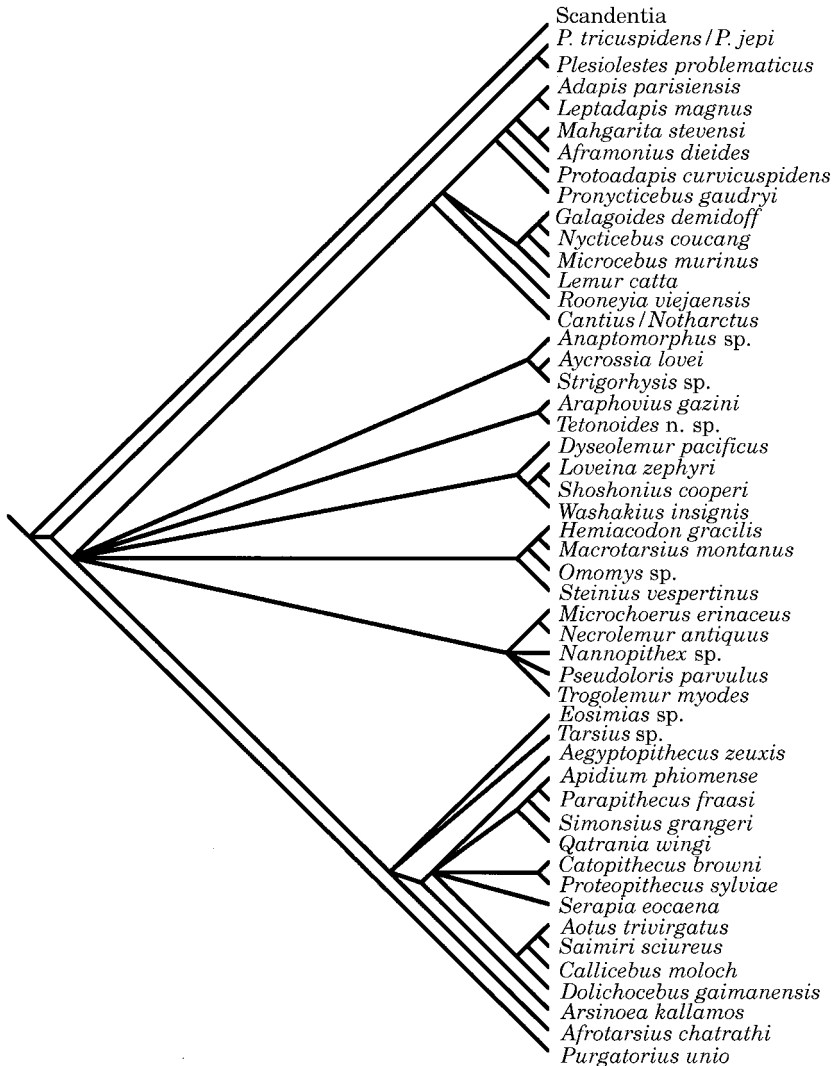


Figure 4. Majority rule (50%) consensus of all Analysis Group 1 consensus trees. This network illustrates the groups found by analysis of all the data regardless of the assumptions made. Primate taxa not united with other taxa are omitted for clarity but would join the polytomy at the base of the primate clade.

(*Strigorhysis*+*Aycrossia*) and usually *Anaptomorphus*; (2) a microchoerine clade including (*Microchoerus*+*Necrolemur*), usually with *Nannopithecus*, *Trogolemur* and *Pseudoloris* in various closely related positions; (3) a washakiine clade including {[(*Shoshonius*+*Loveina*), *Washakius*] *Dyseolemur*}; and (4) a clade consisting of *Arapahovius* and *Teto-*

noides. In addition, an omomyine clade, including *Hemiacodon*, *Macrotarsius*, *Omomys*, and *Steinius*, is found in the majority of cases. The majority of the results described above for omomyid relationships agree with Williams (1994; n.d.). However, because only a sample of omomyid taxa are used here (and in Kay *et al.*, 1997), some details differ.

With regard to Anthropoidea: (1) platyrrhines are found to form a monophyletic group; (2) the parapathecines ((*Apidium*+*Parapithecus*) *Simonsius*) are always monophyletic (Figure 3); (3) catarrhines (i.e. *Aegyptopithecus* in our group) and platyrrhines were not always found to form a monophyletic group (Figure 3), although this was the case in the majority of analyses (Figure 4); (4) in all but one analysis, all living platyrrhines are more closely related to each other than to *Dolichocebus* (Figure 4); (5) the Fayum anthropoids in our sample were usually more closely related to the crown anthropoids than to other primates; (6) the oligopithecines (*Catopithecus*+*Proteopithecus*) were monophyletic in the majority of cases (Figure 4).

The qatraniines are not monophyletic under any of the assumption sets adopted here, and they never fall in with parapathecines in a monophyletic Parapathecoidea (Figure 5). *Qatrania* falls in with parapathecines when unordered analyses are run, whether scaled or equally weighted [Figure 5(a) & (b)]. When ordered analyses are run, majority rule consensus trees find *Serapia*, *Qatrania* and *Arsinoea* to fall out sequentially as sister taxa to a clade consisting of oligopithecines, parapathecines, platyrrhines and catarrhines [Figure 5(c)]. Oligopithecines fall out as the sister taxon to platyrrhines when the data are unordered and scaled [Figure 5(a)], and when they are weighted equally, ordered and constrained; otherwise they are the sister taxon to a clade consisting of parapathecines and crown anthropoids.

Tarsius was only placed as the sister taxon to washakiines when an ordered, constrained and equally weighted data set was used [Figure 6(a)]. *Tarsius* falls out as the sister-taxon to an Anthropoidea+*Eosimias* clade when the data are ordered and unconstrained, whether equally weighted or scaled, and when unordered, constrained and equally weighted [Figure 6(b)]. *Eosimias*

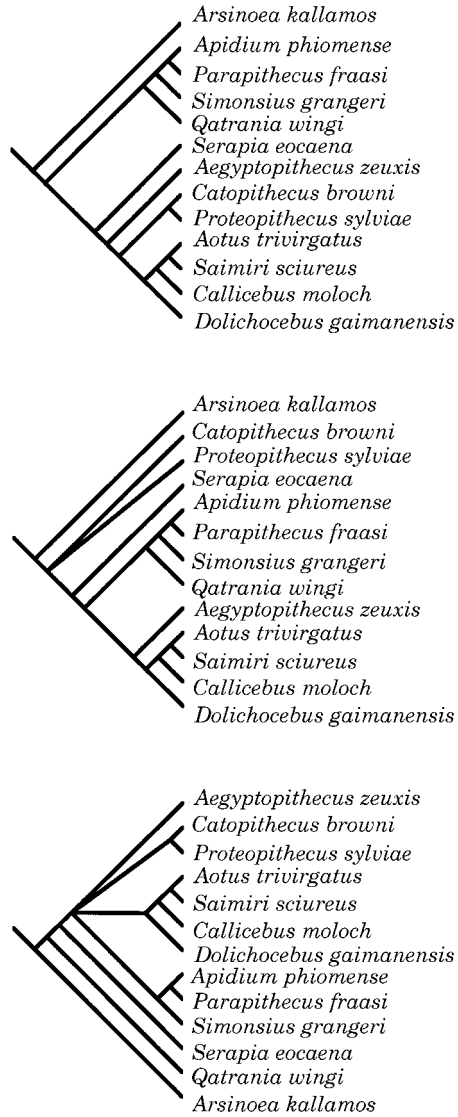


Figure 5. Diagrams illustrating different arrangements of crown and fossil Anthropoidea under different assumption sets in Analysis Group 1. Non-anthropoid taxa omitted. Top: Tree obtained using unordered scaled data. Center: Tree obtained using unordered, equally weighted data. Bottom: Tree obtained using ordered data.

falls out as the sister taxon to a *Tarsius*+Anthropoidea clade when unordered, scaled analyses are run [Figure 6(c)].

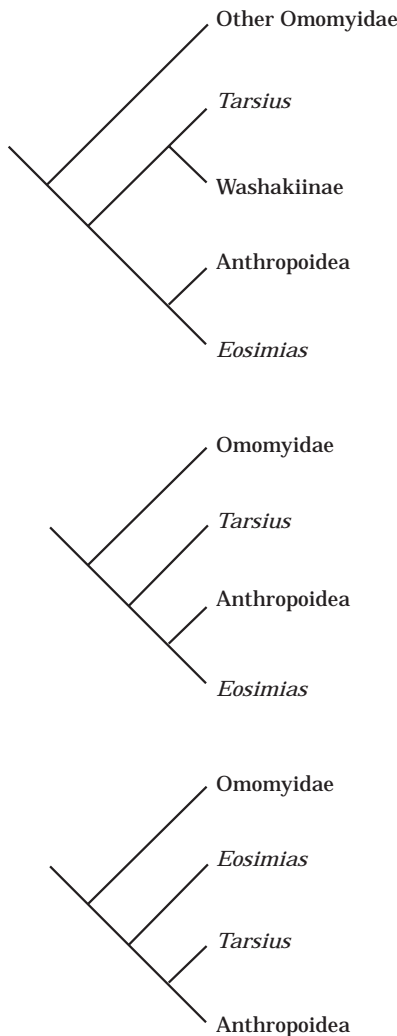


Figure 6. Diagrams illustrating different arrangements of *Tarsius*, Anthropoidea and *Eosimias* under different assumption sets in Analysis Group 1. Top: Tree obtained using ordered, constrained, equally weighted data. Center: Tree obtained using ordered, unconstrained data. Bottom: Tree obtained using unordered, scaled data.

Analysis Group 2: all characters; assuming Shanghuang petrosal not to be Eosimias

The complete data set was also analyzed with the data from the Shanghuang petrosal included as a separate taxon (scaled analyses) and excluded altogether (equally weighted analyses). There are several ele-

ments common to the results of all assumption sets: (1) a clade consisting of *Tarsius*, *Eosimias*, *Afrotarsius* and Anthropoidea; (2) a washakiine clade; (3) a monophyletic crown Anthropoidea; (4) a monophyletic Parapithecinae; (4) an *Adapis+Leptadapis* clade; (5) a *Mahgarita+Aframoni* clade; and (6) a clade consisting of all strepsirrhines, except *Lemur catta* (Figure 7).

When the Shanghuang petrosal was included in the analysis as a separate taxon, the strict consensus trees included a polytomy of all non-washakiine omomyids. The Shanghuang petrosal is very omomyid-like (MacPhee *et al.*, 1995) and could equally easily belong to any of the omomyid lineages except the washakiines. Majority rule consensus trees of these polychotomies produce groups similar to those found in Analysis Group 1 (Figure 8). In all but two cases the (*Tarsius*, *Eosimias*, *Afrotarsius*, Anthropoidea) clade was nested within the omomyids; the unordered and unconstrained analyses produced majority rule consensus trees in which this clade was the sister taxon to the (strepsirrhine+adapid) clade.

Analysis Group 3: cranial characters only

Analysis of the cranial data alone yielded two tree topologies. The first resulted from the unconstrained ordered analysis (Figure 9) (which did not yield primate monophyly), and the second from the other three assumption sets (Figure 10). Both these trees mimic the majority of the complete analyses in having a monophyletic crown Anthropoidea with *Apidium* as the sister taxon, followed by *Catopithecus*, *Tarsius*, then the omomyids. A clade consisting of [(*Adapis+Mahgarita*) *Pronycticebus*] is always found, as are a *Cantius+Lemur* clade and a [(*Galagoides+Nycticebus*) *Microcebus*] clade.

Analysis Group 4: dental characters

Figure 11 illustrates the groups common to all dental trees: (1) strepsirrhine monophyly

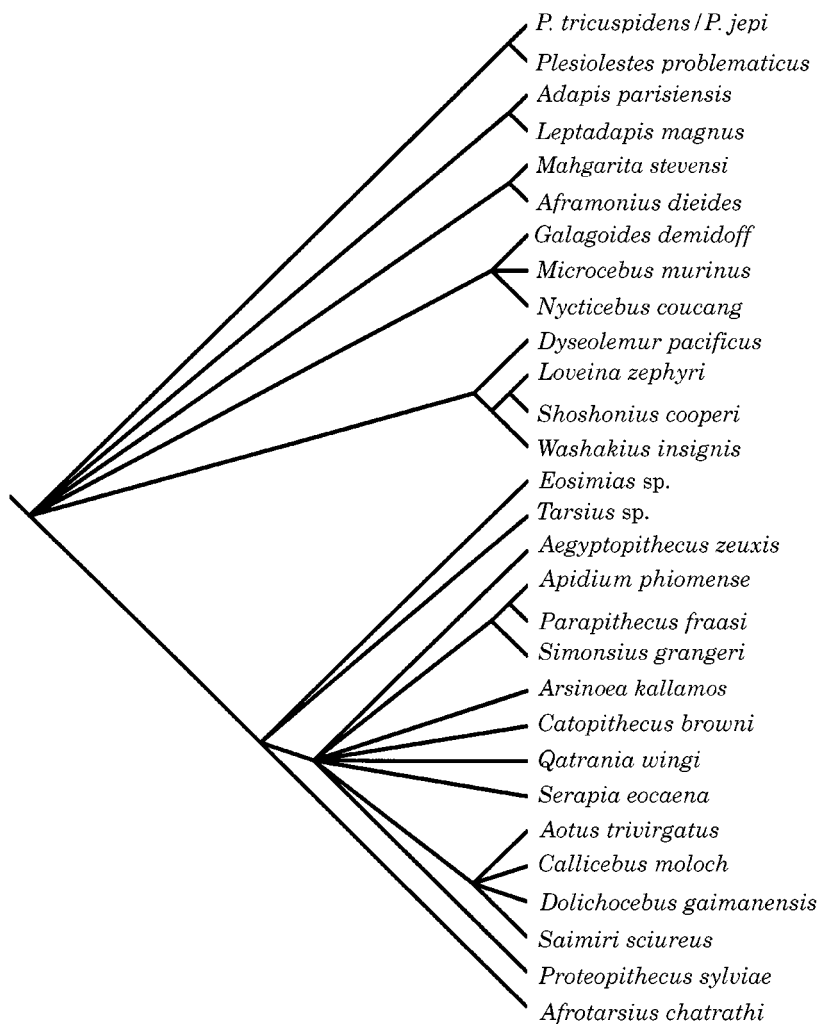


Figure 7. Strict consensus of all Analysis Group 2 consensus trees. This network illustrates the groups found by analysis of all the data regardless of the assumptions made. Taxa not united with other taxa are omitted for clarity but would join the polytomy at the base of the tree.

is supported; (2) anthropoid monophyly is also confirmed, although *Rooneyia* consistently falls in with the parapithecines; (3) the parapithecines and qatraniines form a monophyletic Parapithecoidea (although including *Rooneyia*); (4) *Aegyptopithecus* is the sister taxon of the Parapithecoidea with the platyrrhines as the sister to this clade; (5) the oligopithecids are the most primitive anthropoids. As with the complete

data set, the same groupings of omomyids are supported: (6) anaptomorphines, (7) microchoerines, (8) washakiines and (9) omomyines (Figure 11).

The majority rule consensus tree of all dental trees exhibits increased resolution among the omomyids (Figure 12). Importantly, it also supports the notion of an *Eosimias*+*Tarsius* clade, although this is not closely related to any other group (Figure 12).

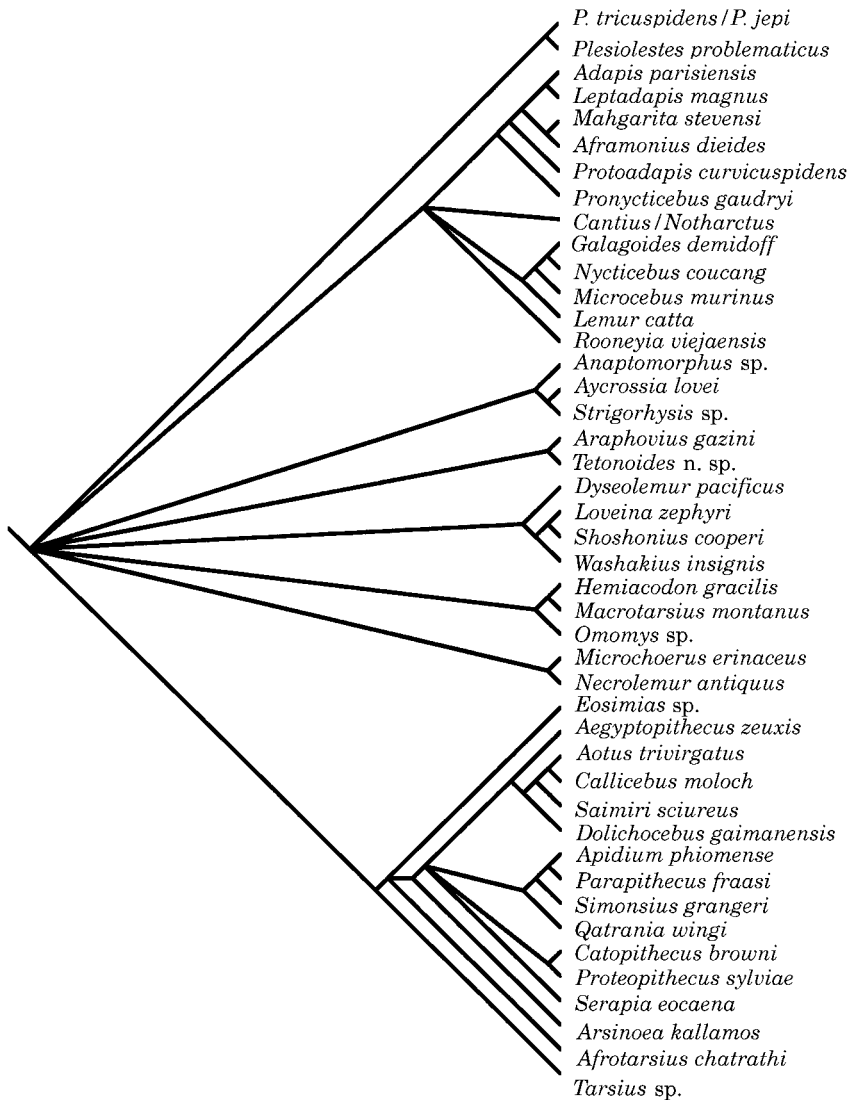


Figure 8. Majority rule (50%) consensus of all Analysis Group 2 consensus trees. This network illustrates the groups found by analysis of all the data regardless of the assumptions made. Primate taxa not united with other taxa are omitted for clarity but would join the polytomy at the base of the primate clade.

Examination of individual trees revealed that some kind of adapid is often more closely related to anthropoids than any omomyid (Table 2). In one case it is *Mahgarita* and *Aframonius*, in two cases it is a clade consisting of cercamoniines and adapines, and in the constrained, unordered case, a clade consisting of [(adapines+

cercamoniines] [*Tarsius*+*Eosimias*)] is the sister clade to (Anthropoidea+*Afrotarsius*).

Analysis Group 5: postcranial characters

The postcranial evidence supports primate monophyly; constrained trees do not display any topological differences from unconstrained trees. Ordered and

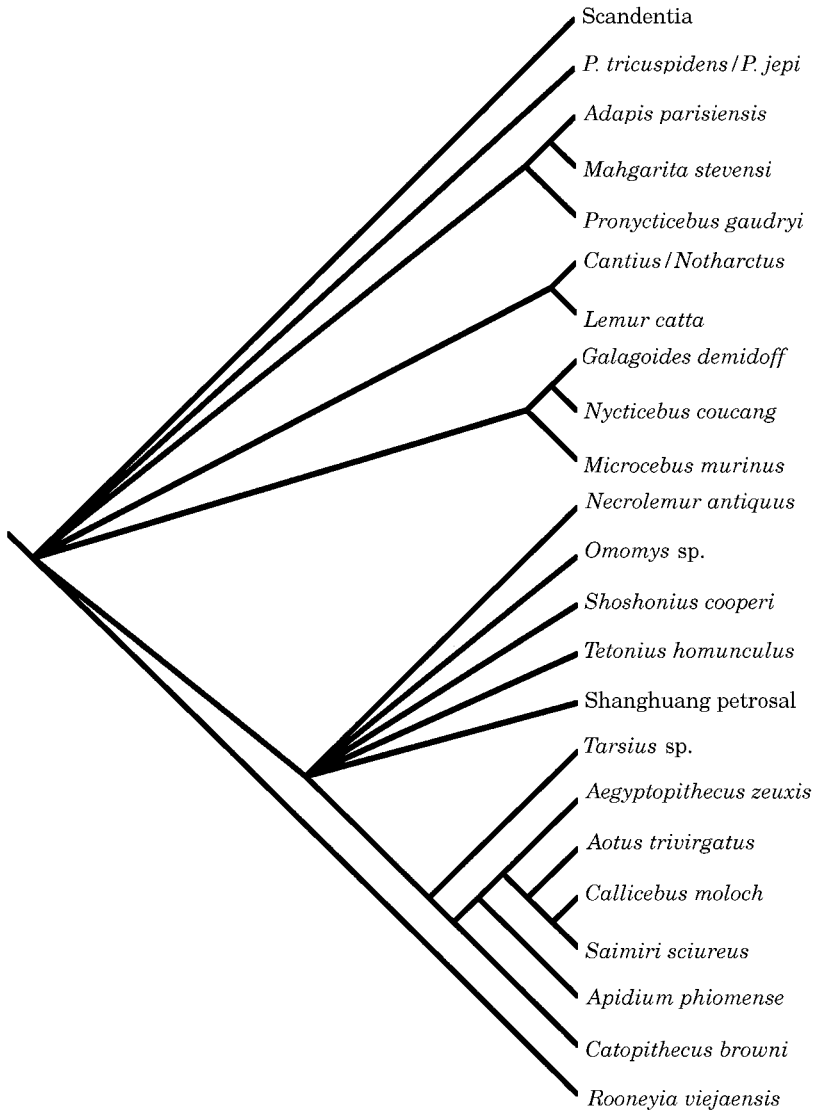


Figure 9. Strict consensus tree of cranial data, unconstrained, ordered, scaled.

unordered analyses are very similar with character ordering having only minor effects on tree topology. Figure 13 illustrates the strict consensus of both trees obtained from the postcranial data: (1) Adapids, omomyids, strepsirrhines and *Tarsius*, form a clade, equivalent to "Prosimii"; (2) Anthropoidea forms a clade; (3) strepsirrhines are more closely

related to adapids than to omomyids; (4) Malagasy primates are monophyletic; (5) *Eosimias* is more closely related to "Prosimii" than to anthropoids; (6) paraithecoids are more closely related to platyrrhines than to catarrhines. Ordering the characters creates a monophyletic Omomyidae with *Tarsius* as the sister-taxon to *Necrolemur*.

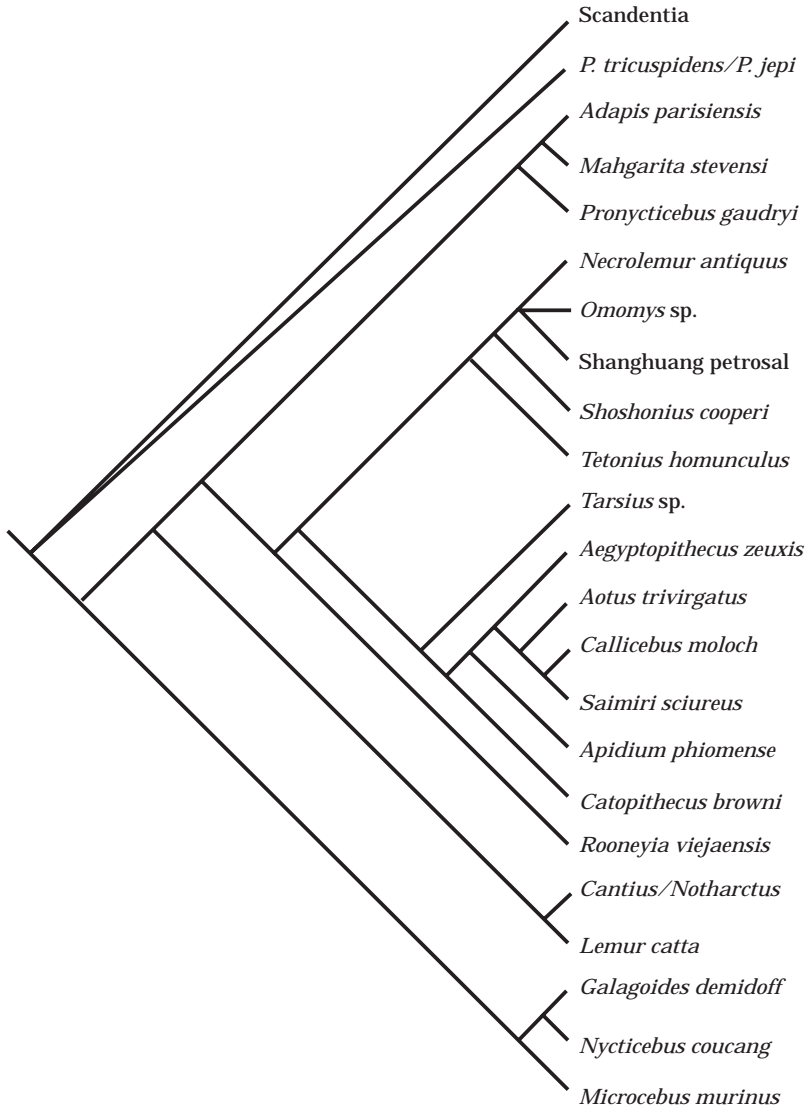


Figure 10. Strict consensus tree of cranial data unconstrained, unordered, scaled; and constrained, ordered, scaled.

Discussion

Separate versus combined analyses

There is currently little agreement regarding the relationships among primate higher taxa. The analyses presented here suggest that this is attributable in part to the fact that all analyses to date have utilized data from only one part of the body and these data sets

evince some rather disjunct phylogenetic signals. The postcranial evidence supports the existence of a monophyletic "Prosimii", consisting of omomyids, adapids, strepsirrhines and *Tarsius*, and a monophyletic Anthropeidea. The cranial data set suggests the existence of a monophyletic Haplorhini, consisting of a *Tarsius*-Anthropeidea clade

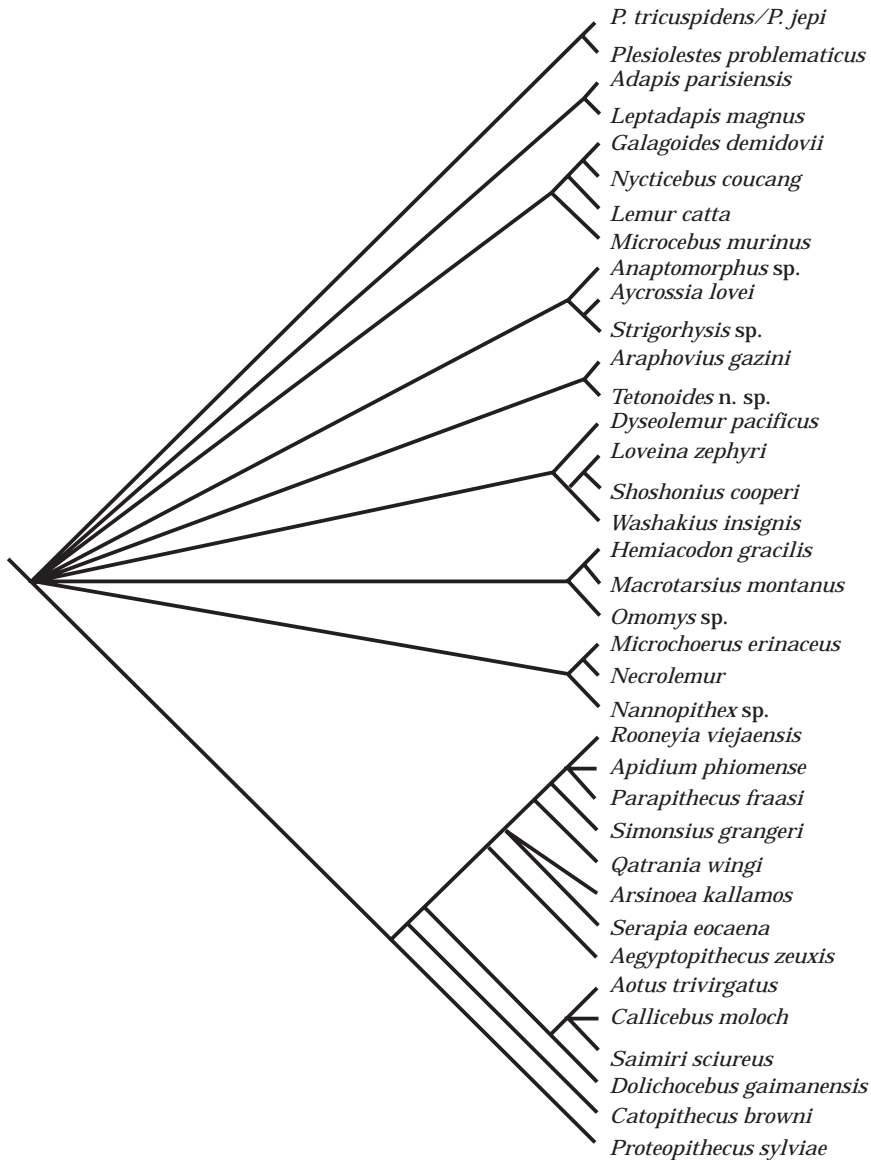


Figure 11. Strict consensus tree of all trees obtained from analysis of the dental data set; i.e., groupings obtained by analysis of dental data regardless of assumption sets.

nested within a paraphyletic Omomyidea, and a monophyletic Strepsirrhini, consisting of adapids and strepsirrhines. The dental evidence provides weak support for the hypothesis of an adapid-anthropoid clade. However, when all the data are analyzed together, a *Tarsius*-Anthropeidea clade is

found under all assumption sets except one.

Various arguments have been advanced for and against the separate analysis of different types of data. Some workers have argued that different classes or "process partitions" of data exist if they have evolved

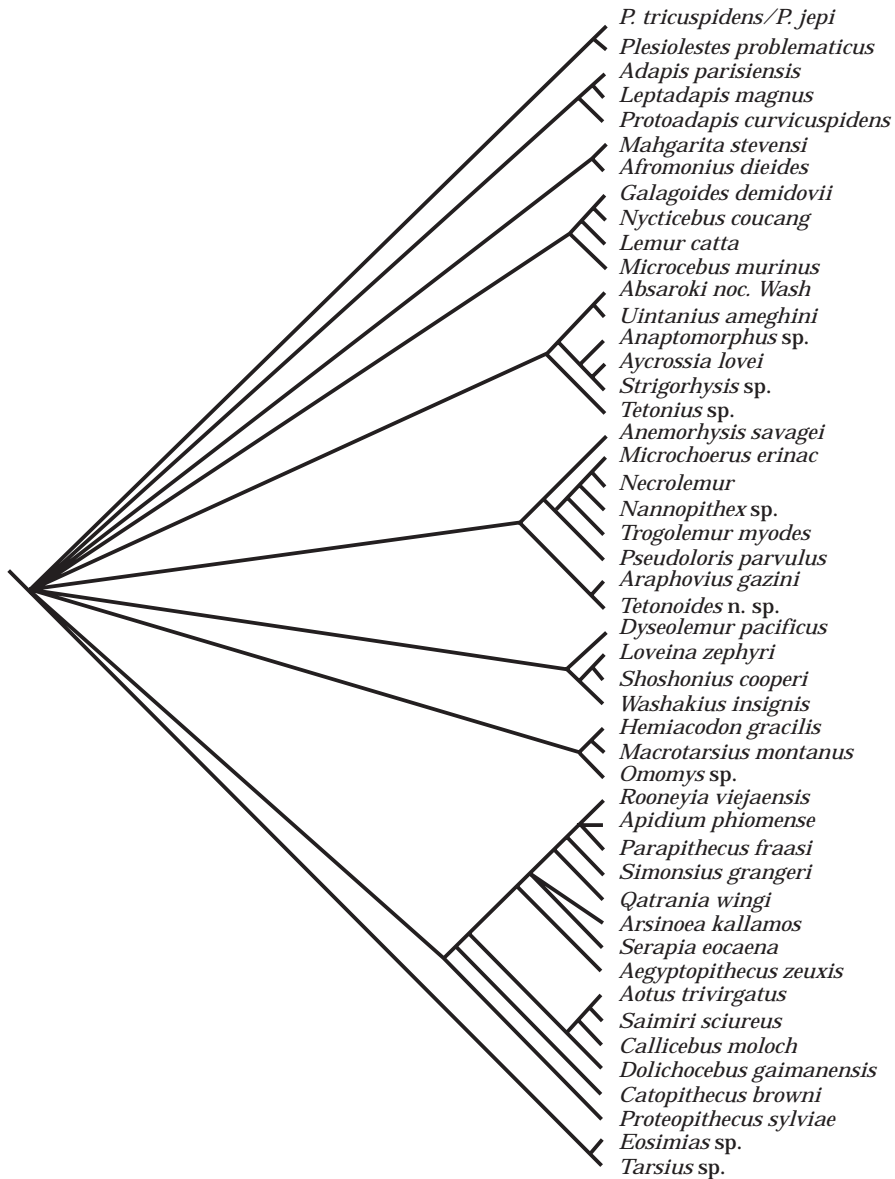


Figure 12. Majority rule (50%) consensus tree of all trees obtained from analysis of the dental data set.

according to different “rules” or evolutionary processes (Bull *et al.*, 1993; De Queiroz *et al.*, 1995; Huelsenbeck *et al.*, 1994; Miyamoto & Fitch, 1995). The advantage of analyzing such partitions or classes separately is that if independence of data sets can be proven, then independent estimates of

phylogeny can be generated. Other workers have suggested that different classes of data do not exist and that all available data should be included in an analysis (Kluge, 1989; Kluge & Wolf, 1993; Chippendale & Wiens, 1994). The question in the present case is: do the dental, cranial and postcranial

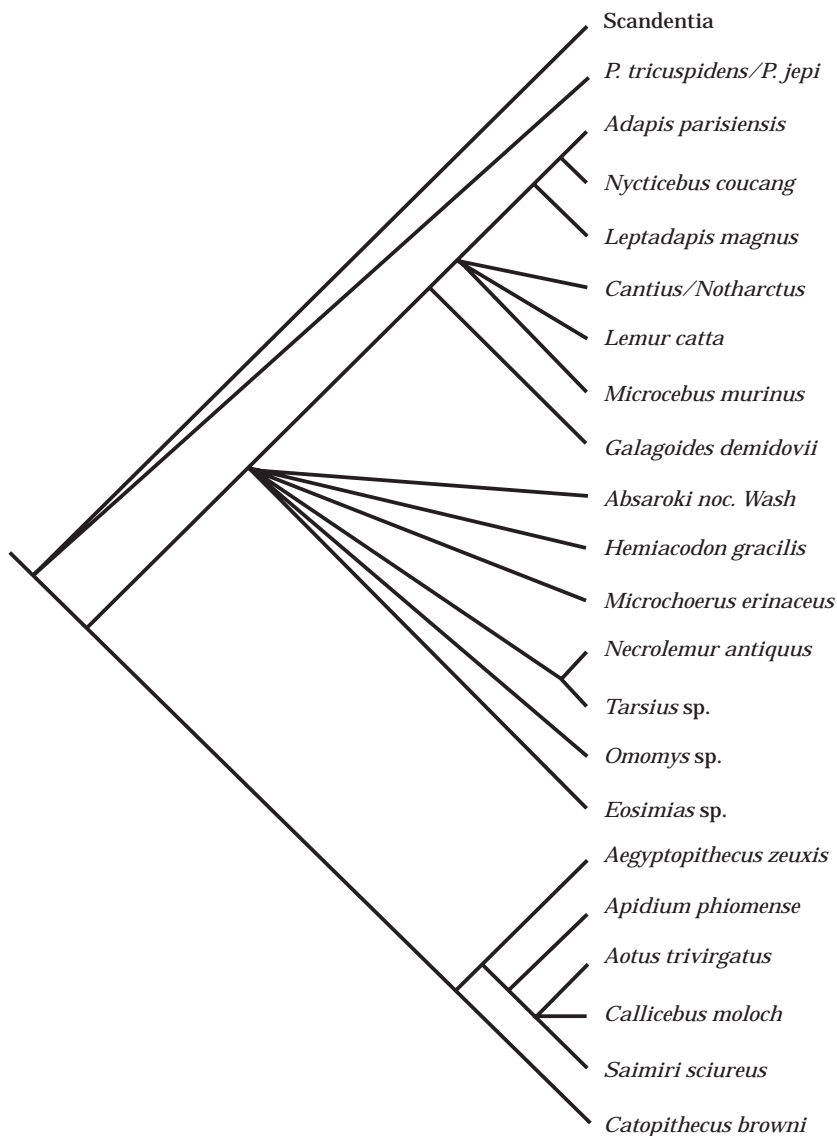


Figure 13. Strict consensus tree of all trees obtained from analysis of the postcranial data set; i.e., groupings obtained by analysis of postcranial data regardless of assumption sets. Note support for "Prosimii".

characters constitute different classes of data?

Miyamoto & Fitch list five criteria for identifying process partitions, three of which are relevant here: independence of genes, gene products and gene "functions" (1995:66). We do not know whether our

dental, cranial and postcranial characters are genetically independent, although we suspect that they may not be, particularly the cranial and dental data sets. Clearly a strong case in favor of partition cannot be made on the basis of these considerations.

Nevertheless, our three classes of data clearly evince different phylogenetic signals, suggesting that they may have been evolving under different rules. Bull *et al.* (1993) demonstrated that combining two data sets that have evolved at different rates can yield incorrect phylogenies. If different parts of the primate body evolved at different rates, this might create problems for our combined analyses. We therefore sought to estimate the relative evolutionary rates in our three data sets: the cranial, dental and postcranial data sets. We selected one tree on which to make these calculations: the most parsimonious tree derived from analysis of all characters, ordered, scaled and unconstrained. A polytomy among the outgroup taxa at the base of the tree was manually resolved so that MacClade could calculate the changes using equivocal cycling. For each of the three data sets, the total changes on this tree were calculated using the Tree Changes calculation in MacClade. The number of changes is appropriate because it is not weighted in any way by the costs of the reconstructed changes. This value was then divided by the number of character *states* in each data partition (i.e., dental, cranial, postcranial). We apportioned the number of changes to states, rather than to characters, otherwise multistate characters would appear to evolve faster merely because they have more states assigned to them.

Table 4 gives the results of these calculations. The dental character states (2.19 changes per state) change nearly twice as often on this tree as the cranial (1.2 changes per state) and postcranial (1.29) character states. Initially these results appear to suggest that the dental traits have evolved twice as fast as the cranial and postcranial. However, for many of the taxa in this data set much of the cranial or postcranial data is missing (Table 3), decreasing the number of changes that occur on the tree. To account for missing data, we also did these calculations only on those 15 taxa represented by at

Table 4 Evolutionary rates in most parsimonious tree from scaled, ordered, unconstrained data

Characters	Number of states	Total changes	Changes per state
All taxa			
All	777	1703–1787	2.19–2.30
Cranial	119	145–146	1.22–1.23
Dental	519	1377–1448	2.65–2.79
Postcranial	139	180–192	1.29–1.38
Taxa 75%+ complete			
All	777	839–910	1.08–1.17
Cranial	119	114–115	0.96–0.97
Dental	519	573–633	1.10–1.22
Postcranial	139	148–158	1.06–1.14

least 75% of the data (Table 3). The number of changes was calculated on the same tree as the previous calculations, but with all but the 15 most complete taxa pruned from it. In this data set, on average, all character states exhibit between 1.08 and 1.1 changes on the tree, with dental characters averaging between 1.1 and 1.2 changes, cranial characters averaging 0.965 changes and postcranial characters averaging 1.06 and 1.14 changes (Table 4).

These estimates of evolutionary rates in different parts of the primate body are rather crude, but they do suggest that the cranial data evolved slightly (10%) slower than the other two data partitions. It is noteworthy that the results derived from analyses of the complete data set are in concordance with the results of the cranial data, not the dental or postcranial data. Perhaps the cranial data, evolving more slowly than the other two data partitions, influence the branching pattern of the tree at basal nodes, whereas the more rapidly evolving dental and postcranial data obscure any pattern at basal nodes, but influence distal nodes on the tree more profoundly (see also Gould, 1997). Another possible explanation for the concordance between the trees derived from the cranial data and those derived from the overall analysis is that the cranial data set

was more selectively compiled than the dental data set. The cranial characters were primarily collated from the literature by Ross (1994), a literature primarily concerned with resolving relationships among primate higher taxa. The dental matrix was assembled with the more catholic aim of resolving relationships among many different groups of primates at different taxonomic levels. An effort to gather a larger, more diverse cranial or postcranial data set might determine the effect of character selection on our analyses of evolutionary rates in different parts of the primate body.

Character ordering

One argument given in support of ordering multistate characters is that it increases tree resolution (Mickevich & Weller, 1990). There seems little reason to prefer a well resolved tree over a poorly resolved one if the well resolved tree is inaccurate (Slowinski, 1993). Nevertheless, it is worthwhile examining the effect that character ordering has in the present case. Does character ordering increase tree resolution in this data set?

Following Hauser & Presch (1991), using the complete data set, comparisons were made between the number of nodes in strict consensus trees of the most parsimonious trees generated using unordered and ordered data sets, holding all other assumptions constant. Out of six comparisons, in three cases the ordered data set produced a more highly resolved tree, and in three cases it did not. There are various possible reasons for this, including the large amounts of missing data and the low proportion of ordered vs. unordered characters. Nevertheless, as found by Hauser & Presch (1991), the ordered data sets did not consistently produce more highly resolved trees than the unordered data sets. Improved resolution cannot be invoked in favor of preferring trees produced using ordered multistate

characters over trees produced using unordered data.

Importance of fossils

Fossils have been shown to be important in phylogenetic analyses, particularly if they are relatively complete, and if they come from a temporal position close to ancestral nodes in the tree (Huelsenbeck, 1991). The reason for this is the particular mixture of derived and primitive features exhibited by fossils (Gauthier *et al.*, 1988). In the present case, the importance of fossils varies. Overall, the fossil evidence supports phylogenetic reconstructions based on evidence from living taxa. There is wide agreement among paleo-primatologists that tarsiers are more closely related to anthropoids than to strepsirrhines (Purvis, 1995). The evidence comes from molecular data (Koop *et al.*, 1989*a,b*; Porter *et al.*, 1997) and soft tissues (Hubrecht, 1897; Luckett, 1975, 1976; Shoshani *et al.*, 1996). The complete data set presented here provides definitive support for this hypothesis: tarsiers and anthropoids are found to be more closely related to each other than to strepsirrhines.

This result is compelling, given that only four soft-tissue characters were included in the data set and run in Analysis Groups 1 and 2. Although we did not attempt to sample the soft-tissue data exhaustively, inclusion of further soft-tissue characters would not alter these results. The most extensive soft-tissue data set pertinent to this problem is that of Shoshani *et al.* (1996). Of the 98 soft-tissue characters in that data set, nine are relevant to the current analysis, one supports a monophyletic Prosimii and eight support a *Tarsius*-Anthropoidea clade among living primates.

The case of the Shanghuang petrosal is more interesting. This petrosal was recovered from the same Shanghuang fissure filling deposit as jaws of *Eosimias sinensis* and has been assigned to this taxon, primarily on the basis of size (MacPhee *et al.*, 1995). Its

morphology is of interest because it lacks the derived features of the petrosal shared by tarsiers and anthropoids. If *Eosimias* is a basal anthropoid—as our analysis suggests—and if the Shanghuang petrosal is that of *Eosimias*, then the otic apomorphies linking tarsiers to anthropoids must be convergences. This possibility is translated in one of our analyses into the collapse of the tarsier–anthropoid clade and the formation of a tarsier–washakiine clade. Notably however, if the Shanghuang petrosal is *not* that of *Eosimias*, then there are no assumption sets applied to the complete data set that can break up the tarsier–anthropoid clade.

The profound influence of the Shanghuang petrosal on tree topology under some assumption sets can be attributed to the two reasons listed above: its specific combination of primitive and derived features and its position close to the root of anthropoids. The dentition of *Eosimias* nests it firmly at the base of the anthropoid clade, close to the node shared with *Tarsius*. The Shanghuang petrosal exhibits nothing to dispute this placement for *Eosimias*, yet it lacks most of the otic apomorphies shared by tarsiers and anthropoids. Consequently, under one set of assumptions it is unparsimonious for *Tarsius* to be the sister taxon to the *Eosimias*–Anthropoidea clade.

Given that the majority of analyses support the notion of a tarsier–anthropoid clade whether the Shanghuang petrosal belongs to *Eosimias* or not, given the uncertainty of the assignment of the petrosal to *Eosimias*, and given that the otic features that it lacks are unique to tarsiers and anthropoids, we believe that the Shanghuang petrosal probably does not belong to *Eosimias*.

Strength of various hypotheses

Adapid–anthropoid hypothesis. This hypothesis receives support from the dental evidence but is not supported by the cranial or postcranial evidence, or the evidence overall. Rather, the majority of the evidence better

supports the hypothesis of an adapid–strepsirrhine clade exclusive of anthropoids and tarsiers. Indeed, of the three hypotheses evaluated here, the adapid–anthropoid hypothesis was by far the least well supported. To estimate the weakness of this hypothesis relative to the *Tarsius*–Anthropoidea hypothesis, we used a heuristic search (1000 replications) to find the shortest tree that contains an adapid–anthropoid clade. We introduced 50 dummy characters into the matrix and ran the complete data set with all characters equally weighted and unordered. The shortest tree found was 1894+steps (excluding dummy characters), compared with 1658+steps for the unconstrained analysis. The adapid–anthropoid tree is 236 steps (14%) longer than the tree containing the *Tarsius*–Anthropoidea clade.

Simons & Rasmussen's (1996) recent paper is the newest and most explicit attempt to link adapids and anthropoids,* and these workers go so far as to venture a new classification of the order Primates. Consequently, their conclusions must be examined in some detail. Resurrecting Wortman's (1903–1904) “informed and cohesive” classification as “a conservative alternative to erecting a new taxon”, they place the Hyporder Anthropoidea within Wortman's suborder Neopithecini (Simons & Rasmussen, 1996:285). In support of their phylogenetic hypothesis, Simons & Rasmussen (1996) present an extensive list of cranial and dental features in which the early anthropoid *Catopithecus* is claimed to more closely resemble “adapoids” (hereafter referred to as adapids) than *Tarsius*. Simons & Rasmussen's table is reproduced here as Table 5. Most of the enumerated characters were included in the present study and their character numbers are given in the table.

Why does the present study not support the adapid–anthropoid hypothesis? Of the

*The adapid–anthropoid hypothesis is also advocated by Shoshani *et al.* (1996), but without any evidence in support of it.

Table 5 Reinterpretation of craniodental features cited by **Simons & Rasmussen (1996)** in support of an anthropoid-adapid clade

Feature ¹	<i>Tarsius</i> ¹	<i>Catopithecus</i> ¹	Adapids ¹	Character # (this study) ²	Status (this study) ³
Upper and lower P2	Yes	No	Yes	25, 26, 134	T-Ad
Incisors spatulate	No	Yes	Yes	14	Convergent
Sexual dimorphism	No	Yes	Yes	20	Convergent
Central incisor jugum	Yes	No	No	?	
Inter canine distance pinched	Yes	No	No	?	Need data
Postorbital closure	Partial	Complete	Absent	206	T-A
Zyg.-alisph. contact	Yes	Yes	No	207	T-A
Lacrimal foramen	On face	In orbit	Variable	212	A. autap.
Maxillary tuberosity	Septal flange	No flange	No flange	?	T. autap.
Zygomatico-facial foramen	No	Moderate	Large	?	T. autap.
Interorbital region	Narrow	Broad	Broad	205	Correlated
Olfactory bulb	Small	Moderate	Large	?	Need data
Sagittal crest	No	Yes	Yes	?	Need data
Ascending process of premaxilla	Narrow	Broad	Broad	231	T. autap.
Mandibular symphysis	Unfused	Unfused	Variable	221	Convergent
Face	Not deep	Deep	Deep	219, 220	T. actually deep
Pyramidal process position	Medial	Lateral	Lateral	217	Primitive
Pyramidal process shape	Delicate	Robust	Robust	?	Need data
Posterior palatine torus	Present	Absent	Absent	216	Convergent
Tympanic shape	Tubular	Unexpanded	Unexpanded	197	Primitive
Tympanic fusion	Yes	Yes	No	196-198	T-A
Suprameatal foramen	Yes	No	No	203	T. autap.
Postglenoid foramen position	Medial	Behind	Behind	222, 223	Correlated
Parotic fissure	Present	Absent	Absent	204	Primitive
Foramen magnum position	Forward	Medium	Back	?	T. autap.
Jugular foramen	Small	Large	Medium	?	Need data
Glenoid fossa shape	Guttered	Flat	Flat	222, 223	Primitive
Occipital condyle shape	Not convex	Convex	Convex	?	Need data
Basilar part of occipital bone	Narrow	Broad	Broad	?	Correlated
Promontory canal	Large	Large	Variable	193	Convergent

¹The first four columns are taken from **Simons & Rasmussen (1996)**.

²Character # (this study): the character numbers(s) referring to the character trait in this study. ?=not included because data were not available, we did not understand the character description, or we believe the trait to be correlated with other characters.

³Status (this study): Our interpretation of the evolution of the trait in question based on the tree derived from analysis of all the data, unordered, constrained and equally weighted. A, Anthroidea; Ad, Adapidae; T, *Tarsius*; autap., autapomorphy; convergent, trait evolved convergently in Anthroidea and Adapidae; correlated, trait hypothesized to be correlated with character listed in column five and therefore not listed as separate character; need data, more data required before definitive score can be made; primitive, trait primitive for primates; T-A, synapomorphy of tarsier-anthropoid clade; T-Ad, convergent similarity between tarsiers and adapids.

30 characters in **Table 5**, one is shared by tarsiers and adapids and is probably primitive for primates (25, 26, 134);* three are

*The number of characters in the text does not match that in parentheses because the character numbers are taken from the data set in the present study, in which the characters were recorded into more characters, not from the **Simons and Rasmussen (1996)** table.

shared by anthropoids and adapids to the exclusion of other primates but are primitive for primates, being present in the outgroups (197, 217, 204); one is shared by anthropoids and adapids and may be derived relative to the primitive primate condition (221); two are shared by tarsiers and anthropoids and are probably derived (196, 197,

198, 206, 207); five are autapomorphies of *Tarsius* and therefore of no value in determining relationships among primates (201, 233); two characters are incorrectly assigned by Simons & Rasmussen [*Tarsius* actually has a deep face (Ross, 1994) and *Catopithecus* has a posterior palatine torus]; five require more comparative study before they can be included in the matrix (occipital condyle shape, jugular foramen size, pyramidal process shape, olfactory bulb size, intercanine distance); three are probably correlated with other characters in the data matrix and similarly require more study (interorbital breadth, breadth of basilar part of occipital bone, and postglenoid foramen position); three provide no phylogenetic signal for various reasons explained in Table 5 (193, 206, 221); and one (central incisor jugum) is not sufficiently well described to be discussed. Overall, these characters do not provide convincing evidence for adapid-anthropoid affinities, drawing the Simons & Rasmussen classification into question. Several additional factors argue against accepting this classification.

First, Wortman's Neopithecini does not include the callitrichids, which are relegated to a different superfamily, the Arctopithecini. Either Simons & Rasmussen are advocating a phylogenetic placement of callitrichids outside of Anthropoidea, or their Neopithecini does not reflect Wortman's original intent. We know of no recent research suggesting that adapids are more closely related to noncallitrichid anthropoids than to callitrichids, as Wortman suggests. It is therefore inappropriate to resurrect a taxonomic division intended to express the contrast between callitrichids (Arctopithecini) and other anthropoids (Neopithecini).

Second, the characters on which Wortman's classification is based include anatomical errors that have been corrected by subsequent research. The most significant of these pertain to the carotid circulation, which Wortman regarded to be of

fundamental importance in primate classification (1903:148). At the beginning of this century, it was believed that two internal carotid arteries existed in mammals, one lying medial to the petrosal bone and one passing through the tympanic cavity (Wible, 1986). Wortman suggested that in lemurs and indriids the medial entocarotid supplied the majority of blood to the brain and that the lateral entocarotid was much reduced. He placed the carotid foramen "at the postero-internal junction of the tympanic bulla and the basioccipital", medial to the jugular foramen (foramen lacerum posticum) (1903:151). In lorises and galagos the "entocarotid" (actually the ascending pharyngeal; Cartmill, 1975) passes through the foramen lacerum at the anteromedial angle of the bulla, as Wortman recognized. Wortman claimed that in all other primates—which he classified as Anthropoidea and which included *Tarsius*, *Omomys*, *Adapidae*, *Callitrichids*, other *Platyrrhines* and *Catarrhines*—the entocarotid traverses the tympanic cavity from a posterior carotid foramen located in various positions in the bulla.

Recent work has demonstrated that mammals only ever have one internal carotid artery, situated either medial to, or on the promontorium within the middle ear cavity (Wible, 1986). In no primate does the internal carotid artery enter the braincase through a foramen "at the postero-internal junction of the tympanic bulla and the basioccipital", medial to the jugular foramen. In lemurs (including indriids) the internal carotid artery pierces the posterolateral corner of the bulla and runs in a short canal to the promontorium. There the relatively large stapedial branch diverges from the internal carotid proper and pierces the stapes to run up into the cranial cavity where it supplies the meninges and orbit. Beyond the divergence of the stapedial artery, the internal carotid *sensu stricto* is relatively small, or even absent in these animals

Table 6 Unambiguous character-state changes supporting omomyid–tarsier–anthropoid clade

Character number	Description	State changes
25. p1	P ₁ /P ¹ presence	Present→absent
34. p13	P ₂ protoconid	Not projecting=to P ₃ →extremely low
56. p37	P ₄ postmetaconid crest	Weak or absent→present
77. m16	M ₁ trigonid to talonid height	Much higher than talonid→slightly higher
199. cr17	Auditory bulla vs. pterygoid fossa	Absent→encroaches via tympanic cavity
202. cr20	Basioccipital bullar flange	Minimal→extensive
205. cr23	Orbit size	Small→large
208. cr26	Zygomatic-lacrimal contact	Present→absent
222. cr40	TMJ morphology	Biconcave and transversely wide→trough-like
263. T1	Tibio-fibular fusion	Absent, small facet→absent, moderate facet

(Conroy & Wible, 1978). All adapids discovered to date resemble lemurs in the posterolateral position of the posterior carotid foramen in the bulla and many resemble lemurs in the relative size of the stapedia artery and internal carotid proper (Ross, 1994). To date, *Mahgarita* is the only adapid that resembles living anthropoids and tarsiers in having a relatively large promontorial branch of the internal carotid (Rasmussen, 1990; Ross, 1994).

In sum, the taxon Neopithecini, if consisting of adapids and all anthropoids, should not be resurrected because it is not supported by the majority of the evidence, is based on errors of anatomical fact, and violates Wortman's original intent, to separate callitrichid anthropoids from other anthropoids and adapids. Simons himself (1997) seems now to recognize the lack of utility of Wortman's classification. In his most recent paper, he places Adapidae (including Cercamoniinae) within the Prosimii (Simons, 1997:180).

Prosimii. A monophyletic Prosimii including strepsirrhines, *Tarsius*, adapids and omomyids is only supported by the postcranial evidence (as found by Dagosto & Gebo, 1994; Ford, 1994). The present data set consists primarily of osteological and dental characters. Were the molecular, karyotypic, and placental data, which suggest close

affinities between tarsiers and anthropoids to the exclusion of strepsirrhines (Hubrecht, 1897; Luckett, 1975, 1976; Koop *et al.*, 1989*a,b*; Porter *et al.*, 1997), to be run with the morphological data set, it would provide even stronger support for the [omomyid (tarsier+anthropoid)] clade.

Omomyid–anthropoid hypothesis. The notion that anthropoids arose from within omomyids is supported by the cranial evidence and by the evidence overall. Ten characters support the monophyly of omomyids, tarsiers and anthropoids (Table 6). These characters come from all parts of the skeleton, including four from the dentition describing the first stages in molarization of the premolars, five from the skull reflecting the evolution of an omomyid-like skull morphology, and one from the hindlimb skeleton, reflecting an increase in leaping as a mode of locomotion.

The most parsimonious arrangement of the data places *Uintanius* as the sister taxon to the tarsier–anthropoid clade. This arrangement is supported by five unambiguous characters of the dentition reflecting changes in cheek tooth shape (primarily broadening) (Table 7). *Uintanius* is known from middle Eocene (Bridgerian) deposits in Wyoming and Colorado. Scoring of our OTU is based on material from *Uintanius ameghini* and on a recently described

Table 7 Unambiguous character state changes supporting *Uintanius* as the sister taxon to the tarsier-anthropoid clade

Character number	Description	Change
69. m8	M ₁ paraconid position	Mesial to metaconid → mesiolingual
70. m9	M ₂ paraconid position	Twin to metaconid → mesiolingual
92. m31	M ₁₋₂ cristid obliqua	Strongly trenchant → very strongly trenchant
154. M3	M ² shape (buccolingual/mesiodistal)	Very broad → transverse
156. M5	<i>Nannopithec</i> fold	Weak → absent

specimen referred to *Uintanius* cf. *rutherfordi* by Gunnell (1995) that preserves portions of the previously unknown anterior alveoli. The jaw is somewhat U-shaped, the incisors appear to have been of approximately the same size and implanted upright. In these features, *Uintanius* resembles washakiin omomyids, anthropoids, and adapids and is unlike many other omomyids. We have argued elsewhere (Covert & Williams, 1991, 1994; Kay & Williams, 1994a) that these features may be primitive for primates and not indicative of a sister group relationship with anthropoids. A number of unambiguous character state changes support *Uintanius* as the sister taxon to the tarsier-anthropoid clade; mesiolingual positioning of the paraconid and an increase in shear on M₁₋₂, broadening of the M₂ and loss of the *Nannopithec*-fold on the upper molars. Mesiolingual positioning of the paraconid and increase in shear are found in many omomyids and loss of the *Nannopithec*-fold is found in many omomyids and adapids as well. Broadening of the M₂ is found in several other omomyids and in the adapid *Pronycticebus*. We do not believe these characters are particularly compelling because each is found in a number of other omomyids and/or adapids. Furthermore, no cranial or postcranial data are known for *Uintanius*. At this time, a sister taxon relationship of *Uintanius* and the tarsier-anthropoid clade should be considered with caution.

Tarsius–Anthropoidea hypothesis

The *Tarsius*–Anthropoidea hypothesis is by far the best supported of all those evaluated. It is supported by (a) the cranial evidence; (b) the dental evidence when a constrained, unordered analysis is run; and (c) the overall evidence for all except one assumption set (all characters, constrained, ordered, equally weighted).

Various tree topologies are compatible with this hypothesis. We choose to discuss one of these: the tree obtained from analysis of the complete data set, all characters scaled to be of equal weight regardless of the number of character states, multistate characters unordered, constrained to ensure primate monophyly and with the data from the Shanghuang petrosal included as a separate taxon. In addition, this tree included two polychotomies, one of which was manually resolved in order to obtain lists of unambiguous character state changes associated with the basal primate node. (The clade including all plesiadapiform outgroup taxa was designated as the primate sister taxon, rather than an unresolved trichotomy between the plesiadapiform clade, Scandentia and Primates.)

Eleven dental characters support the tarsier+anthropoid grouping unambiguously (Table 8). Six other cranial characters would also unambiguously support this clade with their states known for *Uintanius*. Presuming these features were absent in *Uintanius*, they also define the

Table 8 Unambiguous character state changes supporting a tarsier-anthropoid clade (including *Eosimias* and *Afrotarsius*)

Character number	Description	Changes
19. c1	Canine size	Very small canine occlusal area/M ₁ area → small to moderate canine area
43. p22	P ₃ protocristid orientation	Protocristid absent → distolingually oriented
50. p29	Premolar basal inflation	Very inflated → slightly inflated
54. p34	P ₄ antero-buccal cingulum	Absent or trace → strong
61. p44	P ₄ to M ₁ area	0.83 to 0.92 → 0.63 to 0.72/0.73 to 0.82
90. m29	M ₃ hypoconulid size	Large → moderate
93. m32	M ₁ cristid obliqua angle	Distolingual to protoconid → distal to protoconid
94. m33	M ₂ cristid obliqua angle	Distolingual to protoconid → distal to protoconid
107. m46	M ₁ hypoflexid	Deep → moderate
135. P5	P ⁴ /M ¹ area	P ⁴ =M ¹ → P ⁴ <M ¹
171. M22	M ¹⁻³ lingual cingulum	Weak, broken → strong, complete
189. cr7*	Dorso-ventral position of carotid foramen	Dorsal → ventral
190. cr8*	Carotid foramen position vs. fenestra cochleae	Posterior to fenestra cochleae → anterior to fenestra cochleae
196. cr14*	Tympanic bone	Intrabullar (aphaneric) → extrabullar (phaneric)
206. cr24*	Postorbital closure	Postorbital bar → postorbital septum
214. cr32*	Orbital convergence	Orbital convergence >30 degrees → high convergence for relative orbit size
230. cr48*	Epitympanic crest	Broad → narrow

tarsier-anthropoid clade. The cranial characters include the well-known rearrangements of the ear region characteristic of tarsiers and anthropoids, such as ventral and anterior positioning of the carotid foramen and exclusion of the tympanic ring from the bulla. This clade is also characterized by an increase in orbital convergence relative to orbit size, and the evolution of a post-orbital septum and rearrangements of the face long thought to have characterized early anthropoids (e.g., Le Gros Clark, 1959; Martin, 1990; Simons, 1972). These changes are most likely to have characterized the last common ancestor of tarsiers and anthropoids.

Anthropoidea. None of the classical "anthropoid" features, such as the fused mandibular symphysis, fused metopic suture, postorbital closure and highly convergent orbital margins is found at the basal anthropoid node. A fused metopic suture in

older adult specimens may well be primitive for primates and the fused mandibular symphysis unites crown anthropoids and parapathecines to the exclusion of oligopithecines, qatraniines and eosimiids. Postorbital closure evolved at the tarsier-anthropoid node along with extreme orbital convergence. Fossil discoveries and this analysis have effectively broken up this complex of features and demonstrated that they evolved independently of each other at different times.

What then is an anthropoid? The demonstration that the "classic" anthropoid features are in fact synapomorphies at more inclusive levels argues against an apomorphy-based definition of Anthropoidea. Similarly, we have argued elsewhere against the notion of a crown-group based definition on the grounds that it excludes obvious fossil anthropoids from the group and potentially results in a plethora of unstable names for paraphyletic groups.

Table 9 Unambiguous character state changes supporting an anthropoid clade that includes *Eosimias* and *Afrotarsius*

Character number	Description	State change
6. i6	I ₁ : I ₂ proportions (Af?) ¹	I ₁ >I ₂ →I ₁ <I ₂
9. i9	Incisor crown height (Af?)	High→moderate
11. i11	Lower incisor roots (Af?)	Slightly procumbent→erect
12. i12	Lower incisor crowns (Af?)	Procumbent→erect
14. i14	I ₁ crown shape (Af?)	Lanceolate→spatulate
56. p37	P ₄ postmetaconid crest (Af?)	Present→weak or absent
58. p41	P ₃₋₄ protoconid (Af?)	P ₃ much lower than P ₄ /P ₃ slightly lower than P ₄ →P ₃ equal in height to P ₄
68. m7	M ₃ trigonid vs. talonid	Trigonid=talonid→trigonid≫talonid
240. H9	Dorsal placement medial epicondyle (Af?)	Parallel→slightly angled dorsally
286. MT1	Peroneal tubercle (Af?)	Large→small

¹Af?, character state unknown for *Afrotarsius*.

Stem-based definitions have the advantage of maintaining taxonomic stability in the context of a rapidly changing knowledge of the fossil record (Kay & Williams, 1994a,b; Beard & MacPhee, 1994).

Anthropoidea must therefore include all the non-tarsier descendents of the last common ancestor of tarsiers and crown anthropoids. This includes *Eosimias* and *Afrotarsius* within the Anthropoidea. Ten unambiguous character state changes support this grouping (Table 9). The lower incisors and their roots become erect, the crowns become spatulate and of moderate height, and I₁ becomes smaller than I₂. The P₄ trigonid opens up posteriorly and the P₃ protoconid increases in size relative to that of P₄. The M₃ talonid decreases in size markedly. The medial epicondyle on the humerus becomes slightly angled dorsally and the peroneal tubercle on the first metatarsal is reduced in size. Of these characters, only one is preserved in *Afrotarsius*, and the presence of these character states in *Afrotarsius* must be considered a prediction of this hypothesis.

The Fayum anthropoids are united with crown anthropoids to the exclusion of eosimiids by four features of the premolars

and eight features of the molars (Table 10).

Comments on specific taxa

Parapithecoidea. Parapithecoids have been known since the beginning of this century (Osborn, 1908; Schlosser, 1910, 1911) and they are now well represented by numerous specimens from several localities in the Jebel Qatrani Formation in the Fayum. A detailed review of the group in 1987 recognized three, possibly four, para-pithecoid genera and five species: *Apidium phiomense*, *A. moustafai*, *Parapithecus fraasi*, *Parapithecus (Simonsius) grangeri*, and *Qatrania wingi* (Fleagle & Kay, 1987). Since then another species of *Qatrania*, *Q. fleaglei* (Simons & Kay, 1988) and a new species of *Apidium*, *A. bowni* (Simons, 1995) have been described, and two new genera and species from the late Eocene Fayum Quarry L-41 have been placed in the Parapithecoidea: *Serapia eocaena* and *Arsinoea kallamos* (Simons, 1992).

Kay & Williams (1994a) recognized the monophyly of the Parapithecoidea and erected two subfamilies within it: the Parapithecinae, containing *Apidium*, *Parapithecus* and *Simonsius*, and the possibly paraphyletic Qatraniinae, containing *Qatrania*, *Serapia*

Table 10 Unambiguous character state changes supporting the anthropoid clade excluding *Eosimias* and *Afrotarsius*

Character number	Description	Changes
34. p13	P ₂ protoconid	Extremely short→not projecting=to P ₃
51. p30	P ₄ exodaenodonty	Slight→not
52. p31	P ₄ talonid length	Much shorter than trigonid→slightly shorter or equal
59. p42	P ₃ to P ₄ area	0.45 to 0.59→0.60 to 0.69
77. m16	M ₁ trigonid to talonid height	Much higher than talonid/slightly higher→similar height
81. m20	M ₁ paraconid	Large→small
87. m26	M ₁₋₂ postentoconid sulcus	Absent→faint
88. m27	M ₁ hypoconulid	Small→moderate
89. m28	M ₂ hypoconulid	Small→moderate
92. m31	M ₁₋₂ cristid obliqua	Very strong trenchant→weak round
99. m38	M ₁₋₂ hypocristid	Strong→weak
100. m39	M ₃ hypocristid	Strong→weak

and *Arsinoea*. The qatraniines were linked to the parapithecines by five features of the lower cheek teeth, but were excluded from the parapithecines because they lack both wear facet X on the M₂ and a sulcus between the lower molar protoconids and metaconids.

This study confirms the monophyly of the Parapithecinae, but does not provide convincing support for the placement of the qatraniines in a monophyletic group with the parapithecines. The exact placement of the three qatraniine genera relative to oligopithecids and parapithecines varies with the assumption sets used. When all of the data are considered (Analyses 1 and 2), the Shanghuang petrosal is listed as a separate taxon, and an unconstrained, unordered, scaled analysis is run, qatraniines share a last common ancestor with the parapithecines. In the remaining runs in Analyses 1 and 2, *Qatrania* sometimes falls in with the parapithecines, and sometimes falls with *Serapia* and *Arsinoea* outside a clade consisting of platyrrhines, catarrhines, parapithecines, and oligopithecines. This calls into question the monophyly of the Parapithecoidea *sensu* Kay & Williams (1994a) to include *Qatrania*, *Arsinoea*, and *Serapia* and Para-

pithecidae *sensu* Simons & Rasmussen (1991).

We prefer the phyletic arrangement advocated by Kay & Williams which proposes two stages in the evolution of the anthropoid dentition, documented among the early anthropoids of the Fayum, Egypt. In the first stage, most closely approximated by qatraniine parapithecids *Qatrania* and *Serapia*, most changes occurred in molar structure. On the M₁₋₂ the height of molar trigonids was slightly reduced, the paraconids were reduced, the hypocristids were weakened, a postentoconid sulcus appeared, and the hypoconulids were lingually placed. M³ was reduced in size. Additionally, a protocone developed on P². In the second stage, represented by platyrrhines, and catarrhines, changes occurred in the structure of the premolars. The premolars became less mesiodistally crowded in the jaw and P₄ was structurally re-organized, such that the talonid became similar in mesiodistal length to the trigonid and the metaconid was enlarged, repositioned medially, and widely separated from the protoconid (see also Harrison, 1987). Similarly, the M₁ metaconid was shifted to a more transverse position relative to the protoconid

Table 11 Unambiguous character state changes supporting the monophyly of Oligopithecidae

Character number	Description	Changes
1. m30	M ₁₋₂ hypoconulid	Near midline → twinned
130. C4	C ¹ lingual cingulum	Strong → weak absent
145. P15	P ³⁻⁴ parastyles	Absent → present
151. P21	P ³⁻⁴ buccal cingulum development	Absent or weak → strong
172. M24	M ¹⁻² buccal cingulum	Weak → strong

and the molar cusps were more marginally positioned. The lingual moiety of P² was reduced to become a more triangular tooth and the lingual cingula of the upper premolars were strengthened. Additionally, the upper molar metaconules were lost. Finally, body size increased. *Arsinoea* resembles parapithecids in most details but its P₄ (with a strong, more linguallly positioned metaconid) is reminiscent of propliopithecids, oligopithecids, and platyrrhines. When it is known from more complete specimens of the upper dentition, *Arsinoea* may require reassignment as a primitive anthropoid of modern aspect. Fleagle & Kay (1987) list primitive, otherwise nonanthropoid, postcranial features, especially in the femur, tibia, and cuboid that support the argument for parapithecids as primitive anthropoids.

Oligopithecidae. *Oligopithecus savagei* has been known from Quarry E in the lower part of the Jebel Qatrani Formation since 1962 (Simons, 1962). Represented for many years by a mandible preserving C₁–M₂, *Oligopithecus* has been described as a “hominoid” ancestral to *Aegyptopithecus* and *Propliopithecus* (Simons, 1962, 1972; Simons & Pilbeam, 1972), an adapid (Szalay, 1970; Gingerich, 1980), an omomyid (Szalay & Li, 1986), and a basal catarrhine (Szalay & Delson, 1979; Fleagle & Kay, 1987; Simons & Rasmussen, 1994). In the late 1980s, attribution of isolated teeth from Quarry E to *Oligopithecus* (Rasmussen & Simons,

1988) and the discovery of *Proteopithecus sylviae* and *Catopithecus browni* in Quarry L-41 in the Jebel Qatrani Formation (Simons, 1989, 1990) greatly increased our knowledge of oligopithecid diversity and anatomy. *Catopithecus* is now known from several skulls, two distal humeri and a proximal femur, and *Proteopithecus* is known from upper and lower dentitions, a proximal femur and an os coxae (Simons, 1989, 1992; Simons & Rasmussen, 1996; Gebo et al., 1994). As a result of these discoveries and the analysis presented here, the phyletic position of the oligopithecids must be revised.

Our analyses provide unequivocal support for oligopithecid monophyly. All of the majority rule consensus trees and most of the strict consensus trees produced in Analyses 1 and 2 found a monophyletic group consisting of *Catopithecus* and *Proteopithecus*, suggesting that Oligopithecidae is a natural group. The characters defining this group are given in Table 11.

Nevertheless, the presence of three premolars in *Proteopithecus* and only two premolars in *Catopithecus* and *Oligopithecus* suggests that *Proteopithecus* may actually belong in another group. This possibility cannot be evaluated with the data presently at hand.

However, it is no longer tenable to regard the oligopithecids as basal catarrhines (Fleagle & Kay, 1987), broadly ancestral to later catarrhines like *Aegyptopithecus*

(Simons, 1972; Simons & Rasmussen, 1994, 1996). Although a definitive placement for oligopithecids was not found in this study, they only fell within the crown anthropoid clade a few times in Analyses 1 and 2, and then as the sister taxon to platyrrhines. In the majority of cases they fell outside a clade consisting of crown anthropoids and parapithecines, in various placements relative to qatraniines. We therefore advocate the removal of the Oligopithecidae from the Catarrhini, and their placement as *Anthropoidea incertae sedis*.

Eosimias. *Eosimias* was first described by Beard *et al.* (1994) on the basis of an incomplete lower jaw of *Eosimias sinensis*. A nearly complete lower jaw of *E. centennicus* has been described more recently (Beard *et al.*, 1996). *Eosimias* is claimed by Beard and his co-workers to be a stem anthropoid on the basis of several features of the dentition. Our analysis of the *Eosimias* dental and postcranial material confirms that this taxon is likely to be sister to a clade consisting of living anthropoids and the Fayum taxa Oligopithecidae. *Eosimias* occupies this position regardless of the assumption sets employed and regardless of whether the Shanghuang petrosal belongs to this genus or not.

Afrotarsius chatrathi. A small lower jaw preserving M_{1-3} and lower parts of the P_{3-4} crowns was described from Quarry M in the upper part of the Jebel Qatrani Formation in 1985 and attributed to the Tarsiidae (Simons & Bown, 1985). Subsequent workers have suggested that it might actually be the sister taxon of Anthropoidea (Fleagle & Kay, 1987; Ginsburg & Mein, 1987; Kay & Williams, 1994a). Kay & Williams suggested several synapomorphies in support of this grouping: the M_{1-2} cristid obliqua oriented mesiodistally towards the protoconid; metacristid transverse to paraconid; small lower molar hypoconulids; and M_2 larger than M_3 .

The present study suggests that *Afrotarsius* may be related to *Eosimias*. In one analysis *Afrotarsius* was placed outside Primates (Figure 4) and in another, *Afrotarsius* fell out as the sister taxon to *Omomys* (all characters, unordered, constrained, scaled). In the remainder of the analyses, *Afrotarsius* was placed outside the [Anthropoidea+ (*Tarsius*+*Eosimias*)] clade about half the time, and as the sister taxon to *Eosimias* the other half. Only two characters unambiguously support an *Afrotarsius*-*Eosimias* clade, and they may well be related to each other: absence of molar cusp inflation and vertical molar walls. However, there are twenty-four characters that support this clade, although ambiguously. We believe the hypothesis of a close *Afrotarsius*+*Eosimias* relationship is worth serious consideration.

Rooneyia viaejanesis. *Rooneyia* is known by a skull and upper dentition recovered from Eocene deposits in Texas. It has been referred by most researchers to the Omomyidae (Wilson, 1966; Szalay, 1976; Szalay & Delson, 1979), or as a basal "tarsiiform" (Rosenberger, 1985), but anthropoid affinities have also been suggested (Simons, 1968). Recently, analyses of cranial (Beard & MacPhee, 1994; Ross, 1994) and dental (Williams, 1994; n.d.) data suggest that *Rooneyia* falls outside the omomyid radiation. Our combined analysis does not support omomyid affinities for *Rooneyia*, however, and no definite alternative placement can be made. The combined evidence places *Rooneyia* either with extant strepsirrhines, with the adapid/strepsirrhine clade, or in one instance, with Anthropoidea. Cranial data, unconstrained and unordered, positions *Rooneyia* as sister to all other primates, whereas cranial data, constrained and ordered, place this taxon as the outgroup to an omomyid-tarsier-anthropoid clade; dental data support a parapithecine-*Aegyptopithecus* relationship for *Rooneyia*.

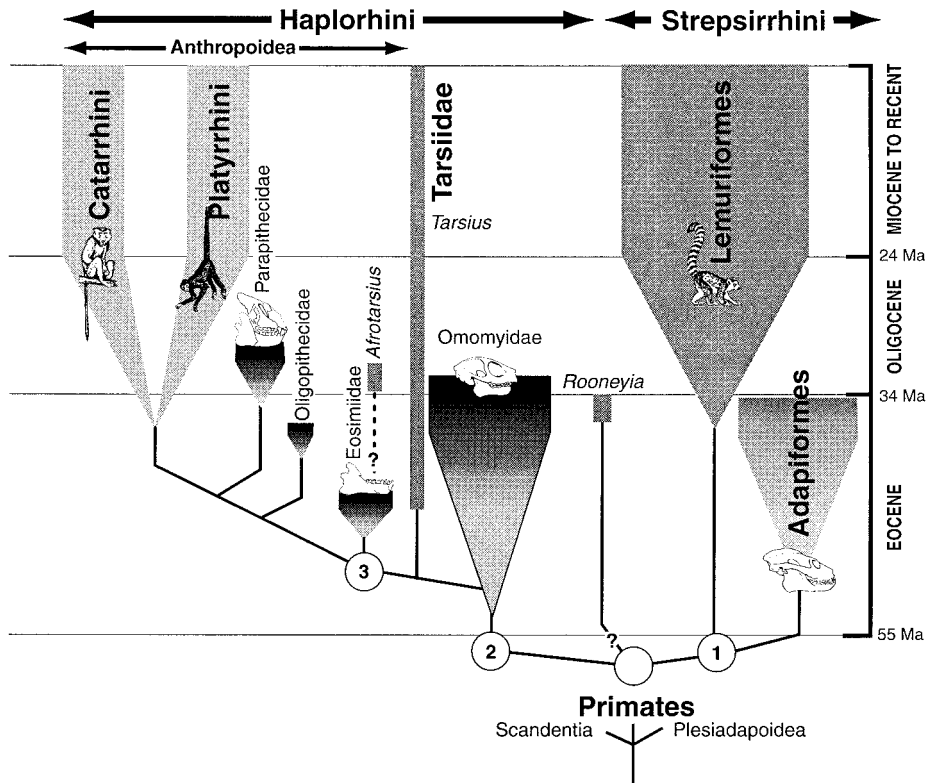


Figure 14. Summary of preferred phylogeny. 1. Adapids are more closely related to extant strepsirrhines than to omomyids, tarsiers or anthropoids. 2. For characters unambiguously supporting this node see Table 6. 3. For characters unambiguously supporting this node, see Table 9.

Clearly the phylogenetic placement of this enigmatic taxon must await the discovery of additional material.

Preferred tree and classification

Our preferred tree is illustrated in Figure 14. We believe the tarsier–anthropoid hypothesis is the best hypothesis of anthropoid relationships at present, for three reasons. First, the tarsier–anthropoid hypothesis is the best-supported by the data presented here. To accept a tarsier–washakiine clade (Beard *et al.*, 1988; Beard & MacPhee, 1994), one very specific set of assumptions must be invoked, including the assumption that the Shanghuang petrosal is that of

Eosimias. All other assumption sets examined here yield a *Tarsius*–Anthropoidea clade. Second, the tarsier–anthropoid hypothesis (and the associated [omomyid–(tarsier–anthropoid)] hypothesis) is corroborated by functional analysis of character transformation series (Ross, 1996). Third, this hypothesis provides the most parsimonious reconstruction of features that are unique to tarsiers and anthropoids; the post-orbital septum and the anterior accessory cavity of the middle ear.

However, although the tarsier–anthropoid hypothesis is best supported by our data, there is only weak support for the *Tarsius*–Anthropoidea clade, as illustrated by bootstrap and decay analyses of our complete data set under one assumption set

(Shanghuang petrosal excluded, all characters unordered, constrained to ensure primate monophyly, all characters equally weighted). The *Tarsius*–Anthropoidea clade was not found in the majority of the trees generated by a bootstrap analysis of 1000 replicates and a decay analysis found the tarsier–anthropoid clade to collapse when parsimony was relaxed by two steps. However, it is noteworthy that the clade consisting of all living and fossil anthropoids also broke down after relaxing parsimony by two steps and the clade consisting of living strepsirrhines collapsed after four steps. Thus, although the *Tarsius*–Anthropoidea hypothesis is not very robustly supported by these data, neither are clades which most primatologists accept almost without question.

Our preferred classification of the primates included in this study is given in Table 1. The strong evidence for a lemuriform–adapiform clade requires the placement of both taxa in the Semiorder Strepsirrhini, an arrangement receiving support from other workers (e.g., Szalay & Delson, 1979; Delson & Tattersall, 1997). The fossil Omomyidae are placed in their own Suborder Omomyiformes, despite evidence suggesting that this may be a paraphyletic taxon, with some taxa more closely related to a *Tarsius*+Anthropoidea clade than to other omomyids. Until the relationships among omomyids, tarsiers and anthropoids are more definitively resolved, we believe this conservative approach is most appropriate.

The Suborder Tarsiiformes should be restricted to the genus *Tarsius* and all fossil taxa more closely related to *Tarsius* than to anthropoids or omomyids (e.g., *Xanthorhysis*). Specifically, despite historical precedent to the contrary (e.g., Szalay & Delson, 1979; Shoshani *et al.*, 1996; Beard, 1998), placement of omomyids in Tarsiiformes is not consistent with data suggesting that tarsiers may be more

closely related to Anthropoidea than to any omomyid, and the fact that most omomyids lack convincing synapomorphies linking them to tarsiers. Previous workers have noted that it is too simplistic to label the omomyid postcranium (Dagosto, 1993) and cranium (Ross, 1994) “tarsier-like”, and similar comments apply to the dentition. Moreover, omomyids have not been shown to be adaptively more similar to *Tarsius* than to cheirogaleids and galagos. Until the evidence linking *Tarsius* to one specific clade of omomyids is more convincing than the evidence linking *Tarsius* to Anthropoidea, it is misleading to refer omomyids to Tarsiiformes.

Summary and Conclusions

To evaluate the phylogenetic position of Anthropoidea, morphological data on 291 dental, cranial and postcranial morphological characters were collected for 57 taxa of living and fossil primates and analyzed using PAUP and MacClade. The dental evidence provides some support for the notion of an adapid origin for anthropoids, the cranial evidence supports the tarsier–anthropoid hypothesis, and the postcranial evidence supports monophyly of Prosimii and Anthropoidea. Combining these data into a single data set demonstrates Anthropoidea to be monophyletic and the traditional anthropoid synapomorphies to have evolved mosaically. Agreement between the most parsimonious trees derived from the cranial and the complete data sets may be attributable to the cranial characters having evolved more slowly than the dental and postcranial characters.

The adapid–anthropoid hypothesis is rejected as much less parsimonious than the alternatives. There is almost universal support for a tarsier–anthropoid clade nested within omomyids. *Eosimias* is certainly a member of the *Tarsius*–Anthropoidea clade, and is probably a basal anthropoid, although

the Shanghuang petrosal may not belong to this taxon. There is support for a relationship between the *Tarsius*-Anthropoidea clade and both washakiines and *Uintanius*. Parapithecines are the sister taxon to crown anthropoids; qatraniines and oligopithecids are more distantly related sister taxa.

Overall, the available data do not allow definitive statements regarding the interrelationships of the haplorhines: *Tarsius*, Omomyidae and Anthropoidea. Many key fossil taxa (e.g., *Eosimias*, *Afrotarsius*) are still poorly known and we lack critical fossils sampling the divergence of the higher taxonomic levels of primates. Clearly, many more fossils are required before we can determine the precise phyletic relationships of tarsiers, omomyids, and anthropoids.

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Appendix A. Character list

Characters followed by an asterisk were considered “ordered” in some analyses.

Dentition

Lower Teeth

Incisors

1. i1*. Lower incisor number

0=three

1=two

2=one: I₁ present, I₂ absent

3=absent.

2. i2. Lower incisor occlusal arrangement

0=arcuate battery in occlusal perspective (U-shaped arcade)

1=cusp tips staggered (V-shaped arcade).

3. i3. Lower incisor crown spacing

0=no spaces

1=spaces present between crowns.

4. i4. I₂-C diastema

0=present

1=absent.

5. i5*. I₁₋₂ size (ratio of I₁₊₂ area to M₁ area)

0=very small ($= < 0.69$)

1=moderate sized ($= > 0.70$, $= < 1.07$)

2=large (> 1.07).

6. i6*. I₁:I₂ proportions (ratio of I₁ area to I₂ area)

0=I₁ much smaller than I₂ (< 0.65)

1=I₁ smaller than I₂ ($= > 0.65$, < 0.82)

2=I₁ almost as large as I₂ ($= > 0.83$, < 1.00)

3=I₁ larger than I₂ ($= > 1.01$, < 1.25)

4=I₁ much larger than I₂ ($= > 1.25$).

7. i7*. I₁ crown width (spatulate incisors only)

0=considerably wider (m-d) than root (spatulate)

1=narrow at apex, wider than root

2=“styliform” (crown apex approximately the same width as the cervical margin).

8. i8. I₂ crown cross-sectional shape (ratio of m-d length to b-l breadth)

0=rounded oval ($= > 0.64$)

1=mesiodistally compressed (< 0.64).

9. i9*. Lower incisors crown height (crown heights judged from cemento-enamel junction to crown tip on the buccal surface)

0=low crowned

1=moderately high crowned

2=high crowned.

10. i10. I₁₋₂ crown buccal outline

0=gently curved in lateral perspective

1=strongly curved.

11. i11*. Lower incisor roots

0=erect or vertical

1=slightly procumbent

2=very procumbent.

12. i12*. Lower incisor crowns

0=erect or vertical

1=procumbent

2=very procumbent.

13. i13. Tooth comb

0=absent

1=with three teeth

2=with two teeth.

14. i14. I₁ crown shape

0=spatulate

1=lanceolate, pointed.

15. i15. I₂ heel development (a lingual

swelling at the base of crown)
0=heel absent
1=heel present.

16. i16. Incisor lingual enamel
0=well developed
1=poorly developed or absent.

17. i17*. Lower first incisor lingual cingulum
0=absent to weak
1=strong but incomplete
2=strong and complete.

18. i19*. I_1 to M_1 area
0= I_1 very small ($I_1 \ll M_1$)
1=moderately enlarged ($I_1 < \text{or} = M_1$)
2=grossly enlarged ($I_1 > M_1$).

Canines

19. c1*. Female $C^1/1$ area (relative to molars)
0=very small ($C_1/M_1 < 0.40$)
1=moderate ($= > 0.4, < 0.80$)
2=large ($= > 0.80, < = 1.20$)
3=very large ($= > 1.20$)

20. c2*. $C^1/1$ dimorphism (square root male C_1 area/square root female C_1 area)
0=low (< 1.07)
1=moderate ($> = 1.07, < 1.17$)
2=high ($> = 1.17$).

21. c3. C_1 cross-sectional shape
0=rounded oval
1=mesiodistally compressed
2=buccolingually compressed.

22. c4. C_1 lingual crest development
0=rounded
1=sharp.

23. c5. Canine paracristid (not scored if species has canine incorporated into a tooth comb)
0=oblique to occlusal plane

1=nearly horizontal to occlusal plane
2=forms part of cropping mechanism with I_{1-2} .

24. c6. Canine height (females)
0=low, squat
1=narrow, short
2=tall, at or above tooth row.

Premolars

25. p1. $P^1/1$
0=present
1=absent.

26. p2. P_2
0=present
1=absent.

27. p3. P_2 roots
0=single
1=double.

28. p4*. P_{3-4} roots
0= P_3 single, P_4 single
1= P_3 single, P_4 double
2= P_3 double, P_4 double.

29. p5*. Premolar crowding (overlapping of crowns)
0=no crowding
1=slightly crowded
2=very crowded.

30. p6*. P_3 paraconid
0=large
1=small
2=absent or vestigial.

31. p7*. P_4 paraconid
0=large
1=small
2=absent or extremely small.

32. p9*. P_4 paraconid position
0=mesial to protoconid
1=mesiolingual, between protoconid and

- metaconid
2=mesial to metaconid; widely spaced from metaconid
3=twinned with metaconid.
33. p11*. P₃₋₄ cristid obliqua
0=absent
1=weak
2=strong.
34. p13. P₂ protoconid height and shape
0=slender, projects above protoconids of P₃₋₄
1=massive, projects above protoconids of P₃₋₄
2=not projecting, in line with P₃
3=extremely short, shorter than P₃.
35. p14. P₄ metaconid position
0=close to protoconid
1=widely spaced from protoconid.
36. p15. P₂ metaconid size
0=absent or trace
1=small.
37. p16*. P₃ metaconid size
0=absent or trace
1=small
2=large.
38. p17*. P₄ metaconid size
0=absent or trace
1=small
2=large.
39. p18. P₄ trigonid—lingual configuration
0=closed
1=open.
40. p19. P₃ entoconid and lingual talonid crest
0=absent
1=lingual talonid crest present but an entoconid does not stand out above it
2=entoconid is a small discrete cusp.
41. p20. P₄ entoconid and lingual talonid crest
0=absent
1=lingual talonid crest present but an entoconid does not stand out above it
2=entoconid is a small discrete cusp.
42. p21. P₄ lateral and medial protocristid
0=continuous between metaconid and protoconid
1=discontinuous between metaconid and protoconid.
43. p22. P₃ lateral protocristid orientation
0=transversely oriented
1=distolingually oriented
2=absent.
44. p23. P₄ lateral protocristid orientation
0=transversely oriented
1=distolingually oriented.
45. p24. P₃₋₄ posterior trigonid wall
0=complete (taxa without metaconids are assigned this character state)
1=deeply notched.
46. p25. P₃₋₄ hypoconid size
0=large
1=small or absent.
47. 50. p26. P₃₋₄ hypoconid (or distal terminus of oblique cristid) position
0=distal to protoconid
1=distal to metaconid, or between protoconid and metaconid.
48. p27*. P₄ hypocristid shearing development
0=absent
1=weak
2=strong.
49. p28*. P₂ buccal cingulum development
0=absent
1=incomplete, broken at protoconid and hypoconid

2=complete.

50. p29*. Lower premolar inflation

0=not basally inflated

1=slightly basally inflated

2=very basally inflated.

51. p30*. P₄ exodaenodonty

0=not exodaenodont

1=slightly exodaenodont

2=very exodaenodont.

52. p31*. P₄ talonid length (ratio of mid-line m-d length of trigonid to m-d length of talonid)

0=extremely short or non-existent

(tri:tal=>1.61)

1=short (much shorter than trigonid)

(tri:tal=>1.27, <1.61)

2=equal or slightly shorter in length to trigonid (tri:tal=>0.92, <1.27)

3=talonid longer than trigonid

(tri:tal<0.91).

53. p33*. premolar orientation

0=crown bases vertical in lateral perspective

1=slightly oblique

2=strongly oblique, projecting medial over the anterior.

54. p34. P₄ anterobuccal cingulum development

0=absent or trace

1=strong.

55. p36. P₄ postprotoconid ridge

0=weak or absent

1=moderate

2=very strong.

56. p37. P₄ postmetaconid ridge

0=weak or absent

1=moderate

2=very strong.

57. p40*. P₄ paraconid height

0=low

1=moderate

2=high (nearly as high as protoconid).

58. p41*. P₃₋₄ protoconid height

0=P₃ much lower than P₄

1=P₃ slightly lower than P₄

2=P₃ equal in height to P₄

3=P₃ higher than P₄.

59. p42*. P₃ to P₄ area

0=0.45-0.59

1=0.60-0.69

2=0.70-0.79

3=>0.80.

60. p43*. P₄ m-d L/b-1 W

0=(<0.95)

1=(=>0.96, <1.14)

2=(=>1.15, <1.20)

3=(=>1.21, <1.35)

4=(=>1.36, <1.46)

5=(>1.47).

61. p44*. P₄ to M₁ area

0=(<0.62)

1=(=>0.63, <0.72)

2=(=>0.73, <0.82)

3=(=>0.83, <0.92)

4=(=>0.93, <1.02)

5=(>1.03).

62. p45. P₃₋₄ root orientation

0=P₃₋₄ roots aligned mesiodistally

1=P₃ root shifted laterally, P₄ mesial root aligned mesiodistally

2=P₃ roots aligned mesiodistally, P₄ mesial root shifted laterally. (Score as missing if roots are single.)

Molars

63. m1. M_{3/3}

0=present

1=absent.

64. m2. M₁ root number

0=one

1=two.

65. m3. M₂ root number
0=one
1=two.
66. m4. M₃ root number
0=one
1=two.
67. m6*. M₂ trigonid width (ratio of buccolingual breadths of trigonid and talonid)
0=much wider than talonid ($= > 1.11$)
1=width similar (< 1.11 , > 0.90)
2=much narrower than talonid ($= < 0.90$).
68. m7*. M₃ trigonid width (based on relative buccolingual breadths)
0=much wider than talonid ($= > 1.20$)
1=trigonid and talonid widths similar ($= < 1.20-1.05$)
2=trigonid narrower than talonid (< 1.05).
69. m8*. M₁ paraconid position
0=mesial to protoconid
1=mesiolingual, between protoconid and metaconid
2=mesial to metaconid but widely spaced from it
3=twinned with metaconid.
70. m9*. M₂ paraconid position
0=mesial to protoconid
1=mesiolingual, between protoconid and metaconid
2=mesial to metaconid but widely spaced from it
3=twinned with metaconid.
71. m10*. M₃ paraconid position
0=mesial to protoconid
1=mesiolingual, between protoconid and metaconid
2=mesial to metaconid but widely spaced from it
3=twinned with metaconid.
72. m11. M₁ parastylid
73. m12*. Molar metastylids
0=absent
1=present.
74. m13. M₃ hypoconulid
0=single
1=double.
75. m14*. M₃ heel
0=absent
1=narrower than talonid
2=approximately equal in width to talonid.
76. m15*. Molar enamel surface
0=smooth
1=slightly crenulated
2=highly crenulated.
77. m16*. M₁ trigonid height (ratio of trigonid height to talonid height)
0=higher than talonid ($= > 1.20$)
1=slightly higher than talonid ($= > 1.10$, < 1.20)
2=trigonid and talonid of similar height (< 1.10).
78. m17. M₁₋₂ cusp relief
0=moderate to high
1=low.
79. m18. M₁ trigonid lingual configuration
0=open
1=closed.
80. m19. M₁ metaconid position
0=lingual to protoconid
1=slightly distolingual to protoconid.
81. m20*. M₁₋₂ paraconid development
0=absent
1=small
2=large.

82. m21. M_{1-2} lateral protocristid orientation
 0=runs toward metaconid
 1=runs toward hypoflexid.
83. m22. M_1 distal trigonid wall
 0=complete
 1=deeply notched by protoconid/metaconid sulcus
 2=medial and lateral protocristid do not meet but no sulcus is discerned.
84. m23. M_2 distal trigonid wall
 0=complete
 1=deeply notched by protoconid/metaconid sulcus
 2=medial and lateral protocristid do not meet but no sulcus is discerned.
85. m24. M_{1-3} wear facet X
 0=present
 1=absent.
86. m25*. M_{1-2} entoconid
 0=absent
 1=barely stands out on lingual talonid marginal crest
 2=a small discrete cusp
 3=a large cusp.
87. m26*. M_{1-2} postentoconid sulcus
 0=prominent
 1=faintly visible
 2=absent.
88. m27*. M_1 hypoconulid size
 0=large
 1=moderate
 2=small
 3=absent.
89. m28*. M_2 hypoconulid size
 0=large
 1=moderate
 2=small
 3=absent.
90. m29*. M_3 hypoconulid size
 0=large
 1=moderate
 2=small
 3=absent.
91. m30*. M_{1-2} hypoconulid position
 0=twinned to entoconid
 1=near midline
 2=slightly buccal to midline.
92. m31*. M_{1-2} cristid obliqua development
 0=weak (rounded)
 1=strong (trenchant)
 2=very strong (trenchant).
93. m32*. M_1 cristid obliqua orientation
 0=reaches trigonid wall at a point distal to protoconid
 1=reaches trigonid wall at a point distolingual to protoconid
 2=reaches trigonid wall at a point distal to metaconid.
94. m33*. M_2 cristid obliqua orientation
 0=reaches trigonid wall at a point distal to protoconid
 1=reaches trigonid wall at a point distolingual to protoconid
 2=reaches trigonid wall at a point distal to metaconid.
95. m34. M_1 cristid obliqua terminus
 0=runs to base of trigonid
 1=runs part way up the distal trigonid wall
 2=connects with protoconid tip or protocristid
 3=connects with metaconid.
96. m35. M_2 cristid obliqua terminus
 0=runs to base of trigonid
 1=runs part way up the distal trigonid wall
 2=connects with protoconid tip or protocristid
 3=connects with metaconid.

97. m36. M_3 cristid obliqua terminus
 0=runs to base of trigonid
 1=runs part way up the distal trigonid wall
 2=connects with protoconid tip or proto-cristid
 3=connects with metaconid.
98. m37. M_{1-2} centroconid development
 0=present
 1=absent but cristid obliqua bends sharply in hypoflexid
 2=absent.
99. m38*. M_{1-2} hypocristid development
 0=absent or seen only as a trace
 1=weak
 2=strong.
100. m39*. M_3 hypocristid development
 0=absent or seen only as a trace
 1=weak
 2=strong.
101. m40*. M_{1-2} talonid–lingual configuration
 0=open
 1=notched lingually but not open
 2=closed.
102. m41. M_{1-2} distal fovea
 0=absent
 1=present.
103. m42. M_{1-2} hypocristid configuration
 0=simple
 1=with accessory cusp close to hypoconid.
104. m43. M_{1-2} cristid obliqua
 0=notched
 1=straight.
105. m44*. Molar cusp inflation
 0=cusps not inflated, marginally positioned
 1=slightly inflated
 2=very inflated.
106. m45*. M_{1-2} buccal cingulum development
 0=absent to trace
 1=partial broken at protoconid and hypoconid
 2=complete.
107. m46*. M_1 hypoflexid depth
 0=very shallow
 1=moderate
 2=deep.
108. m47*. M_2 hypoflexid depth
 0=very shallow
 1=moderate
 2=deep.
109. m53*. M_2 length/ M_3 length
 0= M_3 much longer than M_2 (0.71–0.80)
 1= M_3 longer than M_2 (0.81–0.90)
 2= M_3 equal to M_2 (0.91–1.00)
 3= M_3 smaller than M_2 (1.01–1.12)
 4= M_3 much smaller than M_2 ($= > 1.13$)
 5= M_3 absent.
110. m54*. M_1 area
 0=1.10–2.00 mm
 1=2.10–3.10 mm
 2=3.10–4.00 mm
 3=4.10–5.00 mm
 4=5.10–6.00 mm
 5=6.10–7.00 mm
 6=7.10–8.00 mm
 7=8.10–9.00 mm
 8= > 9.10 .
111. m55*. M_1 length/width
 0=1.0–1.15
 1=1.16–1.22
 2=1.23 \times 1.32
 3= > 1.33 .
112. m56. Molar cusp wall convergence
 0=convergent
 1=vertical.

113. m57. M_{1-2} entoconid position relative to hypoconid
 0=transverse to hypoconid
 1=distal to hypoconid.

Upper Teeth

Incisors

114. I1*. I^1-I^2 interstitial contact
 0=absent teeth widely spaced
 1=present as narrow contact
 2= I^2 tightly packed against I^1 , I^1 prepraecrista abbreviated.

115. I2. I^1-I^1 interstitial contact
 0=present
 1=absent, a wide space occurs in the mid-line between these teeth.

116. I3. I^2-C diastema
 0=present
 1=absent.

117. I4*. I^1 area: I^2 area
 0=areas approximately equal ($= < 1.00$)
 1= I^1 slightly larger than I^2 ($> 1.00, < 1.40$)
 2= I^1 much larger than I^2 (> 1.40).

118. I5*. I^1 size (I^1 area: M^1 area)
 0=small ($= < 0.50$)
 1=moderate ($> 0.50, < 0.56$)
 2=large ($= > 0.56$).

119. I6*. I^1 occlusal shape (mesiodistal length/buccolingual breadth)
 0=rounded oval (< 1.05)
 1=buccolingually compressed ($> 1.05, < 1.30$)
 2=extremely compressed (> 1.30).

120. I7*. I^2 occlusal shape (mesiodistal length/buccolingual breadth)
 0=rounded oval ($= < 1.05$)
 1=slightly buccolingually compressed ($> 1.05, < 1.30$)
 2=extremely buccolingually compressed ($= > 1.30$).

121. I8. I^1 crown shape
 0=spatulate
 no apparent occlusal cusp, mesial and distal edges continuous and rounded
 1=semi-spatulate
 central cusp present but blunt with discernible mesial and distal occlusal crests
 2=central occlusal cusp pointed, occlusal edges steep.

122. I9. I^1 lingual fovea
 0=simple
 1=dual, with midcrown pillar.

123. I10. I¹ occlusal edge orientation (spatulate incisors only)
0=occlusal edge orthogonal to long axis of root
1=occlusal edge wears at a steep angle to long axis of root
2=crown with pronounced mesial asymmetry (=mesial process) in unworn state.
124. I11*. I¹⁻² lingual cingulum
0=weak, discontinuous
1=moderate, continuous
2=strong.
125. I12. I¹ basal lingual cusp
0=absent
1=present.
126. I13. I^{1-I2} buccal cingulum
0=absent
1=present.
127. C1. C¹ cross-sectional shape
0=oval
1=rounded.
128. C2*. Upper canine occlusion
0=C¹ wears against P₁₋₂
1=C¹ wears against P₂
2=C¹ wears against P₂₋₃
3=C¹ wears against P₃.
129. C3. C¹ mesial groove (females)
0=shallow or absent
1=deep.
130. C4*. C¹ lingual cingulum
0=weak or absent
1=strong
2=very strong.
- Premolars**
131. P1*. P² root number
0=one (if tooth is absent, taxon scored "0")
1=two
2=three.
132. P2*. P³ root number
0=one
1=two
2=three.
133. P3*. P⁴ root number
0=one
1=two
2=three.
134. P4*. P² area:P³ area
0=P² much smaller (≤ 0.85) (if tooth is absent, taxon scored "0")
1=P² smaller ($>0.85, <0.95$)
2=P² equal (≥ 0.95).
135. P5*. P⁴ area:M¹ area
0=P⁴ \ll M¹ (≤ 0.66)
1=P⁴ < M¹ ($>0.66, <0.76$)
2=P⁴ = M¹ (0.77-1.05)
3=P⁴ > M¹ (>1.06).
136. P6. P² occlusal outline
0=triangular
1=suboval with the long axis bucco-lingual
2=suboval with the long axis mesio-distal
3=round.
137. P7. P⁴ occlusal outline
0=triangular
1=suboval
2=squared.
138. P8. P³⁻⁴ trigon/talon proportions
0=trigon \geq talon
1=trigon < talon.
139. P9. P³ protocone
0=present
1=absent.
140. P10. P⁴ metacone
0=absent
1=present.
141. P11. P⁴ protocone
0=low relative to paracone
1=high relative to paracone.

142. P12. P² protocone
0=present
1=absent (if tooth absent taxon scored "1").
143. P13. Premolar hypocones
0=absent
1=present on P⁴ only
2=present on P³⁻⁴
3=present on P²⁻⁴.
144. P14*. P⁴ paraconule
0=large
1=small
2=absent.
145. P15. P³⁻⁴ parastyles
0=present
1=absent.
146. P16. P³⁻⁴ metastyles
0=absent
1=present.
147. P17. P³⁻⁴ postprotocrista
0=strong
1=weak, short.
148. P18. P²⁻³ distal crown margin
0=smoothly rounded
1=waisted between buccal and lingual cusps.
149. P19. P³⁻⁴ lingual cingulum
0=absent or weak
1=strong.
150. P20. P³ metacone
0=absent
1=present.
151. P21. P³⁻⁴ buccal cingulum development
0=absent or weak
1=strong.
- Molars**
152. M1*. M¹⁻² root number
0=three, three
1=three, two
2=two, two.
153. M2*. M³ root number
0=three
1=two
2=one.
154. M3*. M² shape (bl/md)
0=very broad (>1.65)
1=broad (<1.65, >1.30)
2=squared (= <1.30).
155. M4*. M¹ area:M² area
0=M¹ ≥ M² (= >1.40)
1=M¹ > M² (<1.40, >1.0)
2=M¹ = < M² (= <1.0).
156. M5*. M¹⁻² *Nannopithec*-fold
0=absent
1=weak
2=strong.
157. M6*. M¹⁻² pseudohypocone
0=absent
1=small
2=large.
158. M7. M¹⁻² metaconule
0=single or absent
1=double.
159. M9*. M¹⁻² preprotoconule
0=absent
1=weak
2=strong.
160. M10*. M¹ hypocone size
0=large
1=small
2=absent.
161. M11*. M² hypocone size
0=large

1 = small
2 = absent.

162. M12. M^{1-2} hypocone position
0 = distal, slightly lingual to protocone
1 = distal, far lingual to protocone.

163. M13*. M^{1-2} prehypocrista development
0 = absent
1 = weak
2 = strong—reaches to postprotocrista, encloses the talon lingually.

164. M14*. M^3 prehypocrista development
0 = absent
1 = weak
2 = strong, reaches to postprotocrista, encloses the talon lingually.

165. M15. M^1 or M^2 paraconule position
0 = attached to preprotocrista
1 = unattached to preprotocrista.

166. M16*. M^{1-2} metaconule size
0 = absent
1 = small
2 = moderate
3 = large.

167. M17. M^{1-2} mesostyle size
0 = absent
1 = present, attached to ectocrista
2 = present on buccal cingulum.

168. M18. M^{1-2} postprotocrista development
0 = strong, runs to base of metaconule or metacone
1 = strong but short does not reach base of metacone
2 = absent.

169. M19. M^{1-2} lateral posterior transverse crista development
0 = sharp
1 = indistinct.

170. M20*. P^4 - M^1 pericone
0 = absent
1 = small
2 = large.

171. M22*. M^{1-3} lingual cingulum development
0 = absent
1 = weak, broken
2 = strong, complete.

172. M24*. M^{1-2} buccal cingulum development
0 = absent
1 = weak
2 = strong.

173. M27. M^{1-2} pre-metaconule cristae
0 = absent or weak
1 = strong.

174. M28. M^{1-2} post-metaconule cristae
0 = absent or weak
1 = strong.

175. M30*. M^3 paraconule
0 = absent
1 = small-moderate
2 = large.

176. M31*. Molar protocone lingual inflation
0 = not inflated
1 = slightly inflated
2 = very inflated.

177. M33*. M^2 buccal expansion of paracone
0 = no expansion
1 = slight expansion
2 = considerable expansion.

178. M34*. M^3 metacone
0 = absent or very small
1 = moderate (but smaller than paracone)
2 = large (equal to paracone).

179. M36*. M³ hypocone

0=absent or very small

1=small

2=large.

180. M37*. M¹ paraconule size

0=absent

1=small-moderate (smaller than paracone)

2=large (nearly as large as or larger than paracone).

181. M44*. M¹⁻³ anterior cingulum

0=strong, complete, long

1=strong, short

2=weak or absent.

182. M46*. M³ size relative to M¹

0=very small (half the size of M¹ or less)

1=small (two thirds)

2=large (approximately as large).

Cranial characters

183. Cr 1. Transverse septum arising from the cochlear housing

0=absent

1=present and forming the lateral wall of an anterior accessory cavity pneumatized from the tympanic cavity

2=present and forming the lateral wall of an anterior accessory cavity pneumatized from the epitympanic recess.

184. Cr 2. Extent of pneumatization of anterior accessory cavity

0=anterior accessory cavity lies anterior to the tympanic cavity and is not trabeculated

1=anterior accessory cavity extends medial to the tympanic cavity, and is trabeculated.

185. Cr 3. Pneumatization of mastoid (from epitympanic recess)

0=absent

1=present.

186. Cr 4. Presence or absence of perbullar pathway

0=absent

1=present and formed exclusively by the petrosal bone.

187. Cr 5. Anteroposterior location of posterior carotid foramen in bulla

0=Posterior to line joining midpoints of tympanic bones

1=anterior to this line.

188. Cr 6. Mediolateral position of posterior carotid foramen in bulla

0=medial

1=midline of the bulla

2=lateral.

189. Cr 7. Ventrodorsal position of the carotid foramen in the bulla

0=dorsal, adjacent to basioccipital or mastoid bone

1=ventral.

190. Cr 8. Position of posterior carotid foramen relative to fenestra cochleae.

0=posterior

1=ventral

2=anterior.

191. Cr 9. Position of the internal carotid canal relative to the fenestra cochleae.

0=runs across ventral lip of the fenestra cochleae, shielding it from ventral view when a canal is present

1=internal carotid canal does not shield the fenestra cochleae from ventral view.

192. Cr 10. Position of the portion of the internal carotid/promontory artery (or its accompanying nerves) lying on the promontorium anterior to the fenestra cochleae.

0=on ventrolateral surface of promontorium

1=contacting only the cupula of the cochlea.

193. Cr 11. Size of stapedial and promontory canals.

0=both stapedial and promontory canals are large and subequal

1=stapedial slightly smaller than promontory
 2=stapedial highly reduced or absent altogether
 3=stapedial larger than promontory
 4=both promontory and stapedial canals absent.

194. Cr 12. Morphology of promontory canal, when present.

0=open trough
 1=complete canal.

195. Cr 13. Presence or absence of canal for internal carotid artery or nerves.

0=absent
 1=present.

196. Cr 14. Position of ventral edge of the tympanic bone.

0=intrabullar, or aphaneric
 1=extrabullar or phaneric.

197. Cr 15. The shape of the tympanic bone.

0=ribbon-like or only slightly expanded
 1=laterally expanded into a collar or tube
 ?=due to fusion with surrounding bones, of unknown shape.

198. Cr 16. Morphology of annular bridge.
 ?=This character is not analyzable in those taxa with an extrabullar tympanic, or those in which this region is not known

0=linea semicircularis or partial annular bridge formed on a entotympanic bulla
 1=linea semicircularis formed on a petrosal bulla
 2=a complete annular bridge.

199. Cr 17. Encroachment of the auditory bulla on the pterygoid fossa.

0=absent
 1=present and formed by anterior accessory cavity
 2=present and formed by the tympanic cavity.

200. Cr 18. Nature of contact between the lateral pterygoid plate and the bulla wall.

0=absent
 1=laminar
 2=abutting.

201. Cr 19. Extent of contact between the lateral pterygoid plate and the bulla wall.

0=slight
 1=very extensive.

202. Cr 20. Flange of basioccipital overlapping medial bulla wall.

0=absent or minimal
 1=extensive.

203. Cr 21. Suprameatal foramen.

0=absent
 1=present, small and in the posterior root of the zygomatic arch
 2=present, large and above the external auditory meatus.

204. Cr 22. Patent parotic fissure.

0=present
 1=absent.

205. Cr 23. Size of orbits*.

0=small
 1=large
 2=extremely large.

206. Cr 24. Postorbital closure*.

0=none
 1=postorbital bar present
 2=postorbital septum present including zygomatic=alisphenoid contact.

207. Cr 25. Composition of the postorbital septum.

0=zygomatic forms most of the septum
 1=frontal forms most of the septum.

208. Cr 26. Zygomatic-lacrimal contact.

0=present
 1=absent.

209. Cr 27. Pronounced interorbital constriction.
0=absent
1=present below olfactory tract.
210. Cr 28. Contact between lacrimal and palatine.
0=present
1=separated by a large fronto-maxillary contact (and in some taxa, a small os planum of the ethmoid)
2=separated by a large os planum.
211. Cr 29. Foramen rotundum.
0=absent
1=present.
212. Cr 30. Position of lacrimal foramen.
0=outside orbital margin
1=within the orbit or on the rim.
213. Cr 31. Metopic suture in adult.
0=unfused
1=fused.
214. Cr 32. Orbital convergence for relative orbit size.
0=below LSR of convergence vs. relative orbit size, and convergence $<30^\circ$
1=below LSR of convergence vs. relative orbit size, and convergence $>30^\circ$
2=above LSR of convergence vs. relative orbit size.
215. Cr 33. Posterior nasal spine*.
0=reduced or absent
1=small but distinct
2=robust and long.
216. Cr 34. Posterior palatine torus.
0=present
1=absent.
217. Cr 35. Pyramidal processes.
0=medially placed
1=laterally placed.
218. Cr 36. Length of medial pterygoid plate*.
0=long medial pterygoid plate extending one-third to one half of the distance to the anterior surface of the bulla
1=short but distinct from lateral pterygoid plate for its entire dorsoventral extent
2=medial pterygoid plate entirely absent, or reduced to a low rugosity.
219. Cr 37. Snout length.
0=long snout
1=short snout.
220. Cr 38. Maxillary depth.
0=deep
1=shallow.
221. Cr 39. Complete symphyseal fusion.
0=absent
1=present.
222. Cr 40. Temporomandibular joint morphology.
0=biconcave and transversely wide
1=anteroposteriorly oriented trough.
223. Cr 41. Entoglenoid process.
0=weak or absent
1=strong.
224. Cr 42. Inter-incisor diastema width.
0=broad and wide
1=narrow.
225. Cr 43. Coronoid height relative to condyle.
0=very far above
1=slightly above or equal.
226. Cr 44. Condyle height relative to toothrow.
0=at level of toothrow
1=slightly above
2=well above toothrow.

227. Cr 45. Mandibular corpus robusticity.
0=shallow
1=deep.

228. Cr 46. Sutural arrangement at pterion.
0=no postorbital closure
1=zygomatico-parietal contact
2=alisphenoid-frontal contact.

229. Cr 47. Enclosure of intratympanic portion of facial nerve in a bony canal.
0=no canal, facial nerve runs in a sulcus
1=bony canal present.

230. Cr 48. Epitympanic crest.
0=absent
1=present.

231. Cr 49. Ascending wing of premaxilla.
0=narrow
1=broad.

Postcranial characters

Humerus characters

232. H1. Shape of humeral trochlea (Ford, 1994; Dagosto & Gebo, 1994; Fleagle & Kay, 1987).
0=cylindrical, distal edge perpendicular to humeral shaft
1=slightly conical, distal edge slightly angled to shaft
2=conical, distal edge very angled to humeral shaft.

233. H2. Relative heights of medial and lateral edges of humeral trochlea.
0=subequal
1=medial flared relative to lateral.

234. H3. Trochleocapitular ridge (Ford, 1994).
0=absent
1=slightly distinct
2=moderately distinct
3=very distinct.

235. H4. Waisted trochlea. Minimum trochlear diameter/maximum trochlear diameter $\times 100$ (Ford, 1994).
0= >70 (unwaisted)
1= ≤ 70 (waisted).

236. H5. Width of capitulum relative to trochlea (ventral capitulum width/ventral trochlear width $\times 100$) (Ford, 1994).
0= <100
1=between 100 and 140
2=140–200
3=above 200.

237. H6. Entepicondylar foramen (Ford, 1986).
0=present
1=variable
2=absent.

238. H7. Entepicondylar foramen position (Ford, 1986).
0=over medial epicondyle
1=above ventral trochlea
2=above dorsal trochlea.

239. H8. Medial epicondyle size (Fleagle & Kay, 1987).
0=small
1=prominent.

240. H9. Dorsal placement of medial epicondyle (Ford, 1994).
0=parallel
1=slight dorsal angle
2=large dorsal angle.

241. H10. Shape of dorsal trochlea (Fleagle, 1995).
0=no pronounced lips on dorsal trochlear edges
1=both medial and lateral edges pronounced
2=very pronounced lateral lip.

242. H11. Dorsoepitrochlear fossa (Fleagle, 1995).
0=present

1 = small, shallow
2 = absent.

243. H12. Olecranon fossa shape (Fleagle, 1995).

0 = shallow
1 = moderate
2 = deep.

244. H13. Supinator crest (Fleagle & Kay, 1987).

0 = prominent
1 = low.

245. H14. Brachialis flange.

0 = broad
1 = moderate
2 = narrow.

246. H15. Bicipital groove morphology (Fleagle & Kay, 1987).

0 = shallow
1 = deep.

247. H16. Deltopectoral crest (Fleagle & Kay, 1987).

0 = prominent
1 = low
2 = flattened superiorly.

248. H17. Deltotriceps crest (Fleagle & Kay, 1987).

0 = low
1 = prominent.

Carpal characters

249. W1. Size of centrale, orientation of centrale–trapezoid facet, and articulation with hamate (Beard & Godinot, 1988).

0 = small centrale, facet faces distally, no articulation with hamate
1 = large centrale, facet faces distoradially, articulation with hamate.

250. W2. Ulnar–pisiform articulation (Beard & Godinot, 1988).

0 = facet on pisiform for ulnar styloid process is roughly equal in size to that for triquetrum

1 = facet on pisiform for ulnar styloid process is much enlarged and deeply excavated.

Femoral characters

251. F1. Length of femoral neck. Neck length #2/BSDLT × 100 (Dagosto & Gebo, 1994; Dagosto & Schmid, 1996)*.

0 = ≤ 75
1 = 75–120
2 = ≥ 120.

252. F2. Angle of femoral neck (Dagosto & Gebo, 1994)*.

0 = < 60°
1 = 60°–70°
2 = > 70°.

253. F3. Angle of lesser trochanter (Dagosto & Gebo, 1994; Dagosto & Schmid, 1996).

0 = medial (0–30°)
1 = posterior (>30°).

254. F4. Size of third trochanter (Dagosto & Gebo, 1994)*.

0 = large
1 = small
2 = crest or absent.

255. F5. Knee index (undefined) (Dagosto & Gebo, 1994)*.

0 = < 90 (shallow knee)
1 = 90–100
2 = > 100 (deep knee).

256. F6. Femoral head shape (Dagosto & Gebo, 1994)*.

0 = spherical
1 = semicylindrical
2 = cylindrical.

257. F7. Anterior extension of greater trochanter (Dagosto & Gebo, 1994).

0 = no extension
1 = extension.

258. F8. Anterior bowing of proximal femur (Dagosto & Gebo, 1994).

0 = none
1 = bowed.

259. F9. Relative length of trochanteric fossa (intertrochanteric fossa length/BSDLT $\times 100$) (Dagosto & Schmid, 1996)*.

0 = long (>125)
1 = moderate (110–125)
2 = very short (<110).

260. F10. Presence of intertrochanteric crest (Dagosto & Gebo, 1994).

0 = no crest
1 = crest.

261. F11. Size of lesser trochanter (Dagosto, 1990)*.

0 = large
1 = intermediate
2 = small.

262. F12. Lateral border of distal femur (Dagosto, 1990).

0 = low
1 = high.

Tibia characters

263. T1. Distal fusion of tibia and fibula.

0 = absent, small articulation
1 = no fusion, moderate articulation
2 = no fusion but extensive articulation
3 = fusion.

264. T3. Shape of distal surface of tibia (Dagosto & Gebo, 1994).

0 = square
1 = triangular.

265. T4. Rotation of the medial malleolus (Dagosto & Gebo, 1994).

0 = none
1 = slight
2 = strong.

266. T5. Shape of medial malleolar articular surface (Dagosto, 1988; Dagosto & Gebo, 1994).

0 = flat

1 = anteriorly convex, posteriorly flat
2 = all convex.

267. T6. Shape of distal tibial shaft (Dagosto & Gebo, 1994).

0 = no compression
1 = anteroposteriorly compressed.

268. T7. Position of tibialis posterior groove (Dagosto & Gebo, 1994).

0 = on medial side of malleolus
1 = on posterior side of malleolus.

Talus characters

269. A1. Position of the flexor fibularis (flexor hallucis longus) groove (Dagosto, 1988).

0 = lateral to the posterior part of the tibio-talar joint
1 = groove is plantar and central to the facet.

270. A2. Slope of talofibular facet (Dagosto & Gebo, 1994).

0 = facet slopes obliquely and gradually laterally
1 = facet is flat [vertical] and has a small pointed process plantarily.

271. A3. Length of the talar–tibial articulation (Dagosto & Gebo, 1994).

0 = short
1 = long.

272. A4. Development of the talar posterior trochlear shelf.

0 = absent or weakly developed posterior trochlear shelf
1 = well developed shelf.

273. A5. Talar neck length (Dagosto & Gebo, 1994).

0 = short (<100)
1 = long (>100).

274. A6. Medial talotibial facet (Dagosto, 1990).

0 = short
1 = long.

Calcaneus characters

275. C1. Anterior calcaneal elongation (length of calcaneus distal to astragalo-calcaneal facet/total calcaneal length \times 100) (Dagosto, 1990)*.

0=not elongate (ACL or anterior calcaneal ratio $<$ 40)

1=moderate (ACL \geq 40–45)

2=long ($>$ 45).

276. C2. Position of the peroneal tubercle relative to posterior astragalocalcaneal joint (Dagosto, 1988)*.

0=distal to joint

1=at joint

2=proximal to joint.

277. C3. Posterior calcaneal bowing (Dagosto & Gebo, 1994).

0=absent

1=present.

Navicular characters

278. N1. Length relative to width \times 100 (Dagosto & Gebo, 1994)*.

0=short ($<$ 90)

1=moderate (100–150)

2=long ($>$ 150).

279. N3. Morphology of the naviculocuboid articulation (Dagosto & Gebo, 1994).

0=cuboid facet on navicular contacts only the ectocuneiform

1=cuboid facet contacts the ectocuneiform and mesocuneiform.

Entocuneiform characters

280. E1. Shape of entocuneiform/MT1 articulation (Szalay & Dagosto, 1988)*.

0=dorsally reduced

1=dorsal moiety of joint enlarged relative to ventral moiety

2=dorsal moiety greatly enlarged.

281. E2. Lateral process of entocuneiform (Szalay & Dagosto, 1988).

0=small

1=large.

General foot characters

282. O1. Foot axis (Dagosto, 1990).

0=mesaxonic

1=paraxonic

2=ectaxonic.

283. O2. Toilet claw (Dagosto, 1990).

0=absent

1=present.

284. O3. Prehallux (Dagosto, 1990).

0=present

1=absent.

285. O4. Metatarsus length (Dagosto, 1990).

0=short

1=long.

Metatarsal character

286. MT1. Peroneal tubercle of MT1 (Szalay & Dagosto, 1988)*.

0=very large

1=large

2=small.

287. MT2. Hallux length relative to digit three length (Schultz, 1963; Dagosto, 1990).

0=short

1=long.

Soft tissue characters

288. Retinal fovea

0=absent

1=present.

289. Haplorhini vs. strepsirhini

0=strepsirhine

1=haplorhine.

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C. ROSS *ET AL.*

290. Tapetum lucidum
0=present
1=absent.

291. Vitamin C synthesis
0=present
1=absent.

Appendix B. Character-taxon matrix

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.
Scandentia	1	9 ¹	9	9	9	9	9	9	9	9	9
<i>P. tricuspidens/P. jepi</i>	1	1	1	9	2	4	9	9	2	9	2
<i>Purgatorius unio</i>	0	9	9	9	9	9	9	9	9	9	9
<i>Plesolestes problematicus</i>	1	9	1	0	1	4	9	0	2	0	2
<i>Adapis parisiensis</i>	1	0	0	1	0	1	0	0	0	0	0
<i>Cantius/Notharctus</i>	1	0	0	1	0	1	0	0	0	0	1
<i>Donrussellia</i> sp.	9	1	9	1	9	9	9	9	9	9	9
<i>Leptadapis magnus</i>	1	9	9	0	9	0	9	9	0	0	0
<i>Mahgarita stevensi</i>	1	9	0	1	0	0	9	9	9	9	1
<i>Aframonius dieides</i>	1	0	9	1	0	9	9	0	9	9	0
<i>Pronycticebus gaudryi</i>	1	9	9	9	0	1	0	9	0	9	0
<i>Protoadapis curvicspidens</i>	1	9	9	9	0	1	9	9	9	9	9
<i>Galagoides demidoff</i>	1	0	0	1	0	2	9	1	2	0	1
<i>Lemur catta</i>	1	0	0	0	0	2	9	1	2	0	1
<i>Microcebus murinus</i>	1	0	0	1	0	2	9	1	2	0	1
<i>Nycticebus coucang</i>	1	0	0	1	0	2	9	1	2	0	1
<i>Absarokius</i> sp.	1	0	0	1	0	2	9	9	9	9	9
<i>Anaptomorphus</i> sp.	1	0	0	1	0	2	9	9	9	9	0
<i>Anemorhysis savagei</i>	1	1	9	1	2	4	9	9	9	9	2
<i>Arapahovius gazini</i>	1	1	0	1	2	4	9	0	2	0	2
<i>Aycrossia lovei</i>	1	0	9	1	0	2	9	0	9	9	0
<i>Dyseolemur pacificus</i>	1	0	0	1	0	3	9	9	1	0	0
<i>Hemiacodon gracilis</i>	1	1	0	1	1	3	9	0	9	9	2
<i>Loveina zephyri</i>	1	0	9	1	0	2	9	9	9	9	0/1
<i>Macrotarsius montanus</i>	1	9	9	1	0	3	9	9	9	9	1
<i>Microchoerus erinaceus</i>	1	1	0	1	2	4	9	9	2	0	1
<i>Nannopithec</i> sp.	1	1	0	1	2	4	9	9	2	0	1
<i>Necrolemur antiquus</i>	1	1	0	1	2	4	9	9	2	0	1
<i>Omomys</i> sp.	1	1	0	1	2	3&4	9	0	1/2	0	1
<i>Pseudoloris parvulus</i>	1	1	9	1	2	4	9	0	9	9	2
<i>Rooneyia viejaensis</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Shoshonius cooperi</i>	1	0	9	1	0	2	9	9	9	9	0
<i>Steinius vespertinus</i>	1	1	9	1	0	3	9	9	9	9	1/2
<i>Teilhardina americana</i>	1	1	0	1	1	3	9	9	9	9	2
<i>Teilhardina belgica</i>	1	1	9	1	0	2/3	9	9	9	9	9
<i>Tetonius</i> sp.	1	1	0	1	2	4	9	0	2	0	2
<i>Tetonoides</i> sp.	1	1	9	1	2	3/4	9	9	9	9	2
<i>Trogolemur myodes</i>	1	1	9	1	2	4	9	9	2	1	2
<i>Washakius insignis</i>	1	0	0	1	0	2	9	0	0/1	9	0
<i>Eosimias</i> sp.	1	0	0	1	0	0	0	0	0	0	0
<i>Tarsius</i> sp.	2	1	9	1	9	4	9	1	2	0	1
<i>Aegyptopithecus zeuxis</i>	1	0	0	0	0	1	0	0	1	0	0
<i>Apidium phiomense</i>	1	0	0	1	0	1	0	0	0	0	0
<i>Arsinoea kallamos</i>	1	0	0	1	1	0/1	9	0	1	0	0
<i>Catopithecus browni</i>	1	9	0	9	9	1	0	0	1	0	0
<i>Parapithecus fraasi</i>	9	0	0	1	0	1	0/1	0	0	0	0
<i>Qatrania wingi</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Serapia eocaena</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Simonsius grangeri</i>	3	9	9	9	9	9	9	9	9	9	9
<i>Aotus trivirgatus</i>	1	0	0	1	1	2	0	0	0	0	0
<i>Callicebus moloch</i>	1	0	0	1	0	1	1	1	1	0	0
<i>Dolichocebus gaimanensis</i>	1	9	9	9	9	9	0	0	0	0	9
<i>Saimiri sciureus</i>	1	0	0	1	2	1	0	0	0	0	0
<i>Proteopithecus sylviae</i>	1	9	9	9	9	9	9	9	9	9	9
<i>Afrotarsius chatrathi</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Strigorhysis</i> sp.	1	0	9	1	1	2	9	9	9	9	0
<i>Uintanius ameghini</i>	1	0	9	1	0	2&3	9	9	9	9	1

¹9=missing data

Appendix B continued

	12.	13.	14.	15.	16.	17.	18.	19.	20.	21.	22.
Scandentia	9	9	9	9	9	9	9	0	0	0	0
<i>P. tricuspidens/P. jepi</i>	1	0	1	9	0	2	2	0	0	9	9
<i>Purgatorius unio</i>	9	9	9	9	9	9	9	0	9	9	9
<i>Plesolestes problematicus</i>	1	0	1	0	0	0	2	0	0	0	0
<i>Adapis parisiensis</i>	0	0	0	1	0	2	0	1	9	0	1
<i>Cantius/Notharctus</i>	1	0	0	1	0	1	0	1	9	0	9
<i>Donrussellia</i> sp.	9	0	9	9	9	9	9	9	9	9	9
<i>Leptadapis magnus</i>	0	0	0	1	9	2	0	1	9	1	1
<i>Mahgarita stevensi</i>	9	0	0	9	9	9	0	1	9	0	0
<i>Aframomius dieides</i>	0	0	9	9	9	9	0	1	9	0	0
<i>Pronycticebus gaudryi</i>	0	0	0	1	0	9	9	1	9	9	9
<i>Protoadapis curvicaudatus</i>	9	9	9	9	9	9	9	1	9	0	0
<i>Galagoideus demidoff</i>	2	1	1	1	0	1	0	0	0	1	0
<i>Lemur catta</i>	2	1	1	1	0	1	0	0	0	1	0
<i>Microcebus murinus</i>	2	1	1	1	0	1	0	0	0	1	0
<i>Nycticebus coucang</i>	2	1	1	1	0	0	0	0	0	1	0
<i>Absarokius</i> sp.	9	0	9	9	9	9	0	0	9	0	9
<i>Anaptomorphus</i> sp.	9	0	9	9	9	9	1	0	9	1	9
<i>Anemorhysis savagei</i>	9	0	9	9	9	9	2	0	9	9	9
<i>Arapahovius gazini</i>	2	0	1	1	0	2	2	0	9	2	0
<i>Aycrossia lovei</i>	9	0	1	1	9	9	1	0	9	0	0
<i>Dyseulemur pacificus</i>	9	0	3	9	0	9	0	0	9	0	0
<i>Hemicacodon gracilis</i>	1/2	0	9	1	9	1/2	1	0	9	2	9
<i>Loveina zephyri</i>	9	0	9	9	9	9	0	9	9	9	9
<i>Macrotarsius montanus</i>	9	0	9	9	9	9	1	9	9	9	9
<i>Microchoerus erinaceus</i>	1	0	1	9	0	2	2	0	9	2	0
<i>Nannopithecus</i> sp.	2	0	1	1	0	2	9	0	9	0	0
<i>Necrolemur antiquus</i>	2	0	1	9	0	2	2	0	9	0	0
<i>Omomys</i> sp.	1	0	1	0	9	2	1	0	9	0	0
<i>Pseudoloris parvulus</i>	9	9	9	9	0	9	2	0	9	0	9
<i>Rooneyia viejaensis</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Shoshonius cooperi</i>	9	0	9	9	9	9	0	0	9	0	0
<i>Steinius vespertinus</i>	9	0	9	9	9	9	9	1	9	9	9
<i>Teilhardina americana</i>	9	0	9	9	9	9	0/1	0	9	0	0
<i>Teilhardina belgica</i>	9	0	9	9	9	9	0	0	9	9	9
<i>Tetonius</i> sp.	2	0	1	1	0	2	2	0	9	0	0
<i>Tetonoides</i> sp.	9	0	9	9	9	9	1	0	9	9	9
<i>Trogolemur myodes</i>	2	0	1	9	0	9	2	0	9	9	0
<i>Washakius insignis</i>	9	0	1	1	0	2	0	0	9	0	0
<i>Eosimias</i> sp.	0	0	0	1	0	0	0	2	9	0	0
<i>Tarsius</i> sp.	1	0	1	9	0	0	0	1	0	0	1
<i>Aegyptopithecus zeuxis</i>	0	0	0	1	0	1	0	1	2	0	0
<i>Apidium phiomense</i>	0	0	0	1	0	2	0	1	2	0	0
<i>Arsinoea kallamos</i>	0	0	0	1	0	2	0	1	9	1	0
<i>Catopithecus browni</i>	0	0	0	1	0	9	9	1	2	0	0
<i>Parapithecus fraasi</i>	0	0	0	1	0	2	0	1	9	0	0
<i>Qatrania wingi</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Serapia eocaena</i>	9	9	9	9	9	9	9	1	9	1	0
<i>Simonsius grangeri</i>	9	0	9	9	9	9	9	1	9	0	0
<i>Aotus trivirgatus</i>	0	0	0	1	0	9	0	1	0	0	0
<i>Callicebus moloch</i>	0	0	0	1	0	9	0	1	0	0	0
<i>Dolichocebus gaimanensis</i>	0	0	0	1	0	9	0	1	1	0	0
<i>Saimiri sciureus</i>	0	0	0	1	0	9	0	2	2	0	0
<i>Proteopithecus sylviae</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Afrotarsius chatrathi</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Strigorhysis</i> sp.	9	0	9	9	9	9	1	0	9	9	9
<i>Uintanius ameghini</i>	9	0	9	9	9	9	0	0	9	9	9

Appendix B *continued*

	23.	24.	25.	26.	27.	28.	29.	30.	31.	32.	33.
Scandentia	9	9	0	0	0	1	1	2	0	1	2
<i>P. tricuspidens/P. jepi</i>	9	1	1	0	0	2	0	2	2	9	0
<i>Purgatorius unio</i>	9	9	0	0	1	2	0	2	0	1	2
<i>Plesolestes problematicus</i>	0	1	1	0	0	2	0	2	0	1	2
<i>Adapis parisiensis</i>	2	2	0	0	1	2	0	2	9	9	2
<i>Cantius/Notharctus</i>	0	2	0	0	1	2	0	2	1	1	1
<i>Donrussellia</i> sp.	9	9	0	0	1	2	0	2	1	1	9
<i>Leptadapis magnus</i>	0	2	0	0	1	2	0	2	1	0	2
<i>Mahgarita stevensi</i>	0	2	1	0	0	2	0	2	2	9	1
<i>Aframonius dieides</i>	0	2	1	0	0	2	0	2	2	9	2
<i>Pronycticebus gaudryi</i>	9	9	0	0	1	2	0	2	1	1	1
<i>Protoadapis curvicaudatus</i>	9	2	0	0	1	2	0	2	2	9	2
<i>Galagoides demidoff</i>	9	9	1	0	0	2	2	2	2	9	2
<i>Lemur catta</i>	9	9	1	0	0	2	0	2	2	9	1
<i>Microcebus murinus</i>	9	9	1	0	0	9	1	2	2	9	0
<i>Nycticebus coucang</i>	9	9	1	0	0	2	1	2	2	9	0
<i>Absarokius</i> sp.	9	9	1	0	0	2	2	2	2	9	1
<i>Anaptomorphus</i> sp.	9	9	1	1	9	2	1	9	2	9	1
<i>Anemorhysis savagei</i>	9	9	1	0	0	2	1	2	1	1	1
<i>Arapahovius gazini</i>	1	0	1	0	0	2	0	2	0	2	1
<i>Aycrossia lovei</i>	1	1	1	0	0	2	2	2	2	9	1
<i>Dyseolemur pacificus</i>	0	9	1	0	0	2	1	2	1	1	1
<i>Hemiacodon gracilis</i>	9	0/1	1	0	0	2	1	2	2	9	2
<i>Loveina zephyri</i>	9	9	1	0	0	2	1	1	0	2	1
<i>Macrotarsius montanus</i>	9	9	1	0	0	2	0	9	0	1	1
<i>Microchoerus erinaceus</i>	1	0	1	1	0	1	2	2	2	1	0
<i>Nannopithecus</i> sp.	1	0	1	1	0	1	2	2	2	0	1
<i>Necrolemur antiquus</i>	1	0	1	1	0	1	2	2	2	1	1
<i>Omomys</i> sp.	0	1	1	0	0	2	0	2	2	1	1
<i>Pseudoloris parvulus</i>	1	9	1	1	0	1	2	2	2	1	1
<i>Rooneyia viejaensis</i>	9	9	9	9	0	9	9	9	9	9	9
<i>Shoshonius cooperi</i>	1	1	1	0	0	2	1	1	0	2	1
<i>Steinius vespertinus</i>	9	9	0	0	0	2	0	2	2	1	1
<i>Teilhardina americana</i>	0	1	0&1	0	0	2	0	2	1	2	1
<i>Teilhardina belgica</i>	9	9	0&1	0	0	2	0	2	1	1	1
<i>Tetonius</i> sp.	1	0	1	0	0	2	2	2	1&2	1	1
<i>Tetonoides</i> sp.	9	9	1	0	0	2	1	0	0	2	1
<i>Trogolemur myodes</i>	9	0	1	1	0	0	2	2	1	1	1
<i>Washakius insignis</i>	9	0/1	1	0	0	2	1	1	0	2	0
<i>Eosimias</i> sp.	0	2	1	0	0	2	1	2	0	0	1&2
<i>Tarsius</i> sp.	0	0	1	0	0	1	2	2	2	9	1
<i>Aegyptopithecus zeuxis</i>	0	2	1	1	9	2	0	2	2	9	1
<i>Apidium phiomense</i>	0	2	1	0	0	2	0	2	2	9	0
<i>Arsinoea kallamos</i>	0	2	1	0	9	9	2	2	2	9	1
<i>Catopithecus browni</i>	0	2	1	1	9	2	0	1	1	1	1
<i>Parapithecus fraasi</i>	0	2	1	0	0	2	0	2	2	9	0
<i>Qatrania wingi</i>	9	9	9	0	0	2	0	9	1	1	1
<i>Serapia eocaena</i>	0	2	1	0	0	2	2	2	1	1	1
<i>Simonsius grangeri</i>	0	2	1	0	0	2	0	1	1	9	0
<i>Aotus trivirgatus</i>	0	2	1	0	0	0	0	2	2	9	1
<i>Callicebus moloch</i>	0	2	1	0	0	0	0	2	2	9	0
<i>Dolichocebus gaimanensis</i>	0	2	1	0	0	0	0	2	2	9	1
<i>Saimiri sciureus</i>	0	0	1	0	0	0	0	2	2	9	0
<i>Proteopithecus sylviae</i>	9	9	1	0	9	9	9	9	9	9	9
<i>Afrotarsius chatrathi</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Strigorhysis</i> sp.	9	9	1	1	0	2	2	9	2	9	1
<i>Uintanius ameghini</i>	9	9	1	0	0	2	2	1	1	0	1

Appendix B continued

	34.	35.	36.	37.	38.	39.	40.	41.	42.	43.	44.
Scandentia	2	0	0	0	0	0	1	1	0	1	1
<i>P. tricuspidens/P. jepi</i>	9	9	0	0	0	1	1	1	9	2	9
<i>Purgatorius unio</i>	2	0	0	0	0	1	1	1	0	1	1
<i>Plesolestes problematicus</i>	2	0	9	1	2	1	2	2	0	1	1
<i>Adapis parisiensis</i>	2	1	0	0	2	1	0	2	0	1	1
<i>Cantius/Notharctus</i>	2	0	0	0	2	0&1	0	0	0	1	1
<i>Donrussellia</i> sp.	9	0	9	0	1	1	9	1	0	9	1
<i>Leptadapis magnus</i>	2	0	0	0	2	1	0	1	0	1	1
<i>Mahgarita stevensi</i>	2	9	0	0	0	1	0	1	9	1	1
<i>Aframonius dieides</i>	3	0	0	0	1	1	1	1	0	9	1
<i>Pronycticebus gaudryi</i>	9	0	9	0	1	1	0	2	0	1	1
<i>Protoadapis curvicauspiciens</i>	2	0	0	0	1	1	1	1	0	1	1
<i>Galagoides demidoff</i>	0	1	0	0	2	1	0	2	0	1	1
<i>Lemur catta</i>	0	1	0	0	1	1	0	0	0	1	1
<i>Microcebus murinus</i>	2	9	0	0	0	1	0	0	9	1	1
<i>Nycticebus coucang</i>	0	9	0	0	0	1	0	0	9	1	1
<i>Absarokius</i> sp.	3	0	0	0	1	1	0&1	1	0	2	1
<i>Anaptomorphus</i> sp.	9	0	9	0	1	1	9	1	0	2	1
<i>Anemorhysis savagei</i>	9	0	9	0	1	1	0	2	0	1	1
<i>Arapahovius gazini</i>	2	0	0	1	2	0&1	2	2	0	1	1
<i>Aycrossia lovei</i>	9	0	9	0	1	1	1	1	0	2	1
<i>Dyseolemur pacificus</i>	9	0	0	0	1	1	0	1	0	1	1
<i>Hemiacodon gracilis</i>	3	1	0	0	2	0&1	2	2	0	1	0
<i>Loveina zephyri</i>	9	1	9	1	1	1	0	0	0	1	1
<i>Macrotarsius montanus</i>	9	1	9	9	2	1	9	2	0	0	0
<i>Microchoerus erinaceus</i>	9	1	9	0	2	0	1	1	0	1	0
<i>Nannopithecus</i> sp.	2	0	9	0	1	1	0	0	0	1	1
<i>Necrolemur antiquus</i>	9	1	9	0	2	0	1	1	0	1	1
<i>Omomys</i> sp.	3	0	0	0	1	0&1	2	2	0	1	0
<i>Pseudoloris parvulus</i>	9	0	9	0	1	0	0	0	0	1	1
<i>Rooneyia viejaensis</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Shoshonius cooperi</i>	3	1	0	1	1	1	0	0&1	0	0	1
<i>Steinius vespertinus</i>	9	0	9	0	1	0&1	2	2	0	1	1
<i>Teilhardina americana</i>	3	0	0	0	1	1	1	1&2	0	1	1
<i>Teilhardina belgica</i>	9	0	9	0	1	1	1	2	0	0	1
<i>Tetonius</i> sp.	3	0	0	0	1	1	1	1	0	2	1
<i>Tetonoides</i> sp.	9	0	9	1	2	1	1	1	0	1	1
<i>Trogolemur myodes</i>	9	0	9	0	1	1	0	0	0	2	1
<i>Washakius insignis</i>	2&3	0	0	1	1	0&1	0	0	0	1	1
<i>Eosimias</i> sp.	3	0	0	0	1	1	0	0	0	1	1
<i>Tarsius</i> sp.	3	0	0	0	1	1	1	1	0	1	1
<i>Aegyptopithecus zeuxis</i>	9	1	9	0	2	0	0	0	0	1	0
<i>Apidium phiomense</i>	0	0	0	1	1	1	0	0	1	1	1
<i>Arsinoea kallamos</i>	2	0	0	1	1	0	1	1	0	1	1
<i>Catopithecus browni</i>	9	1	9	0	2	1	0	1	0	1	0
<i>Parapithecus fraasi</i>	2	0	0	1	1	1	0	0	1	1	1
<i>Qatrania wingi</i>	9	0	9	9	1	1	9	0	1	9	1
<i>Serapia eocaena</i>	0	0	0	0	1	1	0	1	0	1	0
<i>Simonsius grangeri</i>	2	0	0	1	1	1	0	0	1	1	0
<i>Aotus trivirgatus</i>	2	1	0	2	2	0	1	1	0	0	0
<i>Callicebus moloch</i>	2	1	0	2	2	0	1	2	0	0	0
<i>Dolichocebus gaimanensis</i>	2	1	0	1	2	1	0	2	0	1	0
<i>Saimiri sciureus</i>	2	1	0	2	2	0	2	2	0	0	0
<i>Proteopithecus sylviae</i>	9	9	0	0	9	9	9	9	9	9	9
<i>Afrotarsius chatrathi</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Strigorhysis</i> sp.	9	0	9	9	1	1	9	1&2	0	0	1
<i>Untanius ameghini</i>	9	0	9	0	0	1	0	0	0	2	1

Appendix B *continued*

	45.	46.	47.	48.	49.	50.	51.	52.	53.	54.	55.
Scandentia	0	1	1	0	0	0	9	9	9	9	9
<i>P. tricuspidens/P. jepi</i>	9	1	0	0	9	1	1	0	1	0	0
<i>Purgatorius unio</i>	0	1	0	0	0	0	0	2	0	0	0
<i>Plesolestes problematicus</i>	0	1	0	2	9	0	9	9	9	9	9
<i>Adapis parisiensis</i>	0	0	0	2	2	9	0	3	1	1	0
<i>Cantius/Notharctus</i>	0	1	1	1	0	0	0	1	0	1	1
<i>Donrussellia</i> sp.	0	1	0	2	9	0	0	1&2	0	1	2
<i>Leptadapis magnus</i>	0	0	0	2	2	0	0	1	0	1	0
<i>Mahgarita stevensi</i>	0	1	0	0	9	0	0	1	0	1	1
<i>Aframonius dieides</i>	0	9	0	0	0	0	0	2	0	0	1
<i>Pronycticebus gaudryi</i>	0	1	9	0	9	0	0	2	0	1	0
<i>Protoadapis curvicauspiciens</i>	0	0	1	0	9	0	0	2	0	1	0
<i>Galagoides demidoff</i>	0	0	0	1	0	1	0	3	1	0	0
<i>Lemur catta</i>	0	1	0	0	0	1	0	2	0	0	1
<i>Microcebus murinus</i>	0	0	1	0	2	1	0	0	1	1	0
<i>Nycticebus coucang</i>	0	1	0	0	0	1	0	0	0	0	0
<i>Absarokius</i> sp.	0	1	1	0	9	2	2	0	1&2	0	0
<i>Anaptomorphus</i> sp.	0	1	1	0	9	2	1	1	1	0	0
<i>Anemorhysis savagei</i>	0	1	0&1	0	9	1	0	1	2	0	0
<i>Arapahovius gazini</i>	0	1	1	0	0	1	1	0	2	1	1
<i>Aycrossia lovei</i>	0	1	1	0	9	2	1	1	1	0	0
<i>Dyseolemur pacificus</i>	0	1	0	1	9	2	1	1	2	1	1
<i>Hemiacodon gracilis</i>	0	1	0	1	0	0	0	1	1	1	1
<i>Loveina zephyri</i>	0	1	1	1	9	2	1	1	2	1	1
<i>Macrotarsius montanus</i>	0	1	0	1	9	2	1	1	0	1	1
<i>Microchoerus erinaceus</i>	0	1	1	1	9	2	1	1	2	1	1
<i>Nannopithecus</i> sp.	0	1	0	0	9	2	2	1	2	0	0
<i>Necrolemur antiquus</i>	0	1	1	1	9	2	1	1	2	1	1
<i>Omomys</i> sp.	0	1	0	0	0	0	0	1	1	1	1
<i>Pseudoloris parvulus</i>	0	1	0	0	9	1	1	1	2	1	0
<i>Rooneyia viejaensis</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Shoshonius cooperi</i>	0	1	1	0	0	2	1	1	2	1	1
<i>Steinius vespertinus</i>	0	1	0	0	9	0	0	1	2	1	1
<i>Teilhardina americana</i>	0	1	1	0	0	0	1	0&1	1	1	0
<i>Teilhardina belgica</i>	0	1	1	0	9	0	0	1	1	0	0
<i>Tetonius</i> sp.	0	1	1	2	0	2	1	1	1	0	0
<i>Tetonoides</i> sp.	0	1	1	1	9	1	0	0	2	1	0
<i>Trogolemur myodes</i>	0	1	0	0	9	2	2	1	2	1	1
<i>Washakius insignis</i>	0	1	0	0	0	2	1	1	2	1	1
<i>Eosimias</i> sp.	0	0&1	1	0	0	1	1	1	1	1	0
<i>Tarsius</i> sp.	0	1	0	0	2	1	1	0	1	1	1
<i>Aegyptopithecus zeuxis</i>	0	1	0	0	9	1	0	3	0	0	9
<i>Apidium phiomense</i>	1	0	1	0	1	2	0	1	0	0	0
<i>Arsinoea kallamos</i>	0	1	1	0	0	1	0	3	1	1	0
<i>Catopithecus browni</i>	0	1	0	0	9	0	0	2	0	0	1
<i>Parapithecus fraasi</i>	1	0	1	0	1	2	0	2	0	0	0
<i>Qatrania wingi</i>	1	1	1	0	9	0	0	2	0	0	0
<i>Serapia eocaena</i>	0	1	1	0	1	1	0	1	0	0	0
<i>Simonsius grangeri</i>	1	1	0	0	0	1	0	3	0	0	1
<i>Aotus trivirgatus</i>	0	1	9	0	0	0	0	1	0	0	1
<i>Callicebus moloch</i>	0	1	9	0	0	0	0	2	0	1	1
<i>Dolichocebus gaimanensis</i>	0	1	0	0	0	1	0	2	0	0	1
<i>Saimiri sciureus</i>	0	1	9	0	0	1	0	0	0	0	0
<i>Proteopithecus sylviae</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Afrotarsius chatrathi</i>	9	9	9	9	9	9	1	9	9	9	9
<i>Strigorhysis</i> sp.	0	1	1	1	0	2	1	1	1	0	0
<i>Uintanius ameghini</i>	0	1	1	0	9	2	2	0	0	0	0

Appendix B continued

	56.	57.	58.	59.	60.	61.	62.	63.	64.	65.	66.
Scandentia	9	9	9	9	9	9	9	0	1	1	1
<i>P. tricuspidens/P. jepi</i>	9	9	2	3	1	1	0	0	1	1	1
<i>Purgatorius unio</i>	0	0	0	1	5	1	0	0	1	1	1
<i>Plesolestes problematicus</i>	9	9	9	9	9	9	9	0	1	1	1
<i>Adapis parisiensis</i>	0	9	2	1	4	3	0	0	1	1	1
<i>Cantius/Notharctus</i>	0	0	1	1&2	3	2	0	0	1	1	1
<i>Donrussellia</i> sp.	0	0	1	9	5	3	0	0	1	1	1
<i>Leptadapis magnus</i>	0	9	2	3	4	4	1	0	1	1	1
<i>Maharita stevensi</i>	1	9	3	3	5	2	0	0	1	1	1
<i>Aframonius dieides</i>	1	9	3	2	3&4	1	0	0	1	1	1
<i>Pronycticebus gaudryi</i>	0	9	9	2	4	3	0	0	1	1	1
<i>Protoadapis curvicspidens</i>	1	9	3	2&3	3	5	0	0	1	1	1
<i>Galagoides demidoff</i>	0	9	2	3	2	0	1	0	1	1	1
<i>Lemur catta</i>	0	0	1	0	5	3	0	0	1	1	1
<i>Microcebus murinus</i>	9	9	2	3	1	2	9	0	1	1	1
<i>Nycticebus coucang</i>	9	9	2	2	3	1	2	0	1	1	1
<i>Absarokius</i> sp.	0	9	0	0	0	5	0	0	1	1	1
<i>Anaptomorphus</i> sp.	0	9	9	0/1	1	3	0	0	1	1	1
<i>Anemorhysis savagei</i>	0	0	1	1	1&2	1	0	0	1	1	1
<i>Arapahovius gazini</i>	1	1	1	2	2&3	0&1	0	0	1	1	1
<i>Aycrossia lovei</i>	1	9	0	0	1	3	0	0	1	1	1
<i>Dyseolemur pacificus</i>	1	1	9	2	1	1	0	0	1	1	1
<i>Hemicacodon gracilis</i>	1	9	2	3	3	0	0	0	1	1	1
<i>Loveina zephyri</i>	1	1	1	3	2	2	0	0	1	1	1
<i>Macrotarsius montanus</i>	1	0	9	9	1&2	0	0	0	1	1	1
<i>Microchoerus erinaceus</i>	1	9	2	3	1	0	0	0	1	1	1
<i>Nannopithecus</i> sp.	1	9	0	0	2	2	0	0	1	1	1
<i>Necrolemur antiquus</i>	1	9	2	3	1	0	0	0	1	1	1
<i>Omomys</i> sp.	1	9	3	3	3&4	2	0	0	1	1	1
<i>Pseudoloris parvulus</i>	0	9	0	1	3&4	1	0	0	1	1	1
<i>Rooneyia viejaensis</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Shoshonius cooperi</i>	1	1	1	2&3	1&2	2	0	0	1	1	1
<i>Steinius vespertinus</i>	1	9	2	3	3	1	0	0	1	1	1
<i>Teilhardina americana</i>	1	0	1	1&2	2	1	0	0	1	1	1
<i>Teilhardina belgica</i>	0	0	1	1&2	3&4	3	0	0	1	1	1
<i>Tetonius</i> sp.	1	1	0	1	1	2&3	0	0	1	1	1
<i>Tetonoides</i> sp.	1	1	1	2	2&3	1	0	0	1	1	1
<i>Trogolemur myodes</i>	0	0	0	0	1	1	0	0	1	1	1
<i>Washakius insignis</i>	1	1	1	2	1&2	2	0	0	1	1	1
<i>Eosimias</i> sp.	0	0	2	0	3	2	2	0	1	1	1
<i>Tarsius</i> sp.	1	9	0	0	1&2	0&1	1	0	1	1	1
<i>Aegyptopithecus zeuxis</i>	9	9	3	3	0	1	2	0	1	1	1
<i>Apidium phiomense</i>	0	9	1	3	1	1	2	0	1	1	1
<i>Arsinoea kallamos</i>	0	9	2	1	0	1	2	0	1	1	1
<i>Catopithecus browni</i>	1	0	2	2	1	1	2	0	1	1	1
<i>Parapithecus fraasi</i>	0	9	2	2	2	3	2	0	1	1	0
<i>Qatrania wingi</i>	0	0	9	9	0&1	0	2	0	1	1	1
<i>Serapia eocaena</i>	0	0	2	0	0	1	2	0	1	1	1
<i>Simonsius grangeri</i>	1	9	2	3	0	2	2	0	1	1	1
<i>Aotus trivirgatus</i>	1	9	2	2&3	0	1&2	9	0	1	1	0
<i>Callicebus moloch</i>	1	9	2	3	0	0	9	0	1	1	0
<i>Dolichocebus gaimanensis</i>	1	9	9	9	0	9	9	0	9	1	9
<i>Saimiri sciureus</i>	1	9	2	3	0	2&3	9	0	1	1	0
<i>Proteopithecus sylviae</i>	9	9	9	9	9	9	9	0	9	9	9
<i>Afrotarsius chatrathi</i>	9	9	9	9	0	9	2	0	1	1	1
<i>Strigorhysis</i> sp.	1	9	0	0	1	3	0	0	1	1	1
<i>Untanius ameghini</i>	1	2	1	1	0	5	0	0	1	1	1

Appendix B *continued*

	67.	68.	69.	70.	71.	72.	73.	74.	75.	76.	77.
Scandentia	1	0	1	1	1	0	0	0	1	0	0
<i>P. tricuspidens/P. jepi</i>	2	1	2	3	3	0	0	1	2	0	0
<i>Purgatorius unio</i>	1	1	2	2	2	0	0	0	1	0	0
<i>Plesolestes problematicus</i>	2	1	3	3	3	0	0	1	2	0	0
<i>Adapis parisiensis</i>	1	1	9	9	9	9	2	9	9	0	9
<i>Cantius/Notharctus</i>	1	1	2	3	3	0&1	0	0&1	1	0	0&1
<i>Donrussellia</i> sp.	1	1	2	2	2	0&1	0	0	1	0	0
<i>Leptadapis magnus</i>	1	1	9	9	9	0	2	0	1	0	2
<i>Mahgarita stevensi</i>	1	1	9	9	9	0	0	0	1	0	9
<i>Aframonius dieides</i>	1	2	9	9	9	0	0	0	1	0	1
<i>Pronycticebus gaudryi</i>	2	1	2	0	0	1	0	0	0	0	0
<i>Protoadapis curvicauspiciens</i>	2	1	1	1	9	0	0	0	1	0	0
<i>Galagoides demidoff</i>	1	1	9	9	9	0	0	0	1	0	0
<i>Lemur catta</i>	2	2	1	9	9	0	2	9	0	0	2
<i>Microcebus murinus</i>	1	1	9	9	9	0	0	0	1	0	1
<i>Nycticebus coucang</i>	1	0	9	9	9	0	0	0	1	0	1
<i>Absarokius</i> sp.	1	0&1	2	3	3	0	0	0	1	0&1	1
<i>Anaptomorphus</i> sp.	1	1	2	3	3	0	0	0	1	0	1
<i>Anemorhysis savagei</i>	1	1	2	3	2	0	0	0	1&2	0	1
<i>Arapahovius gazini</i>	9	1	1&2	3	3	0	0	0	2	2	1
<i>Aycrossia lovei</i>	1	1	2	3	9	1	0	0	2	1&2	0
<i>Dyseolemur pacificus</i>	1	1	1	1	1	1	2	0	1	1&2	1
<i>Hemiacodon gracilis</i>	2	1	9	9	9	0&1	0	0&1	1&2	2	1
<i>Loveina zephyri</i>	1	1	1&2	1&2	1&2	0	0	0	1	0	1
<i>Macrotarsius montanus</i>	1	2	2	2	2	1	1	0	1	1	2
<i>Microchoerus erinaceus</i>	1	1	2	9	9	0	0	0	2	2	2
<i>Nannopithec</i> sp.	1	1	1	1	1	0	0	0	1	0&1	1
<i>Necrolemur antiquus</i>	1	1	2	9	9	0	0	0	1	2	2
<i>Omomys</i> sp.	1	1	2	1	1	0	0	0	1	0	1
<i>Pseudoloris parvulus</i>	1	1	0	0	0	0	0	0	1	0	0
<i>Rooneyia viejaensis</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Shoshonius cooperi</i>	1	1	1&2	1&2	1&2	0&1	2	0	1&2	1&2	1&2
<i>Steinius vespertinus</i>	2	1	2	3	3	0	0	0	1	0	1
<i>Teilhardina americana</i>	1	0	2	3	3	0	0	0	1	0	0
<i>Teilhardina belgica</i>	1	0	2	3	3	0	0	0	1	0	0
<i>Tetonius</i> sp.	1	0	2	3	3	0	0	0	1	0	0
<i>Tetonoides</i> sp.	1	1	1&2	0&1&3	0&1&3	0	0	0	1&2	0	0&1
<i>Trogolemur myodes</i>	1	1	2	3	3	0	0	0	2	0	0
<i>Washakius insignis</i>	1	1	1	1	1	0&1	1&2	1	2	2	1&2
<i>Eosimias</i> sp.	1	0	2	1	1	0	0	0	1	0	0
<i>Tarsius</i> sp.	1	1	1	1	1	0	0	0	1	0	0
<i>Aegyptopithecus zeuxis</i>	1	1	9	9	9	0	0	0	1	0	2
<i>Apidium phiomense</i>	1	1	9	9	9	0	0	0	2	0	2
<i>Arsinoea kallamos</i>	1	0	2	3	9	0	0	0	1	0	2
<i>Catopithecus browni</i>	1	1	1	9	9	0	0	0	1	0	2
<i>Parapithecus fraasi</i>	0	0	9	9	9	0	0	1	1	0	2
<i>Qatrania wingi</i>	0	0	1	9	9	0	0	0	1	0	1
<i>Serapia eocaena</i>	1	0	1	1	1	0	0	0	1	0	2
<i>Simonsius grangeri</i>	0	0	9	9	9	0	0	0	1	0	2
<i>Aotus trivirgatus</i>	1	1	9	9	9	0	0	9	0	0	2
<i>Callicebus moloch</i>	1	1	9	9	9	0	0	9	0	0	2
<i>Dolichocebus gaimanensis</i>	9	9	9	9	9	9	9	9	9	0	2
<i>Saimiri sciureus</i>	0&1	0	9	9	9	0	0	9	0	0	2
<i>Proteopithecus sylviae</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Afrotarsius chatrathi</i>	1	0	1	1	1	0	0	0	1	0	1
<i>Strigorhysis</i> sp.	1	1	9	3	3	9	0	0	2	2	9
<i>Uintanius ameghini</i>	1	1	1	1	9	0	0	0	1	0	0

Appendix B continued

	78.	79.	80.	81.	82.	83.	84.	85.	86.	87.	88.
Scandentia	0	0	1	2	0	0	0	1	3	0	1
<i>P. tricuspidens/P. jepi</i>	0	0	1	2	0	0	0	1	3	1	1
<i>Purgatorius unio</i>	0	0	1	2	0	0	0	1	3	2	1
<i>Plesolestes problematicus</i>	0	0	1	2	0	0	0	1	3	2	2
<i>Adapis parisiensis</i>	0	0	1	0	0	0	0	1	3	1	3
<i>Cantius/Notharctus</i>	0	0	1	2	0	0	0	1	3	2	2
<i>Donrussellia</i> sp.	0	0	1	2	0	0	0	1	3	2	2
<i>Leptadapis magnus</i>	0	0	1	0	0	0	0	1	2	1	3
<i>Mahgarita stevensi</i>	0	9	1	0/1	0	0	0	1	3	2	9
<i>Aframonius dieides</i>	0	0	1	0	0	0	0	1	3	1	2/3
<i>Pronycticebus gaudryi</i>	0	0	1	1	0	0	0	1	3	2	3
<i>Protoadapis curvicaudatus</i>	0	0	1	1	0	0	0	1	3	2	3
<i>Galagoides demidoff</i>	0	0	1	0	0	0	0	1	3	1	3
<i>Lemur catta</i>	0	0	1	1	0	0	0	1	3	2	3
<i>Microcebus murinus</i>	0	0	1	0	0	0	0	1	3	2	3
<i>Nycticebus coucang</i>	0	0	1	0	0	0	0	1	3	2	3
<i>Absarokius</i> sp.	0	0	1	2	0	0	0	1	3	2	2
<i>Anaptomorphus</i> sp.	0	0	1	2	0	0	0	1	3	2	2
<i>Anemorhysis savagei</i>	0	0	1	2	0	0	0	1	3	2	3
<i>Arapahovius gazini</i>	0	0	1	2	0	0	0	1	3	2	2
<i>Aycrossia lovei</i>	0	0	1	2	0	0	0	1	3	2	2
<i>Dyseulemur pacificus</i>	0	0	1	2	0	0	0	1	3	2	2
<i>Hemiacodon gracilis</i>	0	0	1	2	0	0	0	1	3	1	2
<i>Loveina zephyri</i>	0	0	1	2	0	0	0	1	3	2	2
<i>Macrotarsius montanus</i>	0	0&1	1	2	0	0	0	1	3	1	1
<i>Microchoerus erinaceus</i>	1	0	1	2	0	0	0	1	3	2	3
<i>Nannopithecus</i> sp.	0	0	1	1	0	0	0	1	3	2	3
<i>Necrolemur antiquus</i>	0	0	1	2	0	0	0	1	3	2	3
<i>Omomys</i> sp.	0	0	1	2	0	0	0	1	3	2	2&3
<i>Pseudoloris parvulus</i>	0	1	1	1	0	0	0	1	3	2	3
<i>Rooneyia viejaensis</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Shoshonius cooperi</i>	0	0	1	2	0	0	0	1	3	2	2
<i>Steinius vespertinus</i>	0	0	1	2	0	0	0	1	3	2	2&3
<i>Teilhardina americana</i>	0	0	1	2	0	0	0	1	3	2	2&3
<i>Teilhardina belgica</i>	0	0	1	2	0	0	0	1	3	2	2
<i>Tetonius</i> sp.	0	0	1	2	0	0	0	1	3	2	2
<i>Tetonoides</i> sp.	0	0	1	2	0	0	0	1	3	2	2
<i>Trogolemur myodes</i>	0	0	1	2	0	0	0	1	3	2	3
<i>Washakius insignis</i>	0	0	1	2	0	0	0	1	3	2	1
<i>Eosimias</i> sp.	0	0	1	2	0	0	0	1	1	2	2
<i>Tarsius</i> sp.	0	0	1	2	0	0	0	1	3	2	3
<i>Aegyptopithecus zeuxis</i>	1	1	0	0	1	0	0	0	3	0	0
<i>Apidium phiomense</i>	1	1	1	0	1	1	1	0	3	0	0
<i>Arsinoea kallamos</i>	1	0	1	1	0	0	0	1	3	1	1
<i>Catopithecus browni</i>	0	0	0	1	0	0	0	1	3	1	1
<i>Parapithecus fraasi</i>	1	1	1	0	1	1	1	0	3	0	0
<i>Qatrania wingi</i>	1	0	1	1	0	0	0	1	3	0	0
<i>Serapia eocaena</i>	1	0	1	1	0	0	0	1	3	0	0
<i>Simonsius grangeri</i>	1	1	1	0	1	1	1	0	3	0	0
<i>Aotus trivirgatus</i>	0	1	0	0	0	0	0	1	3	2	3
<i>Callicebus moloch</i>	1	1	0	0	0	0	0	1	3	1	1
<i>Dolichocebus gaimanensis</i>	0	9	9	9	9	9	9	1	9	9	9
<i>Saimiri sciureus</i>	0	1	0	0	0	0	0	1	3	2	2
<i>Proteopithecus sylviae</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Afrotarsius chatrathi</i>	0	0	0	2	0	0	0	1	3	2	2
<i>Strigorhysis</i> sp.	0	0	1	2	0	0	0	1	3	2	9
<i>Untanius ameghini</i>	0	0	1	2	0	0	0	1	3	2	2

Appendix B *continued*

	89.	90.	91.	92.	93.	94.	95.	96.	97.	98.	99.
Scandentia	1	2	0	2	1	1	0	0	0	2	2
<i>P. tricuspidens/P. jepi</i>	2	0	1	1	2	1	3	0	0	2	2
<i>Purgatorius unio</i>	1	0	1	2	2	2	3	3	3	2	2
<i>Plesolestes problematicus</i>	2	0	0	1	1	1	3	0	0	2	2
<i>Adapis parisiensis</i>	3	0	9	1	1	1	2	1	1	2	2
<i>Cantius/Notharctus</i>	2	0	2	1	1	1	3	1	1	2	2
<i>Donrussellia</i> sp.	2	0	2	2	1	1	3	0	0	2	2
<i>Leptadapis magnus</i>	2	0	2	1	1	1	2	1	1	2	2
<i>Mahgarita stevensi</i>	9	1	9	1/2	9	1	9	2	2	2	2
<i>Aframonius dieides</i>	2/3	0	1	2	1	1	2/3	2/3	1	2	2
<i>Pronycticebus gaudryi</i>	3	0	9	1	1	0	2	0	9	2	2
<i>Protoadapis curvicspidens</i>	3	2	9	1	2	1	3	1	1	2	2
<i>Galagoides demidoff</i>	3	0	9	2	1	1	0	0	0	2	2
<i>Lemur catta</i>	3	3	9	1	1	1	0	0	0	2	2
<i>Microcebus murinus</i>	3	0	9	1	1	1	0	0	0	2	2
<i>Nycticebus coucang</i>	3	0	9	1	1	1	2	2	2	2	2
<i>Absarokius</i> sp.	2	0	2	1	1	0&1	0	0	1	2	1
<i>Anaptomorphus</i> sp.	2	0	2	1	1	0&1	3	0	2	2	2
<i>Anemorhysis savagei</i>	3	0	9	2	1	0&1	3	0	0	2	2
<i>Arapahovius gazini</i>	2	0	1&2	2	1	1	3	3	0	2	2
<i>Aycrossia lovei</i>	2	0	2	1	1	0&1	3	0	2	2	2
<i>Dyseolemur pacificus</i>	2	0	2	1	1	1	0	0	0	2	2
<i>Hemicacodon gracilis</i>	2	0	1	2	1	1	0/1	1	1	2	2
<i>Loveina zephyri</i>	2&3	0	1&2	2	1	1	0	0	0	2	2
<i>Macrotarsius montanus</i>	1	0	1	2	1	1	0	0	1	2	2
<i>Microchoerus erinaceus</i>	3	0	9	1	1	1	0	0	2	2	2
<i>Nannopithec</i> sp.	3	0	9	1	1	1	3	0	2	2	2
<i>Necrolemur antiquus</i>	3	0	9	1	1	1	3	0	2	2	2
<i>Omomys</i> sp.	2&3	1	1&2	1	0	0	0	0	0	2	2
<i>Pseudoloris parvulus</i>	3	0	9	2	1	1	0	0	0	2	2
<i>Rooneyia viejaensis</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Shoshonius cooperi</i>	2	0	1	2	1	1	3	0	0	2	2
<i>Steinius vespertinus</i>	2&3	1	1&2	1	1	0	1	0	1	2	2
<i>Teilhardina americana</i>	2&3	0	2	2	1	0&1	1	0	0	2	2
<i>Teilhardina belgica</i>	2	0	2	2	1	0&1	1	0	0	2	2
<i>Tetonius</i> sp.	2	0	2	1	1	0&1	0&1&2	0	0	2	2
<i>Tetonoides</i> sp.	2	0	1&2	1	1	0&1	3	0	0	2	2
<i>Trogolemur myodes</i>	3	0	9	1	1	0&1	3	0	0	2	2
<i>Washakius insignis</i>	1	0	1	2	1	1	2	0	1	1	2
<i>Eosimias</i> sp.	2	1	1	2	1	1	0	0	0	2	2
<i>Tarsius</i> sp.	3	1	9	2	0	0	0	0	0	2	2
<i>Aegyptopithecus zeuxis</i>	0	0	1	0	0	0	0	0	0	2	1
<i>Apidium phiomense</i>	0	0	1	0	1	0	0	0	0	0	1
<i>Arsinoea kallamos</i>	1	1	1	0	0	0	9	9	1	2	1
<i>Catopithecus browni</i>	1	1	0	1	0	0	0	0	0	2	1
<i>Parapithecus fraasi</i>	0	1	1	0	1	1	1	0	0	2	1
<i>Qatrania wingi</i>	0	1	1	0	0	0	0	0	0	2	1
<i>Serapia eocaena</i>	0	1	1	0	0	0	0	0	0	2	2
<i>Simonsius grangeri</i>	0	2	1	1	0	0	0	0	0	2	1
<i>Aotus trivirgatus</i>	3	3	9	1	0	0	2	2	2	2	1
<i>Callicebus moloch</i>	1	3	1	1	0	0	2	2	2	2	1
<i>Dolichocebus gaimanensis</i>	9	9	9	9	9	9	9	9	9	2	9
<i>Saimiri sciureus</i>	2	3	1	1	1	0	0	0	1	2	2
<i>Proteopithecus sylviae</i>	9	9	0	9	9	9	9	9	9	9	9
<i>Afrotarsius chatrathi</i>	2	2	1	2	0	0	0	0	0	2	2
<i>Strigorhysis</i> sp.	2	9	2	1	1	0&1	9	0	9	2	2
<i>Uintanius ameghini</i>	9	0	2	2	1	1	0	0	0	2	2

Appendix B continued

	100.	101.	102.	103.	104.	105.	106.	107.	108.	109.	110.
Scandentia	1	1	0	0	1	0	2	2	2	9	9
<i>P. tricuspidens/P. jepi</i>	2	2	0	0	1	1	1	2	2	0	4
<i>Purgatorius unio</i>	2	2	0	0	1	0	1	2	2	2	1
<i>Plesolestes problematicus</i>	2	1	0	0	1	1	2	2	2	9	9
<i>Adapis parisiensis</i>	2	0	0	0	1	9	1	2	2	0	8
<i>Cantius/Notharctus</i>	2	2	0	0	1	1	2	2	2	0	7
<i>Donrussellia</i> sp.	2	2	0	0	1	0&1	1	2	2	0&2	3
<i>Leptadapis magnus</i>	2	0	0	0	1	0	2	2	2	0	7
<i>Mahgarita stevensi</i>	2	2	0	0	1	0	1	2	2	1	7
<i>Aframonius dieides</i>	2	0	0	0	1	0	0	2	2	1	9
<i>Pronycticebus gaudryi</i>	2	1	0	0	1	0	1	2	2	0	7
<i>Protoadapis curvicauspiciens</i>	2	2	0	0	1	1	1	2	2	0	8
<i>Galagoides demidoff</i>	2	2	1	0	1	0	0	2	2	1	1
<i>Lemur catta</i>	2	0	0	0	1	1	0	2	2	2	8
<i>Microcebus murinus</i>	2	2	0	0	1	0	1	2	2	0	0
<i>Nycticebus coucang</i>	2	2	0	0	1	1	0	2	2	1	8
<i>Absarokius</i> sp.	1	2	0	0	1	1	0&1	2	2	2	3
<i>Anaptomorphus</i> sp.	2	1	0	0	1	1	0&1	2	1&2	2	4&5
<i>Anemorhysis savagei</i>	2	2	0	0	1	1	2	2	1	1	1
<i>Arapahovius gazini</i>	2	2	0	0	1	0	2	2	2	1	3
<i>Aycrossia lovei</i>	2	1	0	0	1	1&2	0&1	2	1&2	2	3
<i>Dyseolemur pacificus</i>	2	0	0	0	1	1&2	2	2	2	0	2
<i>Hemicacodon gracilis</i>	2	1	0	0	0	1	2	2	1&2	1	7
<i>Loveina zephyri</i>	2	1	0	0	1	1	1&2	2	2	0	1&2
<i>Macrotarsius montanus</i>	2	2	0	0	1	1	1	2	2	0	7
<i>Microchoerus erinaceus</i>	2	0	0	0	1	1	2	2	2	1	7
<i>Nannopithecus</i> sp.	2	2	0	0	1	1	2	2	2	1	2
<i>Necrolemur antiquus</i>	2	0	0	0	1	1	2	2	2	1	4&5
<i>Omomys</i> sp.	2	1	0	0	1	0&1	1	2	1	1	4
<i>Pseudoloris parvulus</i>	2	1	0	0	1	0	2	2	2	1	0
<i>Rooneyia viejaensis</i>	9	9	9	9	9	9	9	9	9	9	7
<i>Shoshonius cooperi</i>	2	0	0	0	1	1	1	2	2	0	2&3
<i>Steinius vespertinus</i>	2	1	0	0	1	0	2	2	1	1	3
<i>Teilhardina americana</i>	2	2	0	0	1	1	1&2	2	2	1	2
<i>Teilhardina belgica</i>	2	2	0	0	1	1	1	2	2	1	1
<i>Tetonius</i> sp.	2	2	0	0	1	1&2	0&1	2	1&2	2	3
<i>Tetonoides</i> sp.	2	2	0	0	1	1	2	2	1&2	1	0
<i>Trogolemur myodes</i>	2	2	0	0	1	1	2	0	1	0	1
<i>Washakius insignis</i>	2	0	0	0	1	1	1	2	2	0	3
<i>Eosimias</i> sp.	2	1	0	0	1	0	1	1	1	1	1
<i>Tarsius</i> sp.	2	2	0	0	1	1	2	1	1	1	5
<i>Aegyptopithecus zeuxis</i>	1	1	1	0	1	1	1	1	1	1	8
<i>Apidium phiomense</i>	1	1	1	0	1	2	1	2	1	2	8
<i>Arsinoea kallamos</i>	1	2	0	0	1	2	0	1	1	2	4
<i>Catopithecus browni</i>	1	0	0	0	1	0	0	1	1	3	7
<i>Parapithecus fraasi</i>	1	1	1	0	1	2	1	2	1	2	8
<i>Qatrania wingi</i>	1	1	1	0	1	0	1	2	1	0	3
<i>Serapia eocaena</i>	1	0	1	0	1	1	1	1	1	3	7
<i>Simonsius grangeri</i>	1	1	1	0	1	1	1	1	1	2	8
<i>Aotus trivirgatus</i>	0	1	0	0	1	0	0	1	1	3	7&8
<i>Callicebus moloch</i>	0	1	1	0	0	0	0	1	1	3	8
<i>Dolichocebus gaimanensis</i>	9	9	9	9	1	9	0	9	1	9	8
<i>Saimiri sciureus</i>	0	1	0	0	1	1	1	2	1	4	6
<i>Proteopithecus sylviae</i>	9	9	9	9	9	9	9	9	9	3	9
<i>Afrotarsius chatrathi</i>	2	1	0	0	1	0	2	2	2	2	3
<i>Strigorhysis</i> sp.	2	9	0	0	1	2	0&1	2	1&2	1&2	3
<i>Untanius ameghini</i>	2	2	0	0	1	1	1	2	1	9	1

Appendix B *continued*

	133.	134.	135.	136.	137.	138.	139.	140.	141.	142.	143.
Scandentia	2	0	0	2	0	0	1	0	0	1	0
<i>P. tricuspidens/P. jepi</i>	2	9	1	9	1	0	0	1	1	9	0
<i>Purgatorius unio</i>	2	9	1	9	0	0	9	1	1	9	0
<i>Plesolestes problematicus</i>	2	9	2	9	0	1	9	1	1	9	0
<i>Adapis parisiensis</i>	2	1	1	2	2	0	1	1	1	1	0
<i>Cantius/Notharctus</i>	2	0/1	1	2	1	0	0	0	1	1	0
<i>Donrussellia</i> sp.	2	9	1	9	1	0	9	0	0	9	0
<i>Leptadapis magnus</i>	2	0	2	2	2	1	0	1	1	1	0
<i>Mahgarita stevensi</i>	2	0	1	3	1	0	0	0	1	1	0
<i>Aframonius dieides</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Pronycticebus gaudryi</i>	2	9	0	9	1	0	0	0	1	9	0
<i>Protoadapis curvicspidens</i>	2	9	9	9	1	0	9	0	1	9	3
<i>Galagoides demidoff</i>	2	1	1	1	1	1	0	1	0	1	1
<i>Lemur catta</i>	2	0	1	1	0	0	1	0	0	1	0
<i>Microcebus murinus</i>	2	0	1	3	0	0	1	0	0	1	0
<i>Nycticebus coucang</i>	2	2	0	3	1	1	0	0	0	1	1
<i>Absarokius</i> sp.	2	0	3	9	1	0	0	0	0	1	0
<i>Anaptomorphus</i> sp.	2	9	9	9	1	0	9	0	0	9	0
<i>Anemorhysis savagei</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Arapahovius gazini</i>	2	0	0	2	1	0	0	0	0	1	0
<i>Aycrossia lovei</i>	2	0	9	1	9	0	0	9	9	1	0
<i>Dyseolemur pacificus</i>	2	2	0	3	1	0	0	0	0	1	2
<i>Hemiacodon gracilis</i>	2	0/1	0	9	1	0	0	0	0	9	0
<i>Loveina zephyri</i>	2	9	9	9	1	0	9	9	1	9	0
<i>Macrotarsius montanus</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Microchoerus erinaceus</i>	2	0	1	2	2	1	0	0	0	1	1&2
<i>Nannopithec</i> sp.	2	0	1	1	1	0	0	0	0	1	0
<i>Necrolemur antiquus</i>	2	0	1	2	1&2	1	0	0	0	1	1
<i>Omomys</i> sp.	2	0	2	2	1	0	0	0	0	1	0
<i>Pseudoloris parvulus</i>	2	1	0	2	1	0	0	0	0	1	0
<i>Rooneyia viejaensis</i>	2	0	0	9	1	0&1	0	9	1	1	2
<i>Shoshonius cooperi</i>	2	0	1	1	1	0	0	0&1	1	1	0
<i>Steinius vespertinus</i>	2	9	2	9	1	0	0	0	0	9	0
<i>Teilhardina americana</i>	2	9	0&1	9	1	0	0	0	0	9	0
<i>Teilhardina belgica</i>	2	9	0/1	2	1	0	0	0	1	9	0
<i>Tetonius</i> sp.	2	0	2	9	1	0	0	0	0	1	0
<i>Tetonoides</i> sp.	2	9	0/1	9	1	0	0	1	0	9	0
<i>Trogolemur myodes</i>	2	9	9	9	1	0	9	0	9	0	0
<i>Washakius insignis</i>	2	0	1	1	1	0	0	0&1	0	0	2
<i>Eosimias</i> sp.	9	9	9	9	9	9	9	9	9	9	9
<i>Tarsius</i> sp.	2	0	0	3	1	0	1	0	0	1	0
<i>Aegyptopithecus zeuxis</i>	2	0	1	9	1	0	0	0	0	9	2
<i>Apidium phiomense</i>	2	1	1	1	1	0	0	0	0	0	3
<i>Arsinoea kallamos</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Catopithecus browni</i>	2	0	1	9	1	0	0	0	0	1	0
<i>Parapithecus fraasi</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Qatrania wingi</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Serapia eocaena</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Simonsius grangeri</i>	2	0	1	1	1	0	0	0	0	0	0
<i>Aotus trivirgatus</i>	1	2	0&1	0	1	0	0	0	0	0	0
<i>Callicebus moloch</i>	1	1	0	0	1	0	0	0	0	0	3
<i>Dolichocebus gaimanensis</i>	1	9	0	0	1	0	0	0	0	9	2
<i>Saimiri sciureus</i>	1	1	1&2	0	1	0	0	0	0	1	1
<i>Proteopithecus sylviae</i>	2	0	2	0	0	0	0	0	0	1	1
<i>Afrotarsius chatrathi</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Strigorhysis</i> sp.	2	0	2	9	1	0	0	0	0	1	0
<i>Uintanius ameghini</i>	2	9	2	9	0	0	1	0	0	9	0

Appendix B continued

	144.	145.	146.	147.	148.	149.	150.	151.	152.	153.	154.
Scandentia	2	0	1	0	1	0	9	9	0	0	0
<i>P. tricuspidens/P. jepi</i>	0	0	0	1	9	0	9	1	0	0	0
<i>Purgatorius unio</i>	2	0	0	0	9	0	9	9	0	9	0
<i>Plesolestes problematicus</i>	1	0	0	1	9	0	9	9	0	0	1
<i>Adapis parisiensis</i>	2	1	0	1	0	1	1	1	0	0	2
<i>Cantius/Notharctus</i>	2	0&1	0&1	0	1	0	0	1	0	0	0
<i>Donrussellia</i> sp.	2	1	9	9	9	9	9	9	9	9	9
<i>Leptadapis magnus</i>	2	0	0	1	0	1	0	1	0	0	2
<i>Mahgarita stevensi</i>	1	1	1	0	1	1	0	1	0	0	2
<i>Aframomus dieides</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Pronycticebus gaudryi</i>	2	0	0	1	1	0	0	0	0	0	1
<i>Protoadapis curvicaudatus</i>	2	1	0	0	0	0	0	1	0	9	2
<i>Galagoides demidoff</i>	1	1	0	0	1	0	0	0	0	0	1
<i>Lemur catta</i>	2	0	0	1	1	0	0	0	0	0	2
<i>Microcebus murinus</i>	2	0	0	1	0	1	0	1	0	0	1
<i>Nycticebus coucang</i>	2	0	1	1	1	1	0	0	0	0	1
<i>Absarokius</i> sp.	2	0&1	0	0	1	0	1	0	0	0	0
<i>Anaptomorphus</i> sp.	2	0	0	0	9	9	0	9	0	0	9
<i>Anemorhysis savagei</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Arapahovius gazini</i>	2	0	0	0	1	0	0	1	0	0	9
<i>Aycrossia lovei</i>	2	0	0	0	1	0	1	0	0	0	0&1
<i>Dyseolemur pacificus</i>	2	0	0	2	1	0	0	1	0	0	0&1
<i>Hemicacodon gracilis</i>	2	0	0	2	1	0	0&1	1	0	0	1
<i>Loveina zephyri</i>	2	0	9	2	9	0	9	1	0	0	0
<i>Macrotarsius montanus</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Microchoerus erinaceus</i>	2	0	1	0	0	0	0	1	0	0	2
<i>Nannopithecus</i> sp.	2	0	1	0	0	0	0	0	0	0	0&1
<i>Necrolemur antiquus</i>	2	0	1	0	0	0	0	1	0	0	2
<i>Omomys</i> sp.	2	0	0	2	1	0	0	0&1	0	0	1
<i>Pseudoloris parvulus</i>	2	0&1	0	0&2	1	9	0	1	0	0	1
<i>Rooneyia viejaensis</i>	0	0	0	0	1	0	1	0	0	0	1
<i>Shoshonius cooperi</i>	2	0	0	2	1	0	1	1	0	0	0&1
<i>Steinius vespertinus</i>	2	0	1	0	1	0	0	1	0	0	0
<i>Teilhardina americana</i>	2	1	0	0	1	0	9	1	0	0	0
<i>Teilhardina belgica</i>	2	1	0	1	1	0	0	0	0	0	0
<i>Tetonius</i> sp.	2	0&1	0	0	1	0&1	0&1	0&1	0	0	0
<i>Tetonoides</i> sp.	2	0	0	1	1	9	1	1	0	0	9
<i>Trogolemur myodes</i>	2	0	0	9	9	0	9	0	0	0	1
<i>Washakius insignis</i>	2	0	1	1	1	0	0	1	0	0	0&1
<i>Eosimias</i> sp.	9	9	9	9	9	9	9	9	0	9	0
<i>Tarsius</i> sp.	2	1	0	0	1	0	9	9	0	0	1
<i>Aegyptopithecus zeuxis</i>	2	1	0	0	0	1	0	0	0	0	1
<i>Apidium phiomense</i>	0	0	0	0	0	0	0	0	0	0	1
<i>Arsinoea kallamos</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Catopithecus browni</i>	2	0	0	0	1	1	0	1	0	0	1
<i>Parapithecus fraasi</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Qatrania wingi</i>	9	9	9	9	9	9	9	9	0	9	1
<i>Serapia eocaena</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Simonsius grangeri</i>	0	1	0	0	0	0	0	0	0	0	2
<i>Aotus trivirgatus</i>	2	1	0	0	0	0	0	0	1	2	2
<i>Callicebus moloch</i>	2	1	0	0	0	1	0	0	0	1	1&2
<i>Dolichocebus gaimanensis</i>	2	0	1	1	0	1	0	0	0	1	0
<i>Saimiri sciureus</i>	2	1	0	0	0	1	0	0	1	2	0&1
<i>Proteopithecus sylviae</i>	9	0	1	1	1	0	9	1	0	1	0
<i>Afrotarsius chatrathi</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Strigorhysis</i> sp.	2	0	0	0	1	0	1	0	0	0	0
<i>Untanius ameghini</i>	0	1	0	0	1	0	0	0	0	0	1

Appendix B *continued*

	155.	156.	157.	158.	159.	160.	161.	162.	163.	164.	165.
Scandentia	2	0	0	9	0	1	1	1	0	0	0
<i>P. tricuspidens/P. jepi</i>	2	2	0	0	0	2	2	9	0	0	0
<i>Purgatorius unio</i>	2	1	0	0	0	1	1	0	0	0	0
<i>Plesolestes problematicus</i>	2	2	0	0	0	2	2	9	0	0	0
<i>Adapis parisiensis</i>	2	0	0	0	0	0	0	0	0	0	0
<i>Cantius/Notharctus</i>	2	1	0	0	0	2	2	9	0	0	0
<i>Donrussellia</i> sp.	9	9	0	0	9	9	9	9	9	0	9
<i>Leptadapis magnus</i>	2	1	0	0	0	0	1	0	0	0	0
<i>Mahgarita stevensi</i>	2	0	0	0	0	0	0	0	2	0	0
<i>Aframonius dieides</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Pronycticebus gaudryi</i>	2	0	0	0	0	1	1	1	0	0	0
<i>Protoadapis curvicaudatus</i>	9	0	0	9	0	1	1	1	0	9	0
<i>Galagoides demidoff</i>	1	0	0	0	0	0	0	0	1	0	0
<i>Lemur catta</i>	1	0	0	0	0	1	1	1	0	0	9
<i>Microcebus murinus</i>	2	0	0	0	0	1	1	1	0	0	9
<i>Nycticebus coucang</i>	1	0	0	0	0	0	0	1	1	0	0
<i>Absarokius</i> sp.	9	1	0	0	0	2	2	9	0	0	0
<i>Anaptomorphus</i> sp.	9	1	0	0	0	2	2	9	0	0	0
<i>Anemorhysis savagei</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Arapahovius gazini</i>	9	1&2	0	0	0	2	2	9	0	0	0
<i>Aycrossia lovei</i>	9	1	0	0	0	2	2	9	0	0	0
<i>Dyseulemur pacificus</i>	9	1	0	0	0	1	1	1	0	0	0
<i>Hemicacodon gracilis</i>	9	1	0	0	0	1	1	1	0	0	0
<i>Loveina zephyri</i>	9	0&1	0	0	0	2	2	9	0	0	0
<i>Macrotarsius montanus</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Microchoerus erinaceus</i>	2	1	0	1	0	0	0	0	0	0	1
<i>Nannopithecus</i> sp.	1	1&2	0	0	0	1	1&2	0	0	0	0
<i>Necrolemur antiquus</i>	1&2	1	0	1	0	0	0	0	0	1&2	0&1
<i>Omomys</i> sp.	2	0	0	0	0	1	1	1	0	0	0
<i>Pseudoloris parvulus</i>	9	0	0	0	0	0	0	0	1	0	0
<i>Rooneyia viejaensis</i>	9	0	0	0	0	0	0	0	1	0	1
<i>Shoshonius cooperi</i>	9	1	0	0	0	2	2	9	0	0	0
<i>Steinius vespertinus</i>	2	1&2	0	0	0	2	2	9	0	0	0
<i>Teilhardina americana</i>	2	1&2	0	0	0	2	2	9	0	0	0
<i>Teilhardina belgica</i>	9	0	0	0	0	2	2	9	0	0	0
<i>Tetonius</i> sp.	9	1	0	0	0	2	2	9	0	0	0
<i>Tetonoides</i> sp.	9	1	0	0	0	2	2	9	0	0	0
<i>Trogolemur myodes</i>	9	2	0	0	0	2	2	9	0	0	9
<i>Washakius insignis</i>	2	1	0	1	0	1	1	1	0	0	0
<i>Eosimias</i> sp.	2	0	0	0	0	2	2	9	9	9	0
<i>Tarsius</i> sp.	1	0	0	0	0	2	2	9	0	0	0
<i>Aegyptopithecus zeuxis</i>	2	0	0	0	1	0	0	0	0	0	0
<i>Apidium phiomense</i>	2	0	0	0	2	0	0	1	1	0	1
<i>Arsinoea kallamos</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Catopithecus browni</i>	2	0	0	0	0	1	1	0	0	0	9
<i>Parapithecus fraasi</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Qatrania wingi</i>	9	0	0	0	0	0	9	0	0	9	0
<i>Serapia eocaena</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Simonsius grangeri</i>	1	0	0	0	0	0	0	0	0	0	1
<i>Aotus trivirgatus</i>	1	0	0	0	0	0	0	0	2	9	9
<i>Callicebus moloch</i>	1	0	0	0	0	0	0	0	2	2	9
<i>Dolichocebus gaimanensis</i>	2	0	0	9	0	0	0	0	1	9	0
<i>Saimiri sciureus</i>	1	0	0	0	0	0	0	0	1	9	9
<i>Proteopithecus sylviae</i>	1	0	0	0	0	1	1	0	0	0	9
<i>Afrotarsius chatrathi</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Strigorhysis</i> sp.	9	2	0	0	0	2	2	9	0	0	0
<i>Uintanius ameghini</i>	9	0	0	0	0	2	2	9	0	0	0

Appendix B continued

	166.	167.	168.	169.	170.	171.	172.	173.	174.	175.	176.
Scandentia	0	0	0	1	0	2	9	9	9	9	9
<i>P. tricuspidens/P. jepi</i>	1	2	0	1	0	0	2	0	0	9	0
<i>Purgatorius unio</i>	2	0	0	1	0	2	1/2	1	1	9	0
<i>Plesolestes problematicus</i>	1	0	0	1	0	0	2	9	9	9	9
<i>Adapis parisiensis</i>	0	0	0	1	0	2	2	0	0	1	0
<i>Cantius/Notharctus</i>	2	0	0&2	1	0	2	1&2	1	0	0&1	1
<i>Donrussellia</i> sp.	9	9	9	1	9	1	1&2	9	0	9	0
<i>Leptadapis magnus</i>	0	0	1	1	0	2	2	0	0	1	0
<i>Maharita stevensi</i>	1	0	0	1	0	2	2	1	0	0	0
<i>Aframonius dieides</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Pronycticebus gaudryi</i>	1	0	0	1	0	2	2	0	0	9	1
<i>Protoadapis curvicaudatus</i>	0	0	0	0	0	2	1&2	0	0	9	0
<i>Galagoides demidoff</i>	2	0	0	1	0	0	0	0	1	0	1
<i>Lemur catta</i>	0	0	0	1	2	2	0	0	9	0	1
<i>Microcebus murinus</i>	1	0	0	0	0	2	1	0	0	0	0
<i>Nycticebus coucang</i>	1	0	0	1	0	1	2	0	0	0	1
<i>Absarokius</i> sp.	1	0	0	1	0	1	1	1	0	0&1	1&2
<i>Anaptomorphus</i> sp.	1	0	0	1	0	1	1	0	0	0&1	2
<i>Anemorhysis savagei</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Arapahovius gazini</i>	2	0	0	1	0	2	2	1	1	1	1
<i>Aycrossia lovei</i>	1	0	9	1	0	1	1	0	0	0&1	2
<i>Dyseulemur pacificus</i>	2	0	2	1	0	2	2	0	0	0	0
<i>Hemicacodon gracilis</i>	2	0	1	1	0&1	2	2	1	0	2	0
<i>Loveina zephyri</i>	1	2	0	1	0	2	2	0	0	1	0
<i>Macrotarsius montanus</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Microchoerus erinaceus</i>	3	1&2	1	1	0	2	2	0	0	1	1
<i>Nannopithecus</i> sp.	1	2	0	1	0	2	0&1	1	0	0&1	0
<i>Necrolemur antiquus</i>	2	0	1	1	0	2	2	0	0	0	1
<i>Omomys</i> sp.	1	0	0	1	0&1	2	1&2	1	0	1	0
<i>Pseudoloris parvulus</i>	2	0	0	1	0	2	2	1	1	1	0
<i>Rooneyia viejaensis</i>	3	0	2	1	0	1	1	0	0	2	1
<i>Shoshonius cooperi</i>	2	1&2	0	1	1	2	2	0	0	1	0
<i>Steinius vespertinus</i>	1	0	0	1	0	2	2	1	0	0&1	0
<i>Teilhardina americana</i>	1	0	0	1	0	2	2	1	1	0&1	1
<i>Teilhardina belgica</i>	1	0	0	1	0	1	0	1	1	0&1	1
<i>Tetonius</i> sp.	1	0	0	1	0	1	2	1	1	0&1	1
<i>Tetonoides</i> sp.	1	0&1	0	1	0	2	2	1	1	0&1	1
<i>Trogolemur myodes</i>	0/1	0	0	1	0	1	9	1	0	0	2
<i>Washakius insignis</i>	2	2	1	1	1	2	2	0	0	2	0
<i>Eosimias</i> sp.	0	0	0	0	0	2	2	0	0	9	9
<i>Tarsius</i> sp.	1	0	0	0	0	2	1&2	0	0	0	0
<i>Aegyptopithecus zeuxis</i>	1	0	0	0	0	1	1	0	0	0	1
<i>Apidium phiomense</i>	3	0	2	1	2	1	1	0	0	2	1
<i>Arsinoea kallamos</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Catopithecus browni</i>	0	0	0	1	0	2	2	0	0	0	1
<i>Parapithecus fraasi</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Qatrania wingi</i>	2	0	1	9	0	9	0	0	0	9	1
<i>Serapia eocaena</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Simonsius grangeri</i>	2	0	2	1	0	2	1&2	0	0	1	1
<i>Aotus trivirgatus</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Callicebus moloch</i>	2	0	1	1	0	0	0	0	0	0	0
<i>Dolichocebus gaimanensis</i>	0	2	0	0	0	1	1	0	0	0	0
<i>Saimiri sciureus</i>	0	0	0	9	1	9	0&1	0	0	0	0
<i>Proteopithecus sylviae</i>	0/1	0	0	1	0	2	2	0	0	0	0
<i>Afrotarsius chatrathi</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Strigorhysis</i> sp.	1	0	0	1	0	1	1	0	0	0&1	2
<i>Untanius ameghini</i>	2	0	9	9	0	0&1	0&1	0	0	1	0

Appendix B *continued*

	177.	178.	179.	180.	181.	182.	183.	184.	185.	186.	187.
Scandentia	9	9	9	9	9	9	0	9	0	0	0
<i>P. tricuspidens/P. jepi</i>	0	9	0	1	0	1	0	9	9	0	0
<i>Purgatorius unio</i>	9	9	9	1	9	9	9	9	9	9	9
<i>Plesolestes problematicus</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Adapis parisiensis</i>	0	2	0	1	0	2	0	9	1	0	0
<i>Cantius/Notharctus</i>	1	1	0	1	0	1	0	9	9	0	9
<i>Donrussellia</i> sp.	0	9	9	9	0	9	9	9	9	9	9
<i>Leptadapis magnus</i>	0	2	1	1	0	2	9	9	9	9	9
<i>Maharita stevensi</i>	0	2	1	1	0	1	0	9	1	0	0
<i>Aframonius dieides</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Pronycticebus gaudryi</i>	1	2	1	1	0	2	9	9	0	0	0
<i>Protoadapis curviuspidens</i>	0	9	9	1	0	9	9	9	9	9	9
<i>Galagoides demidoff</i>	0	1	0	1	2	0	2	9	1	0	0
<i>Lemur catta</i>	0	1	0	0	0	1	0	9	0	0	0
<i>Microcebus murinus</i>	0	2	0	0	1	1	0	9	0	0	0
<i>Nycticebus coucang</i>	1	1	0	1	2	0	2	9	1	0	0
<i>Absarokius</i> sp.	1	1	0	0&1	0	0	9	9	9	9	9
<i>Anaptomorphus</i> sp.	1	1	9	9	0	1	9	9	9	9	9
<i>Anemorhysis savagei</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Arapahovius gazini</i>	0	1&2	0	9	0	1&2	9	9	9	9	9
<i>Aycrossia lovei</i>	1	1	0	0&1	2	1&2	9	9	9	9	9
<i>Dyseolemur pacificus</i>	9	1	0	1	0	1	9	9	9	9	9
<i>Hemicacodon gracilis</i>	0&1	2	0	1&2	0	1&2	9	9	9	9	9
<i>Loveina zephyri</i>	1	1	0	1	0	2	9	9	9	9	9
<i>Macrotarsius montanus</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Microchoerus erinaceus</i>	0	1	0	1	0	1	9	9	9	9	9
<i>Nannopithec</i> sp.	1	1	0	1	0	1&2	9	9	9	9	9
<i>Necrolemur antiquus</i>	1	1	0	1	0	1	0	9	1	0	0
<i>Omomys</i> sp.	0	2	0	1	0	2	0	9	1	0	0
<i>Pseudoloris parvulus</i>	0	2	0	1	2	2	9	9	9	9	9
<i>Rooneyia viejaensis</i>	0	1	0/1	1&2	0	1	0	9	0	0	0
<i>Shoshonius cooperi</i>	1	1	0	1&2	0	2	0	9	0	0	0
<i>Steinius vespertinus</i>	0	1	0	0&1	0	1	9	9	9	9	9
<i>Teilhardina americana</i>	1	1	0	0&1	0	1	9	9	9	9	9
<i>Teilhardina belgica</i>	0	1	0	0&1	0	0	9	9	9	9	9
<i>Tetonius</i> sp.	1	1	0	0&1	0	1	0	9	9	0	0
<i>Tetonoides</i> sp.	1	1	0	9	9	1&2	9	9	9	9	9
<i>Trogolemur myodes</i>	1	1	0	9	9	1/2	9	9	9	9	9
<i>Washakius insignis</i>	0	1	0	1&2	0	2	9	9	9	9	9
<i>Eosimias</i> sp.	9	9	9	1	9	0	0	9	1	0	9
<i>Tarsius</i> sp.	0	2	0	1	0	2	1	1	0	1	1
<i>Aegyptopithecus zeuxis</i>	2	0	0	0	1	2	1	0	1	9	0
<i>Apidium phiomense</i>	0	0	2	2	1	1	1	1	1	1	9
<i>Arsinoea kallamos</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Catopithecus browni</i>	1	9	9	9	1	2	9	9	1	9	0
<i>Parapithecus fraasi</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Qatrania wingi</i>	9	9	9	1	0	9	9	9	9	9	9
<i>Serapia eocaena</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Simonsius grangeri</i>	1	0	0	1	1	0	9	9	9	9	9
<i>Aotus trivirgatus</i>	1	0	1	0	1	0	1	0	1	1	0
<i>Callicebus moloch</i>	0	0	0	0	2	0	1	0	1	1	0
<i>Dolichocebus gaimanensis</i>	1	1	1	1	2	0	9	9	9	9	9
<i>Saimiri sciureus</i>	0	0	1	0	2	0	1	0	1	1	0
<i>Proteopithecus sylviae</i>	1	0	0	0	1	0	9	9	9	9	9
<i>Afrotarsius chatrathi</i>	9	9	9	9	9	9	9	9	9	9	9
<i>Strigorhysis</i> sp.	1	1	0	1	2	1	9	9	9	9	9
<i>Uintanius ameghini</i>	9	1	0	1	0&1	1&2	9	9	9	9	9

Appendix B *continued*

	287.	288.	289.	290.	291.
Scandentia	0	0	0	0	0
<i>P. tricuspidens/P. jepi</i>	9	9	9	9	9
<i>Purgatorius unio</i>	9	9	9	9	9
<i>Plesolestes problematicus</i>	9	9	9	9	9
<i>Adapis parisiensis</i>	9	9	9	9	9
<i>Cantius/Notharctus</i>	9	9	9	9	9
<i>Donrussellia</i> sp.	9	9	9	9	9
<i>Leptadapis magnus</i>	9	9	9	9	9
<i>Mahgarita stevensi</i>	9	9	9	9	9
<i>Aframonius dieides</i>	9	9	9	9	9
<i>Pronycticebus gaudryi</i>	9	9	9	9	9
<i>Protoadapis curvicspidens</i>	9	9	9	9	9
<i>Galagoides demidoff</i>	1	0	0	0	0
<i>Lemur catta</i>	1	0	0	0	0
<i>Microcebus murinus</i>	1	0	0	0	0
<i>Nycticebus coucang</i>	1	0	0	0	0
<i>Absarokius</i> sp.	9	9	9	9	9
<i>Anaptomorphus</i> sp.	9	9	9	9	9
<i>Anemorhysis savagei</i>	9	9	9	9	9
<i>Arapahovius gazini</i>	9	9	9	9	9
<i>Aycrossia lovei</i>	9	9	9	9	9
<i>Dyseolemur pacificus</i>	9	9	9	9	9
<i>Hemiacodon gracilis</i>	9	9	9	9	9
<i>Loveina zephyri</i>	9	9	9	9	9
<i>Macrotarsius montanus</i>	9	9	9	9	9
<i>Microchoerus erinaceus</i>	9	9	9	9	9
<i>Nannopithecus</i> sp.	9	9	9	9	9
<i>Necrolemur antiquus</i>	9	9	9	9	9
<i>Omomys</i> sp.	9	9	9	9	9
<i>Pseudoloris parvulus</i>	9	9	9	9	9
<i>Rooneyia viejaensis</i>	9	9	9	9	9
<i>Shoshonius cooperi</i>	9	9	9	9	9
<i>Steinius vespertinus</i>	9	9	9	9	9
<i>Teilhardina americana</i>	9	9	9	9	9
<i>Teilhardina belgica</i>	9	9	9	9	9
<i>Tetonius</i> sp.	9	9	9	9	9
<i>Tetonoides</i> sp.	9	9	9	9	9
<i>Trogolemur myodes</i>	9	9	9	9	9
<i>Washakius insignis</i>	9	9	9	9	9
<i>Eosimias</i> sp.	9	9	9	9	9
<i>Tarsius</i> sp.	1	1	1	1	1
<i>Aegyptopithecus zeuxis</i>	0	1	9	9	9
<i>Apidium phiomense</i>	0	9	9	9	9
<i>Arsinoea kallamos</i>	9	9	9	9	9
<i>Catopithecus browni</i>	9	9	9	9	9
<i>Parapithecus fraasi</i>	9	9	9	9	9
<i>Qatrania wingi</i>	9	9	9	9	9
<i>Serapia eocaena</i>	9	9	9	9	9
<i>Simonsius grangeri</i>	9	9	9	9	9
<i>Aotus trivirgatus</i>	0	1	1	1	1
<i>Callicebus moloch</i>	0	1	1	1	1
<i>Dolichocebus gaimanensis</i>	9	9	9	9	9
<i>Saimiri sciureus</i>	0	1	1	1	1
<i>Proteopithecus sylviae</i>	9	9	9	9	9
<i>Afrotarsius chatrathi</i>	9	9	9	9	9
<i>Strigorhysis</i> sp.	9	9	9	9	9
<i>Uintanius ameghini</i>	9	9	9	9	9