

1 Primate Origins and Supraordinal Relationships: Morphological Evidence

Mary T. Silcox · Eric J. Sargis · Jonathan I. Bloch · Doug M. Boyer

Abstract

There are five major scenarios that have been advanced to account for the early events in the origination of the order Primates: a transition from terrestriality to arboreality, the adoption of a grasp-leaping mode of locomotion, the evolution of features for visual predation, an adaptation to terminal branch feeding occurring during angiosperm diversification, or a combination involving terminal branch feeding followed by visual predation. These hypotheses are assessed using both neontological and fossil data. Of the five scenarios, the angiosperm diversification hypothesis is not contradicted by modern data and is found to be the most consistent with the fossil record. In particular, the evolution of features for manual grasping and dental processing of fruit in the earliest primates (primitive plesiadapiforms), and the subsequent development of features for better grasping and more intense frugivory in the common ancestor of Euprimates and Plesiadapoidea, is consistent with a close relationship between early primate and angiosperm evolution. All the other scenarios are less consistent with the pattern of trait acquisition through time observed in the fossil record. Consideration of non-euprimates (e.g., scandentians and plesiadapiforms) is found to be essential to viewing primate origins as an evolutionary process rather than as an event.

1.1 Introduction: what is a primate?

Perhaps the most fundamental issue facing students of primate origins can be summarized by a simple question: what *is* a primate? A clear concept of the diagnosis and taxonomic composition of Primates is essential to providing a coherent understanding of when and why the order separated from the rest of Mammalia. Attempts to define the order Primates have typically started by considering which features of modern primates are present in multiple primate species and are distinctive relative to other mammals. Four major adaptive

complexes of traits have been recognized as characteristic of primates of modern aspect (=Euprimates Hoffstetter 1977; see Mivart 1873; Le Gros Clark 1959; Napier and Napier 1967; Martin 1968, 1986, 1990; Szalay 1968; Cartmill 1972, 1992; Szalay et al. 1987):

- (1) Traits associated with grasping. These include relatively longer hand and foot phalanges, a divergent thumb and big toe, and digits tipped with nails rather than claws.
- (2) Traits associated with leaping. Although such features have been lost in some extant primates (e.g., *Homo sapiens*), the most primitive euprimates have leaping characteristics that include hindlimbs that are long relative to the forelimbs and modified ankle bones.
- (3) Traits associated with improvements to the visual system. These features include large eyes, convergent orbits, and a postorbital bar or septum. The larger and more complex brain of modern primates compared to other euarchontans (see below) may also be associated, in part, with this complex. A smaller apparatus for the sense of smell is presumably associated with an increasing reliance on vision as well, leading to a short snout and proportionally reduced related areas of the brain.
- (4) Dental traits associated with herbivory. Relative to specialized insectivores, primates possess teeth that are low crowned, with blunt and bulbous (bunodont) cusps and broad talonid basins, which are features related to eating non-leafy plant materials (e.g., fruit) rather than insects or meat.

Presence of a petrosal bulla has also often been cited as an ordinal diagnostic primate trait (e.g., Cartmill 1972) but its adaptive significance (if any) is unclear.

Defining the order Primates using observations on living taxa as a starting point is problematic because these traits are unlikely to have evolved simultaneously. Instead, a definition that recognizes the process of primate evolution and that encompasses the earliest, possibly stem, members of the order will have greater explanatory power. We will return to this problem below.

1.2 Ecological scenarios for primate and euprimate origins

Researchers investigating primate origins have typically focused on building an ecological scenario that could explain the evolution of one or more of these adaptive complexes. The earliest such scenario is the arboreal hypothesis of

primate origins, which traces its roots back to the work of G. Elliot Smith and F. Wood Jones in the early part of the twentieth century. The arboreal hypothesis was extended and broadly popularized by W.E. Le Gros Clark (1959). In this hypothesis, grasping extremities were seen as having value for more secure climbing, and the distinctive primate orbital features were explained as being useful for judging distances in the trees during leaping.

All of the other ecological scenarios that have been developed assume a life in the trees for ancestral primates but seek to go beyond simple arboreality to consider more specific types of behavior. Szalay and colleagues (Szalay and Delson 1979; Szalay and Dagosto 1980, 1988; Szalay et al. 1987; Dagosto 1988) considered a derived locomotor mode, grasp-leaping, to have driven the evolution of most of the features that characterize euprimates, including those of the visual apparatus. They linked the ability to rapidly jump from branch to branch with the need to be "... subsequently securely anchored" (Szalay and Delson 1979 p 561) to the landing point. Visual changes were relevant to judging distances in rapid, leaping locomotion (Szalay and Dagosto 1980). In this hypothesis, anatomical changes for grasp-leaping were preceded by a shift to a more herbivorous diet in the primitive primates (i.e., plesiadapiforms) ancestral to Euprimates (Szalay 1968, 1972; Szalay and Dagosto 1980; Szalay et al. 1987).

Cartmill (1972, 1974, 1992) focused on visual predation as key to the origin of Euprimates. The visual predation hypothesis linked visual features beneficial to accurately gauging the distance to prey items with grasping, clawless hands and feet that could provide both a secure hold on narrow supports, and a prehensile apparatus for snatching prey. Because he thought they lacked orbital specializations and grasping features, Cartmill advocated excluding plesiadapiforms from Primates.

Sussman (1991; Sussman and Raven 1978) suggested a link between the origin of Primates and the Cenozoic diversification of angiosperms (i.e., trees that produce fruit and flowers). He agreed with Szalay that a key event in early primate evolution was the invasion of the "arboreal mixed feeding adaptive zones" (Sussman and Raven 1978 p 734) in the Paleocene. This involved increased use of non-leafy plant resources by early primates as angiosperms developed features that made them more tempting to non-insect seed and pollen dispersers, such as specialized flowers and larger fruit. With the appearance of still larger propagative plant organs (e.g., fruit, seeds) near the Paleocene–Eocene boundary, the ancestral Euprimates developed features for entering terminal branches to better exploit these resources.

There are two major classes of data that have been used to assess the relative validity of these various ecological scenarios. The first "tests" various ecological functions assigned to character complexes in the different models using the

comparative method. The second employs the fossil record to document the sequence of anatomical changes that occurred in primate evolution and seeks to tie these changes to adaptive shifts.

1.2.1 Comparative method

Cartmill (1970, 1972, 1974) assessed the then prevalent arboreal hypothesis from the point of view of the diversity of modern arboreal animals. He argued that if living in an arboreal habitat could explain the distinctive features of primates, then these traits should also be found in other arboreal forms, and particularly in the arboreal members of groups that also include terrestrial species. Cartmill found that arboreal animals in general do not have features similar to those seen in modern primates. For example, arboreal squirrels are not more primate-like than terrestrial squirrels in grasping traits, such as a reduction of the claws, or in vision-related features like the degree of orbital convergence. Nonetheless, arboreal squirrels are successful at many of the same behaviors practiced by primates, including making reasonably long jumps and foraging among slender branches. He argued that forward facing orbits, while enhancing stereoscopy, decrease parallax and with it the ability to judge distance at longer ranges. For this reason, orbital convergence is not a very useful trait for gauging distances in a jump but is very effective for visualizing objects close to the face. On the basis of these comparisons, it seems unlikely that the distinctive adaptive complex of euprimates can be simply linked to a shift to an arboreal mode of life.

Cartmill's own hypothesis of primate origins, visual predation, has also been attacked from the standpoint of modern analogy. Garber's (1980) (but see Crompton 1995) work on the tamarin *Saguinus oedipus* revealed a feeding mode similar to that discussed by Cartmill in an animal that possesses claw-like nails. The evolution of claw-like nails in callitrichines, who nonetheless practice visual predation, undermines the association between this feeding behavior and specialized grasping. Sussman (1991) (see also Crompton 1995) pointed out that most living primates are omnivores, not specialized insectivores, and that their methods of prey capture often emphasize scent and hearing over vision—tarsiers have actually been observed to capture their prey with their eyes closed (Niemitz 1979)! Furthermore, many of the insects eaten by extant primates are crawling forms captured on the ground, not flying forms plucked from the air. If living primates are not typically specialized visual predators, it is not clear why we would expect morphologically similar extinct species to be.

Alternatively, some authors (Sussman and Raven 1978; Sussman 1991; Crompton 1995) have sought analogues for early primates among frugivores, such as old world fruit bats. However, Ravosa and Savakova (2004) recently found no relationship between the degree of orbital convergence and the level of frugivory in a broad array of modern taxa. Nonetheless, the absence of primate-like visual features in some modern visual predators (e.g., mongooses and tupaiid treeshrews; Cartmill 1992) suggests that there is no simple relationship between forward facing orbits and this mechanism for prey capture in mammals. A possible “solution” to this criticism, that the euprimate-like mechanism of orbital convergence for prey capture is only needed in nocturnal animals (Allman 1977; Cartmill 1992), would be refuted if the earliest euprimates were not nocturnal (see below).

Sussman’s (1991; Sussman and Raven 1978) angiosperm diversification hypothesis has been criticized based on the lack of an association between the diversification of angiosperms and the evolution of adaptations in arboreal marsupials that converge on those seen in primates (Cartmill 1992). Nonetheless, in a study of the somewhat primate-like South American didelphid marsupial *Caluromys derbianus*, Rasmussen (1990) did find some support for Sussman’s model, in that a substantial part of its diet comes from terminal branch fruit feeding in a manner similar to modern primates. This study additionally provided some support for Cartmill’s model, in that *Caluromys* is also a visual predator that occasionally grasps prey with its hands. However, *Caluromys* does not have particularly convergent orbits (Rasmussen 1990), weakening substantially the link between this anatomical feature and visual predation. Rasmussen’s study can be seen as providing a fifth composite scenario for primate origins that has ancestral primates initially venturing out onto terminal branches to find fruit and other plant parts, with the secondary evolution of features for prey capture to capitalize on the insect resources they found in this milieu (Rasmussen 1990; Cartmill 1992).

The grasp-leaping scenario of primate origins (Szalay and Delson 1979; Szalay and Dagosto 1980, 1988; Szalay et al. 1987; Dagosto 1988) is less susceptible to criticisms based on modern analogy than the other ecological scenarios because it does not depend on a general ecological relationship for its validity. Rather, it stems from a “fossil-first” approach to considering adaptive change, beginning with the evolutionary transitions documented in the fossil record, and then attempting to determine their adaptive meaning in a form-functional context. This highlights a major contrast in approaches to the question of primate origins between the major combatants in the debate. Under Szalay’s approach, the unique origins, constraints, and evolutionary histories of different mammalian

lineages mean that adaptive explanations applied to one group need not apply to any other. Cartmill, however, argues that “[t]he only evolutionary changes we can hope to explain are . . . parallelisms: recurrent modifications that show up over and over again in different lineages for the same structural or adaptive reasons . . .” (Cartmill 1993 p 226).

One problem with Cartmill’s approach is that it assumes that all adaptive shifts of interest must be parallelisms because otherwise there would be no possibility of explaining them. This reflects a more general problem with the use of modern analogy to “test” hypotheses about evolution. Any historical event is by definition a unique occurrence, even if it is more or less similar to other such unique occurrences that have taken place in other lineages. There is no reason to believe that everything that has happened once has necessarily happened twice. The evolutionary process that produced primates began at a unique starting point (i.e., the divergence of this clade from the rest of Mammalia) and finished at a unique endpoint (i.e., the diversity of extant species). The starting point was heavily constrained by the evolutionary history of what went before, and the adaptive significance of the features evident at the current endpoint is dependent not only on the current usage of a given trait, but also on the biological needs of all the animals that existed along the evolutionary lineage leading to a particular modern species. Modern non-primates that appear similar to primates might have passed through series of adaptive stages quite different from those experienced by our distant ancestors and thus may have arrived at their current form by a very different path. For this reason, arguments that ancient marsupials did not acquire their primate-like traits as a result of angiosperm diversification are not directly relevant to the question of whether or not primates did. The study of modern primates, or modern non-primate analogues, in isolation cannot provide a demonstrably accurate picture of the process of primate origins—it can only yield hypotheses that are more or less plausible for subsequent testing by the fossil record.

A somewhat analogous situation occurred in the early history of human paleontology. In the early part of the twentieth century, quite plausible scenarios were proposed that suggested either a large brain or bipedal locomotion as being the first-occurring distinct human trait (Lewin 1987). With the discovery of the australopiths—primitive human ancestors with adaptations for bipedal locomotion but relatively small brains (McHenry and Coffing 2000)—any “brains first” scenario was decisively falsified, no matter how plausible it may have seemed on the surface. And so too must any ecological scenario of primate origins be considered falsified if the predicted pattern of trait acquisition is not matched by the fossil record.

1.2.2 Fossil record

1.2.2.1 Primate supraordinal relationships

The origin of Primates was a process, not a single event. The distinctive primate traits listed in the introduction likely did not arise in an evolutionary instant. If this is true, the elucidation of the adaptive process of primate origins relies centrally on knowing the relationships of taxa at the base of the primate tree to understand the evolutionary steps taken to build the first euprimate.

In recent years, the supraordinal relationships of primates among living mammals have been sought in Archonta, a group named by Gregory (1910) to include primates, dermopterans (flying lemurs or colugos), treeshrews, chiropterans (bats), and elephant shrews. Modern conceptions of Archonta (McKenna 1975; Szalay 1977; Novacek and Wyss 1986; Novacek 1992; McKenna and Bell 1997) exclude elephant shrews but postulate a close evolutionary relationship between the first four groups based on morphological similarities (Silcox et al. 2005). Within Archonta, primates have traditionally been allied with treeshrews, a group that was for many years included in the order Primates (Carlsson 1922; Le Gros Clark 1925, 1926, 1959), but which are now classified in their own order, Scandentia (Butler 1972; McKenna and Bell 1997). Novacek (1992) provided a consensus morphological solution for archontan relationships, with links between Scandentia and Primates on the one hand and Dermoptera and Chiroptera (=Volitantia) on the other.

More recent molecular and morphological studies have questioned this view. Molecular studies have consistently failed to find a close relationship between bats and the other archontans—rather, chiropterans have generally grouped with carnivores and ungulates (Pumo et al. 1998; Miyamoto et al. 2000; Liu et al. 2001; Murphy et al. 2001a, b; Springer et al. 2003, 2004). The other three orders have clustered together in many recent molecular studies (Adkins and Honeycutt 1991; Waddell et al. 1999; Liu et al. 2001; Murphy et al. 2001a, b; Springer et al. 2003, 2004), leading Waddell et al. (1999) to propose the name Euarchonta for a group including Primates, Dermoptera, and Scandentia. Within Euarchonta, consistent molecular support for the traditional grouping of primates and treeshrews has also been lacking, with a Scandentia-Dermoptera (=Sundatheria; Olson et al. 2005) link being supported by several recent analyses (Liu et al. 2001; Murphy et al. 2001a, b; Springer et al. 2003, 2004). If this hypothesis is correct, it implies that the best model for the ancestor of primates based on extant forms is represented by the reconstructed common ancestor of Euarchonta, not by treeshrews in isolation. In particular tupaiids, the diurnal family of treeshrews most often used for comparison to primates (Beard 1993a), become less relevant as

ancestral primate models. The sole living member of the family Ptilocercidae, *Ptilocercus lowii*, is the extant treeshrew closest to the base of Scandentia (Olson et al. 2004, 2005) and shares many more features than tupaiids with dermopterans (Sargis 2001a, 2002a, b, c, d, 2004, in press). These shared features are present in *Ptilocercus* and dermopterans in spite of some fundamental differences between their locomotor modes (gliding in dermopterans, arboreal quadrupedalism in *Ptilocercus*; Sargis 2001a, 2002a, b, c, d, 2004, in press), implying that they may be ancestral for the common ancestor of Sundatheria, or even of Euarchonta. As such, *P. lowii* might provide us with the best living model for the common ancestor of Primates (▶ [Figure 1.1](#)).

■ **Figure 1.1**

Illustration of *P. lowii*, the pen-tailed treeshrew. This arboreal species may be the best living model for the ancestor of Euarchonta and of Primates. Photo by Annette Zitzmann © 1995



Discovery of new fossil specimens has also led to significant challenges to the view of archontan relationships portrayed by Novacek (1992). In 1990, two papers (Beard 1990; Kay et al. 1990) documented specimens of taxa classified in the plesiadapiform family Paromomyidae that were interpreted as providing strong support for a plesiadapiform–dermopteran relationship. Beard (1989,

1990, 1993a, b) even went so far as to postulate that paromomyids and another plesiadapiform family, Micromomyidae, practiced a dermopteran-like, mitten-gliding mode of locomotion.

The relevance of these views to primate origins is related to the systematic position of plesiadapiforms. “Plesiadapiformes” is a paraphyletic grouping of extinct fossil mammals known from the Paleocene and Eocene of North America, Europe, Asia, and possibly Africa (Russell 1964; Beard and Wang 1995; Fu et al. 2002; Smith et al. 2004; Tabuce et al. 2004; Silcox and Gunnell in press). Represented by more than 120 species classified into 11 or 12 families (depending on whether or not the enigmatic African azibiids are included: Silcox 2001; Tabuce et al. 2004), plesiadapiforms represent a very diverse radiation and form a significant component of the faunal record from many Paleocene localities (Rose 1981; Gunnell et al. 1995). The systematic position of plesiadapiforms has been a long-standing matter of debate. Most early workers classified plesiadapiforms in Primates, often specifically in Tarsiidae (Matthew and Granger 1921; Gidley 1923), based largely on dental similarities. More recent workers have often viewed plesiadapiforms as the first radiation of the order Primates, more primitive than any modern group (Szalay and Delson 1979; MacPhee et al. 1983; Szalay et al. 1987). This hypothesized plesiadapiform–euprimate relationship is not without its detractors. Martin (1968) and Cartmill (1972) were the first to seriously question the primate status of plesiadapiforms. In both of these cases, each worker’s emphasis was on forming a clearer definition of the order Primates, rather than providing an outline of primate supraordinal relationships, leaving plesiadapiforms either in limbo or classified as part of a wastebasket “Insectivora.” Such an approach ignores the possibility that identifying ancestral fossil forms would be essential to understanding the adaptive steps leading to the common ancestor of Euprimates.

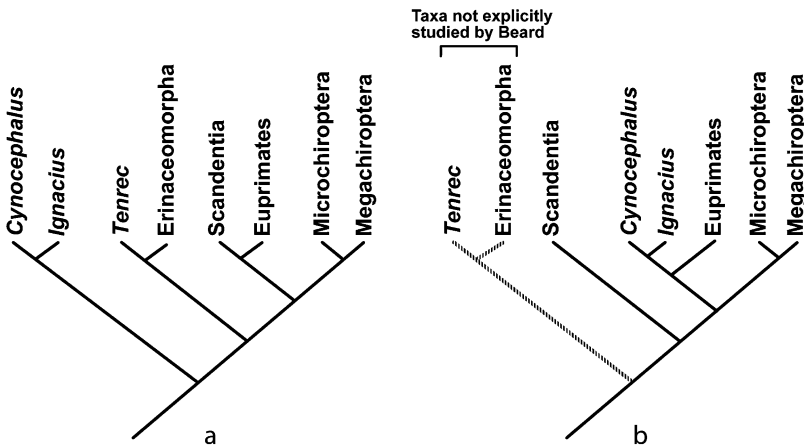
Wible and Covert (1987) also suggested removing plesiadapiforms from the order Primates on the grounds that cranial evidence was more supportive of a scandentian–euprimate tie than a plesiadapiform–euprimate one. They argued that the dental evidence linking plesiadapiforms to euprimates consisted only of ill-defined “trends” (Wible and Covert 1987 p 9). This conclusion was not based on any *detailed* consideration of teeth, however, which is particularly problematic since the euprimate–plesiadapiform relationship had always been supported largely by dental evidence. Furthermore, one of the critical basicranial features that they cited in support of a Scandentia–Euprimates clade excluding plesiadapiforms has since been found in a paromomyid plesiadapiform (a bony tube for the internal carotid nerves and/or artery; Silcox 2003).

Beard’s (1989, 1990, 1993a, b) and Kay et al.’s (1990, 1992) suggestion of a plesiadapiform–dermopteran relationship offered a novel reason for excluding

plesiadapiforms from Primates. Although their papers agreed on the plesiadapiform–dermopteran tie, the analyses performed by these authors produced hypotheses of relationships for the rest of Archonta, including the placement of Euprimates, which were otherwise almost entirely contradictory (► [Figure 1.2](#)).

■ **Figure 1.2**

(a) Kay et al.’s (1992: fig. 11) maximum parsimony cladogram, redrawn with “Euprimates” substituted for their “Primates” following the terminology in use here; (b) relationships of taxa included by Kay et al. taken from Beard’s (1993a: fig. 10.1) analysis. Beard did not explicitly include any lipotyphlan insectivores, implying that he considered them to lie outside of the ingroup. The only areas of congruence between these hypotheses are the monophyly of Chiroptera and the relationship between the paromomyid *Ignacius* and the dermopteran *Cynocephalus*. Otherwise they are entirely in conflict



Kay et al. (1992) failed to support Archonta or Euarchonta, with plesiadapiforms and dermopteran falling outside of lipotyphlan insectivores on their cladogram, and presumably far distant from bats, primates, and treeshrews (► [Figure 1.2a](#)). Likely because of their common focus on cranial data, Kay et al. (1992) agreed with Wible and Covert (1987) that Scandentia is the sister taxon to Euprimates. Beard (1993a; ► [Figure 1.2b](#)), on the other hand, found a close relationship between modern dermopteran and plesiadapiforms (his “Dermoptera”; Beard 1993a, b) and euprimates, a group he named Primatomorpha. The sister group to this clade in Beard’s (1993a) analysis was Chiroptera, with Scandentia falling out as the basal-most group of archontans. These two analyses suggested very different taxa as being central to issues of primate origins—plesiadapiforms and dermopteran on the part of Beard and treeshrews on the part of Kay and colleagues.

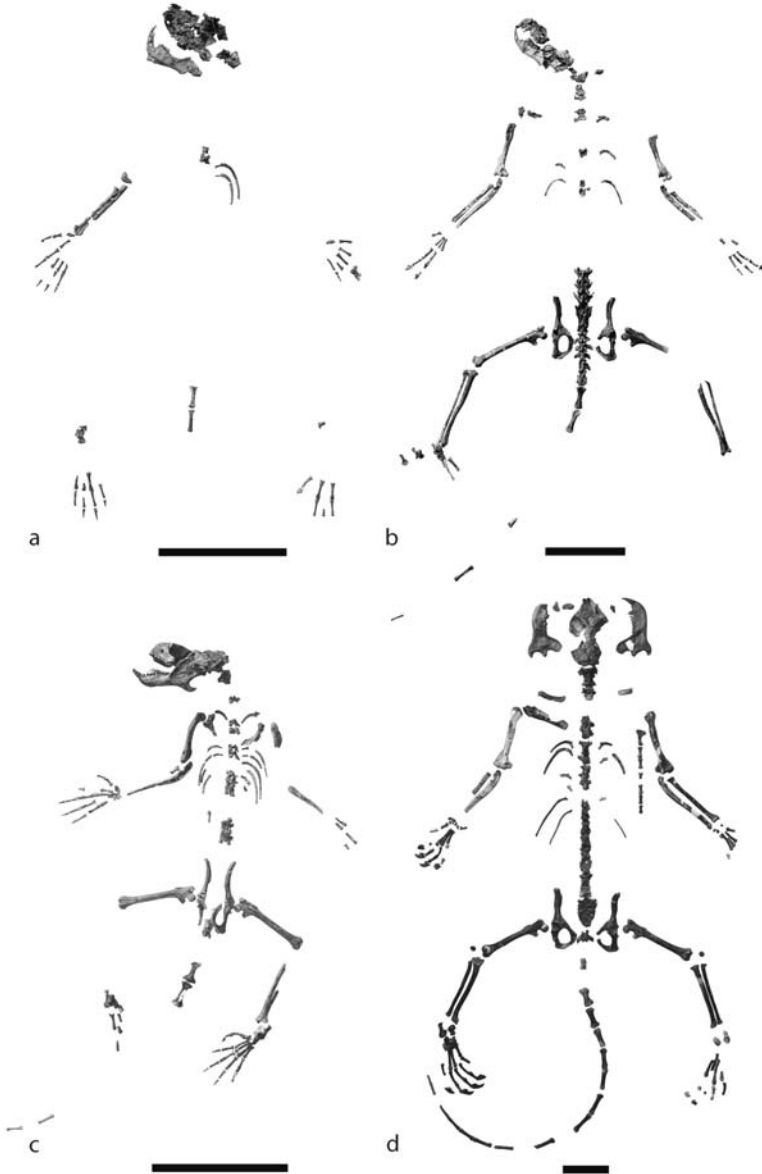
Beard's (1989, 1990, 1993a, b) and Kay et al.'s (1990, 1992) conclusions have been challenged by numerous studies on both phylogenetic and functional grounds (Krause 1991; Szalay and Lucas 1993, 1996; Wible 1993; Wible and Martin 1993; Van Valen 1994; Runestad and Ruff 1995; Stafford and Thorington 1998; Hamrick et al. 1999; Stafford and Szalay 2000; Boyer et al. 2001; Bloch and Silcox 2001, 2006; Silcox 2001, 2003; Bloch and Boyer 2002, 2003; Sargis 2002d, in press; Silcox et al. 2005). Some of the shortcomings identified by these authors include a lack of appropriate sampling of Scandentia (Sargis 2002d, in press), problems with the identifications of specimens (Krause 1991; Hamrick et al. 1999; Boyer et al. 2001), features that were missed or misinterpreted (Simmons 1994; Stafford and Thorington 1998; Bloch and Silcox 2001; Silcox 2001, 2003; Sargis 2002d), and a lack of appropriate character sampling in their almost entire exclusion of dental data and omission of hypothesized volitantian synapomorphies (Silcox 2001; Sargis 2002d, in press; Silcox et al. 2005). Since the publication of Kay et al. (1992) and Beard (1993a, b), numerous new specimens of plesiadapiforms have been uncovered, documenting previously poorly known or totally unknown anatomical regions (Boyer et al. 2001; Bloch and Silcox 2001, 2003, 2006; Bloch and Boyer 2002, 2003; [▶ Figure 1.3](#)). The impact of these specimens also needs to be considered in terms of their relevance to plesiadapiform and euprimate relationships and taxonomy.

Silcox (2001) sought to remedy some of the problems identified above with more extensive character and taxon sampling, including a large dental dataset, inclusion of hypothesized volitantian synapomorphies, reconsideration of all characters, and codings for cranial and dental features of the scandentian *P. lowii*. She examined 181 dental, postcranial, and cranial characters for 85 species. Her results ([▶ Figure 1.4a](#)) supported a plesiadapiform–euprimate relationship to the exclusion of dermopterans. Dermoptera grouped with Chiroptera when bats were included and with Scandentia when Chiroptera was excluded from the analysis. The Dermoptera–Scandentia grouping is also found in many other recent molecular and morphological studies (Liu et al. 2001; Murphy et al. 2001a, b; Springer et al. 2003, 2004; Sargis 2002d, in press).

We have since expanded Silcox's data matrix by including data from new plesiadapiform skeletons, new postcranial characters, and novel postcranial data from *P. lowii* (Bloch and Boyer 2003; see also Bloch et al. 2002, submitted; [▶ Figure 1.4b](#)). This analysis supports a more basal position for micromomyids and a sister group relationship between Plesiadapoidea (including Plesiadapidae, Carpolestidae, Saxonellidae, and the basal form *Chronolestes simul* from Asia) and Euprimates. Thus, this analysis also supports the idea that plesiadapiforms were a paraphyletic stem group at the base of the order Primates. Plesiadapiforms,

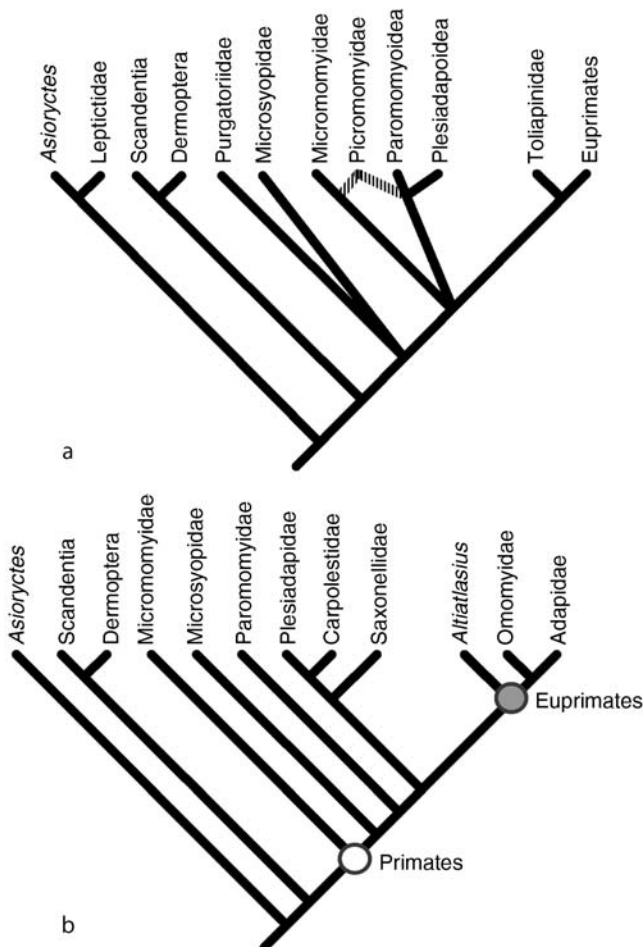
Figure 1.3

Skeletons representing three plesiadapiform families were recovered from Late Paleocene limestones (Bloch and Boyer in press: fig. 3). Paromomyidae is represented by (a) *Acidomomys hebeticus* (UM 108207) and (b) *Ignacius cf. I. graybullianus* (UM 108210). Carpolestidae is represented by (c) *Carpolestes simpsoni* (UM 101963; Bloch and Boyer 2002: fig. 2a). Plesiadapidae is represented by (d) *Plesiadapis cookei* (UM 87990). Scales = 5 cm



■ Figure 1.4

(a) Summary figure from Silcox (2001) based on the Adams consensus tree from a maximum parsimony analysis of 181 dental, cranial, and postcranial characters, excluding chiropterans. In this tree, Euprimates includes (*Altiatlasius*, Omomyidae (Adapidae, and *Altanius*)); Plesiadapoidea includes (*Chronolestes simul* (Saxonellidae (Carpolestidae, Plesiadapidae))); Paromomyoidea includes Picrodontidae, Paromomyidae, and "Palaechthonidae" (a non-monophyletic group); Dermoptera includes Cynocephalidae and Plagiomenidae. (b) Preliminary results from a maximum parsimony analysis of 173 dental, cranial, and postcranial characters by Bloch et al. (Bloch et al. 2002; Bloch and Boyer 2003; Bloch et al. submitted). We consider this tree to be better supported than (a) because it includes data from new plesiadapiform skeletons and more complete data for *Ptilocercus lowii*



and specifically plesiadapoids, are crucial for establishing primitive states for Euprimates in this hypothesis.

One implication of these results is that plesiadapiforms might be best included in the order Primates (Silcox 2001, in press), in a return to earlier

conceptions of how to define the group (Szalay 1975; Szalay and Delson 1979; Szalay et al. 1987). This notion has received some recent support from a previous proponent of the plesiadapiform–dermopteran clade (Kay 2003). The ecological scenarios discussed above take as their starting point the common features of modern primates. Plesiadapiforms do not possess all of these traits. With the recognition that plesiadapiforms constitute the primate stem lineage, discussing “primate origins” then involves dealing with at least two sets of evolutionary transitions—first, the branching off of the primate stem and evolution of the earliest primate (*Purgatorius*; Van Valen and Sloan 1965; Johnston and Fox 1984) and second, the origin of Euprimates. Earlier discussions of “primate origins” that explicitly endeavored to explain only the latter transition (Cartmill 1972; Rasmussen 1990; Sussman 1991) are inherently flawed in trying to account for the concerted evolution of character complexes that did not arise at the same time, mixing the effect of multiple evolutionary transitions. This is true even if one chooses to classify plesiadapiforms as a non-primate sister group to the order.

It is possible to formulate and test predictions about the sequence in which anatomical transformations occurred pursuant to the various ecological scenarios discussed above (Bloch et al., submitted) by the use of the hypothesis of primate supraordinal relationships given in [Figure 1.4b](#). In the same way that “brains first” scenarios of human origins relied on the evolution of large brains before features for bipedalism, so the ecological scenarios of primate origins require a certain order for the addition of traits through time for them to be considered valid.

1.2.2.2 Predictions for ecological scenarios of primate and euprimate origins

Under the arboreal hypothesis, the prediction is inherent in the model that the evolution of characteristically primate traits coincided with a move into an arboreal habitus. If, on the other hand, the ancestors of Primates were already arboreal while lacking such traits, then the arboreal hypothesis would be effectively falsified. It would also be falsified if the evolution of characteristic primate features pre-dated a move to the trees, for example if forward facing orbits were found in an animal otherwise adapted for a terrestrial habitus.

The grasp-leaping hypothesis posits a relationship between the evolution of features for grasping with those for leaping. As such, if grasp-leaping is to function as an explanatory hypothesis for euprimate origins, then the evolution of these features should coincide in time. Visual features for improved stereoscopy should also coincide with the adoption of a more rapid, leaping,

locomotor mode. Although it may still be true that early euprimates were functionally grasp-leapers, if such a coincident evolution of the relevant traits is not found then this hypothesis would lose its explanatory power as a central motivating force in euprimate origins.

Cartmill (1992), in discussing the development of his visual predation hypothesis, wrote,

- ▶ Noting that marked optic convergence is also a characteristic of cats and many other predators that rely on vision in tracking and nabbing prey, Cartmill sought the adaptive significance of this trait in the predatory habits of small prosimian primates like *Microcebus*, *Loris*, and *Tarsius*, which track insect prey by sight and seize them in their hands. Grasping extremities and claw loss, he suggested, had also originated as **predatory adaptations** ... (Cartmill 1992 p 107; emphasis ours)

This statement implies that these features should be tied together temporally, since they were acquired as part of the same adaptive shift to a more predatory pattern of behavior. Kirk, Cartmill, Kay, and Lemelin (2003 p 741b) claimed that Bloch and Boyer (2002) mischaracterized visual predation suggesting that “As originally formulated (Cartmill 1972), Cartmill’s thesis interprets the prehensile, clawless extremities of primates as adaptations for locomotion on slender arboreal supports.” Regardless of these authors’ current opinions, this is directly contradicted by Cartmill’s own account (1992), quoted above, of what he meant when he formulated this hypothesis.

Since visual predation involves an increasing reliance on insect prey, this should also be reflected in the teeth of the earliest euprimates. This is true even if these forms were grasping prey with their hands rather than teeth (contra Cartmill 1972, 1974) because dental features for insectivory reflect not only prey capture but also processing of food items with the unique physical properties of insects. If, however, early primates or euprimates were found to be equally or less insectivorous than their forbears, or a disassociation were to be found between grasping and visual traits, then visual predation would be refuted as a central motivating force in early primate evolution. Since visual predation also relies to some degree on nocturnality (Allman 1977; Cartmill 1992), a finding that the earliest primates or euprimates were diurnal would substantially weaken this hypothesis.

The angiosperm diversification hypothesis predicts two stages in the evolution of primates. First, with the initial exploitation of the arboreal mixed feeding adaptive zone, a dental shift reflecting more use of plant resources should be seen. Second, as the terminal branches were invaded and the use of the food resources from this milieu was intensified, grasping and dental features reflecting these changes should appear. Disassociation between dental traits for eating fruit or

flowers, and those indicating the ability to access terminal branches, would weaken the explanatory power of this hypothesis.

Similarly, the combined hypothesis involving first terminal branch feeding on fruit, and then visual predation, suggested by Rasmussen (1990), requires that “the earliest euprimates had grasping feet and blunt teeth adapted for eating fruit, but retained small, divergent orbits like those of *Plesiadapis*” (Cartmill 1992 p 111). Subsequent evolution should add features for visual predation, such as forward facing orbits and teeth with improved capabilities for processing insects, to this basic model. If, however, convergent orbits evolved at the same time as grasping feet or blunt teeth, or their appearance was not coincident with the evolution of teeth better designed for eating insects, then this model would be effectively falsified.

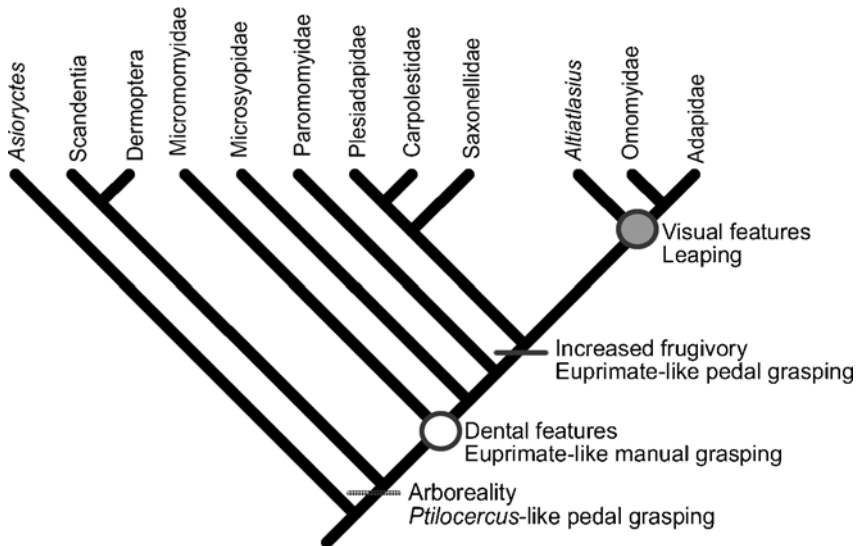
1.2.2.3 Assessment of ecological scenarios

With the well-supported pattern of relationships found by the current authors (🔗 [Figure 1.4b](#)), it becomes possible to consider the predictions outlined above in light of what we know about the fossil record (🔗 [Figure 1.5](#)). In terms of the arboreal hypothesis, the inferred arboreal habits of all plesiadapiforms known from postcranials (Szalay and Decker 1974; Szalay et al. 1975; Szalay and Dagosto 1980; Szalay 1981; Szalay and Drawhorn 1980; Beard 1989; Gingerich and Gunnell 1992; Boyer et al. 2001; Bloch and Boyer 2002, 2003, in press) make it clear that the ancestors of Euprimates were already arboreal. This is further indicated by the inclusion of Primates in Archonta or Euarchonta because this supraordinal group likely had an arboreal ancestor (Szalay and Drawhorn 1980; Sargis 2001a, 2002e). As such, distinctively euprimate traits cannot be linked to a simple move from a terrestrial to an arboreal habitus. The fact that *P. lowii*, an arboreal mammal, may be the best living model for the ancestor of Archonta or Euarchonta and possibly for Primates (Sargis 2001a, 2002e; Bloch et al. 2003), strongly suggests that arboreality is a feature that evolved prior to the base of the primate radiation (Szalay and Drawhorn 1980). Many of the features that have been cited as possible archontan or euarchontan synapomorphies (Szalay and Drawhorn 1980; Szalay and Lucas 1996; Sargis 2002d; Silcox et al. 2005) can also be linked to arboreal locomotion. It is likely that arboreality evolved in the ancestor of Euarchonta (Szalay and Drawhorn 1980; Sargis 2001a, 2002e), and that this trait was retained (but did not originate) in the ancestor of Primates.

The evolution of grasping is central to the assessment of both the grasp-leaping and visual predation hypotheses. With a better fossil record for plesiadapiforms, it is now clear that grasping is not a single character state or set of

■ Figure 1.5

Preliminary results from a maximum parsimony analysis of 173 dental, cranial, and postcranial characters by Bloch et al. (Bloch et al. 2002; Bloch and Boyer 2003; Bloch et al. submitted), with the most significant evolutionary transitions for primates mapped on. "Dental features" include molars that are low crowned, with bunodont cusps and broad talonid basins (all three of which are related to increased herbivory; Szalay 1968), an enlarged M_3 hypoconulid, and a postprotocingulum (=nannopithec or postprotocone fold) on P^4 . Evidence for euprimate-like manual grasping includes an increase in the relative length of the digits. Pedal grasping involves the evolution of a divergent big toe with a nail. Visual features include increased orbital convergence and the postorbital bar. Note that these transitions occur in a step-like fashion, with only visual features and leaping being added at the euprimate node



coordinated transformations. The ancestral euarchontan was likely capable of *Ptilocercus*-like grasping (Szalay and Dagosto 1988; Sargis 2001b, 2002b, e, 2004). As Bloch and Boyer (2002, 2003) demonstrated, the evolution of fully euprimate-like grasping was at least a two-stage process. Features for manual grasping, including relatively long digits of the hand, are present in all plesiadapiforms known from relevant material, with the exception of plesiadapids who have secondarily lost this trait (Bloch and Boyer 2002, 2003; Boyer et al. 2004). Euprimate-like pedal grasping, including a divergent big toe with a nail, is present in *Carpolestes simpsoni*, and can be reconstructed as having evolved in the common ancestor of Plesiadapoidea and Euprimates (Bloch and Boyer 2003).

No plesiadapiforms known show any features associated with specialized leaping (Szalay et al. 1975; Szalay and Dagosto 1980; Beard 1989; Gingerich and Gunnell 1992; Bloch and Boyer 2002, in press). *Carpolestes simpsoni*, for example,

lacks the relatively long legs typically seen in a leaping mammal, indicating that it was a more generalized arboreal quadruped (► [Figure 1.3](#); Bloch and Boyer 2002). The first primate taxa with clear leaping characteristics are early euprimates such as *Cantius* and *Omomys* (Rose and Walker 1985; Anemone and Covert 2000). Although current evidence suggests that leaping and visual traits did evolve at the same time, there is a distinct offset between the evolution of features related to grasping and those for leaping. In light of this, although early euprimates were likely grasp-leapers and leaping may have evolved in the ancestral euprimate (Szalay and Dagosto 1980, 1988; Dagosto 1988), the evolution of grasp-leaping was not the event that shaped the origin of primates or euprimates.

Similarly, no known plesiadapiforms show any of the specialized features of the orbital system that are associated with euprimate-like vision, including a complete postorbital bar, convergent orbits, reduced snout, or an enlarged and reorganized brain (Russell 1964; McKenna 1966; Szalay 1969, 1972; Kay and Cartmill 1977; Kay et al. 1992; Bloch and Silcox 2003, 2006). Therefore, there is an offset between the evolution of grasping and visual features. As such, their coordinated acquisition as part of a shift to a new mode of feeding, visual predation, was not the decisive event in shaping primate or euprimate origins.

It is still possible that adding visual predation to the behavioral repertoire of euprimates was an important event in the evolution of this group, in which grasping features effectively acted as an exaptation (=preadaptation). However, there is evidence that leads one to doubt this scenario, however. First, as discussed above, visual predation becomes mechanistically implausible if the earliest euprimates were diurnal (Allman 1977; Cartmill 1992). Ni et al. (2004) recently published a primitive euprimate skull from Asia that they interpreted as having been diurnal. Although there are some problems with this conclusion (Heesy and Ross 2004; Martin 2004; Bloch and Silcox 2006), it draws attention to the fact that the ancestral activity period for euprimates remains a matter of debate. Second, if euprimates did undergo a transition to becoming more focused on visual predation, then they should have teeth that are indicative of a more insectivorous diet than their precursors. This is not demonstrably true. The earliest known euprimate, *Altiatlasius koulchii*, has extremely low-crowned teeth with very bunodont cusps (Sigé et al. 1990), which is not consistent with a predominantly insectivorous diet. Of the two best-documented groups of early euprimates, adapids are usually viewed as being frugivorous and omomyids as omnivorous or frugivorous (Rose 1995; Strait 2001). The only gut contents known for a primitive fossil primate (from the adapid *Godinotia* from Messel) include fruit remains and no insects. This is likely a real reflection of diet rather than a taphonomic artifact because in other Messel specimens insect remains preserve well (Franzen and Wilde 2003).

Cartmill (1972) attempted to counter this objection by arguing that features such as lower crowned teeth and a reduced styler shelf, interpreted as being associated with a more herbivorous diet (Szalay 1968), do not "... contradict the hypothesis that the ancestral primates were primarily insectivorous" (Cartmill 1972 p 117). Although it is certainly very probable that early euprimates ate some insects, as do all modern small primates (Fleagle 1999), this observation is irrelevant for two reasons. First, the key information for assessing evidence for an evolutionary transition is not static reconstruction of diet but verification of a *change* in diet. Just demonstrating that early euprimates ate some insects is not sufficient—if visual predation is to be supported as an important formative force in euprimate evolution, a shift to greater insectivory must be demonstrated. Unambiguous evidence for such a shift is lacking from the fossil record.

Second, the relevant comparative sample for early euprimates is not living primates but contemporary insectivores. If early euprimates were succeeding and diversifying primarily because they were improving their insect-harvesting abilities, then they should show dental features that indicate that they were at least as well adapted for processing insects as insectivorous mammals living at the same time. This is not the case—most specialized insectivores from the Paleocene and Eocene have much higher crowned teeth and sharper cusps than early primates. It is precisely the absence of such features and the presence of characteristics for processing non-leafy plant material, such as low-crowned molars with broad talonid basins, which make it possible to separate primitive primate and insectivoran teeth in the fossil record. The insectivorans most similar to primates in dental form can be reconstructed as having a more omnivorous diet than their specialized insectivorous kin. For example, the erinaceomorph *Macrocranium tupaiodon* from Eocene deposits at Messel, which has superficially primate-like teeth, is known from stomach contents to have eaten not only insects but also plant material and substantial quantities of fish (Storch and Richter 1994).

The features suggesting a more herbivorous diet in early primates and euprimates are supportive of the angiosperm diversification hypothesis. Since fully euprimate-like pedal grasping pre-dates the origin of Euprimates, the pattern of acquisition of adaptive features does not match precisely the timing of events envisioned by Sussman (1991; Sussman and Raven 1978). Nonetheless, his main points do still have merit. The origin of the order Primates is associated with dental changes for increased herbivory (Szalay 1968). This was likely associated with specializations for terminal branch feeding, including grasping traits, in an omnivorous animal. Within various plesiadapiform lineages and early euprimate groups, improved features for exploiting plant propagative organs continue to appear through the Paleocene and Eocene (Gingerich 1976; Biknevicius 1986; Rose 1995; Bloch and Boyer 2002).

The one major shortcoming of the angiosperm diversification hypothesis is that it may fail to explain the rest of the distinctive traits seen in modern primates (i.e., visual features and leaping). Sussman (1991 p 219) did try to build an explanation for visual traits into his ideas by linking the manipulation of small food items in low light conditions and on tenuous substrates to a need for “acute powers of discrimination and precise co-ordination.” The lack of evidence in modern analogues such as bats for a solid link between frugivory and convergent orbits has led to this view largely being discounted (Ravosa and Savakova 2004). However, perhaps modern models, such as bats, are not appropriate for comparisons to early euprimates, who undoubtedly used a different feeding mode. As Crompton (1995 p 18, emphasis his) pointed out, euprimate visual traits may have evolved for their power in breaking crypsis (i.e., picking out camouflaged food items from the background), and as such could have been beneficial in allowing detection of the “small, *and often very inconspicuous*” food items taken by small primates. In terms of leaping, Rasmussen’s (1990 p 273) observations of *Caluromys* also offer a potential explanation for the value of this locomotor mode to a terminal branch feeder: “The grasping and leaping acrobatics exhibited by *C. derbianus* in Costa Rica enabled them to gain access to fruit that was apparently off limits to most of the other nocturnal frugivores of the study area.” Perhaps it was refinements to terminal branch feeding techniques, offering new access to previously inaccessible food sources and greater abilities for discriminating food choice, which marked the transition to Euprimates. This would only be a difference from Sussman’s scenario in the traits that are emphasized, not in the ecological events that were key.

Rasmussen’s combination hypothesis could be seen as offering an alternative to the angiosperm origins scenario that explains first the grasping and fruit-eating dental features of basal primates and then the visual characteristics of euprimates. However, this combination hypothesis suffers from the same problems as visual predation in linking the evolution of orbital traits to increased insectivory in the absence of evidence for such a dietary shift. On the basis of the current evidence, the angiosperm diversification hypothesis applies best to the evolution of early primates. Furthermore, Szalay’s (1968) view of the key event in primate origins being a dietary transition to a more plant-dominated repertoire is also supported by the current evidence.

1.3 Timing and place of origin of primates and euprimates

The earliest occurring primate known is *Purgatorius*, from either the latest Cretaceous (Van Valen and Sloan 1965; Van Valen 1994) or earliest Paleocene

(Johnston and Fox 1984; Lofgren 1995) of North America. Most of the rest of the early primate fossil record is North American, including all definitive micro-momyids and palaechthonids, most microsyopids, and all the most primitive paromomyids, carpolestids, plesiadapids, and possibly saxonellids (Fox 1991). Plesiadapiforms have only been known from Asia since 1995 (Beard and Wang 1995), which suggests that this geographic bias may be a sampling phenomenon. However, the lack of Asian (or European or African) taxa as primitive as *Purgatorius* is supportive of a North American origin for the order Primates (Bloch et al. submitted).

In terms of the place of origin of Euprimates, Beard (1998) argued that it could be reconstructed as unequivocally Asian. We view this assertion as excessively confident. Silcox (2001) reached a very different conclusion, with origins in Asia, Africa, North America, or even Europe being possible in the context of the current record. Causes for this equivocation include the African location of the earliest known euprimate, *Altiatlasius koulchii*, the Asian location of the primitive euprimate *Altanius orlovi*, the North American location of much of the primitive plesiadapoid and euprimate record, and the European location of both some early euprimates (*Donrussellia*) and of the poorly sampled plesiadapiform family Toliapinidae, which may be related to early euprimates (Silcox 2001; [▶ Figure 1.4a](#)).

The time of origin of the two major clades under discussion here (Primates and Euprimates) can only be minimally constrained using fossil data. As noted above, the earliest known primate, *Purgatorius*, is approximately 65 Myr old. In light of the primitive nature of this taxon, the fossil record is not consistent with a date much earlier than this, putting the origin of the group in the latest Cretaceous, somewhat later than even the most conservative molecular estimates (Springer et al. 2003). The earliest occurring euprimate, *Altiatlasius koulchii*, is Late Paleocene in age (Sigé et al. 1990; Gheerbrant et al. 1998), implying a divergence for euprimates before the Early Eocene. Furthermore, since the sister group to Euprimates (i.e., Plesiadapoidea) had diverged from their common stem by the latest Early Paleocene, Euprimates must be at least that old.

1.4 Conclusions: what is a primate? (Coda)

When Cartmill developed the visual predation hypothesis, he suggested the removal from Primates of any taxa that lacked modern primate-like orbital and grasping features, and thus presumably had not used this mode of feeding (Cartmill 1972, 1974, 1992). This was the primary basis for Cartmill's suggested removal of plesiadapiforms from Primates. Such an approach to defining Primates was perhaps an overoptimistic view of the support for visual predation—if,

as suggested here, an evolutionary transition to this pattern of behavior is not clearly indicated by the fossil record, then this is surely not an appropriate criterion by which to determine inclusion or exclusion of taxa in the order Primates. This view is underscored by the fact that of the three “ordinally diagnostic” traits that Cartmill (1972 p 121) named to diagnose a plesiadapiform-free order Primates—“. . . the petrosal bulla, complete postorbital bar, and divergent hallux or pollex bearing a flattened nail . . .”—two are now known in plesiadapoid plesiadapiforms (Bloch and Boyer 2002, 2003; Bloch and Silcox 2006). The fossil record demonstrates that the characteristic primate traits listed in the introduction arose in a step-like fashion (▶ [Figure 1.5](#)). Thus, the criterion that all of these features must be present in a particular taxon for it to be considered a primate is biologically unnatural. Doing so would exclude taxa on the primate stem who have some, but not all, of these traits, but who postdate the divergence of the primate lineage from the rest of Mammalia. As demonstrated above, such stem taxa are critical for understanding the origin and early evolution of Primates, as well as the accumulation and modification of crucial features within this lineage.

As advocates of phylogenetic taxonomy have made clear, there are some distinct advantages to formal taxonomic definitions that are based on specifying a particular ancestor rather than on a list of mutable characters (Rowe 1987; De Queiroz and Gauthier 1990; Silcox in press). For this reason, although compiling lists of distinctive primate traits is useful to the process of understanding primate origins, it is inappropriate to consider them formal definitions. Using the precepts of phylogenetic taxonomy, Silcox (in press) suggested the following definition for Primates: “the clade stemming from the most recent common ancestor of *Purgatorius* and Euprimates.”

New discoveries will almost certainly change our views on the early parts of primate evolution. There are a number of substantial holes in the fossil record for primate origins, which when filled may fundamentally shift our perceptions of primate evolutionary history. First, there is a sizeable spatial discontinuity in the fossils currently available. Plesiadapiforms have only been discovered in Asia in the last 10 years (Beard and Wang 1995). Since we consider *Altiatlasius* to be a euprimate, the only potential plesiadapiforms from Africa are the poorly known *Azibius* and *Draolestes* (Tabuce et al. 2004). For early euprimates, the few specimens of primitive forms known from Asia and Africa are suggestive of a much larger radiation that is almost completely unknown (Silcox 2001). Even in North America, the geotemporal patterning of the plesiadapiform and euprimate fossil records means that there are still substantial areas at crucial times that remain unsampled.

Second, some taxonomic groups are also undersampled. Two families of plesiadapiforms, Palaechthonidae and Toliapinidae, have the potential to be crucial to an understanding of early primate and euprimate evolution, but both are very poorly known. The best-known plesiadapoids are all relatively derived members of their respective families. In light of the important position of Plesiadapoidea, as the sister taxon to Euprimates, finding more, and more complete, primitive plesiadapoid specimens is vital (Boyer et al. 2004). Perhaps most importantly, a gap still exists between the known plesiadapiforms and the earliest euprimates. No known plesiadapoid has the morphology that would be expected in a euprimate ancestor—they are all too derived in features such as dental reduction, enlargement of the anterior-most incisors, and/or the shape of P_4 . Because the earliest plesiadapoids are late Early Paleocene in age, Euprimates must have a ghost lineage stretching through the Middle and Late Paleocene, which is entirely unsampled. Filling this particular gap will be central to clarifying the evolutionary and adaptive significance of traits for euprimate-like vision and leaping. In light of the complete absence of taxa to fill this gap from the comparatively well-sampled North American record, it seems most plausible that they were living in the Old World.

Finally, since understanding the supraordinal relationships of Primates is central to reconstructing events at the base of the order, a better fossil record for other euarchontan groups is also central to the problem of primate origins. As it stands, the Paleogene fossil record for scandentians and dermopterans is virtually nonexistent, with the exception of a single dermopteran specimen from the Eocene of Thailand (Ducrocq et al. 1992), fragments of scandentian teeth from the Eocene of China (Tong 1988), and plagiomenids, which may be fossil dermopterans. Furthermore, a better understanding of various other fossil groups for whom a tie to Archonta, or specifically to Primates, has been suggested (apatemyids, nyctitheriids, mixodectids; Szalay and Lucas 1996; Hooker 2001; Silcox 2001; Silcox et al. 2005), has the potential to further clarify the evolutionary events downstream from Primates in the euarchontan evolutionary tree.

Although this discussion of holes in the fossil record may seem disheartening, the enormous progress that has been made in the last 10 years for our understanding of primate origins suggests we may not have to wait long for some of these holes to be filled. We have moved from a position analogous to that of early anthropologists arguing about whether brains or bipedalism arose first in human evolution, without having any relevant data to choose between the two, to being able to actually test hypotheses about the order of acquisition of traits in early primate evolution. We can only hope that continuing diligence on the part of researchers interested in primate origins will serve to fill some of these

gaps and allow us to continue expanding our knowledge of the earliest chapters in our own evolution.

Acknowledgments

Our thanks to P.D. Gingerich, K.D. Rose, F.S. Szalay, A.C. Walker, and J.G. Fleagle for conversations relevant to this chapter. We thank Annette Zitzmann for providing the photo of *Ptilocercus* in [▶ Figure 1.1](#). Research was funded by grants from NSERC, Wenner-Gren, the Paleobiological Fund, Sigma Xi, NSF (SBR-9815884), and the University of Winnipeg to MTS; NSF (BCS-0129601) to G.F. Gunnell, P.D. Gingerich, and JIB; NSF (SBR-9616194), Field Museum of Natural History, Sigma Xi, and the Yale University Social Science Faculty Research Fund to EJS; 2002 NSFGRF to DMB.

References

- Adkins RM, Honeycutt RL (1991) Molecular phylogeny of the superorder Archonta. *Proc Natl Acad Sci USA* 88: 10317–10321
- Allman J (1977) Evolution of the visual system in the early primates. *Prog Psychobiol Physiol Psychol* 7: 1–53
- Anemone RL, Covert HH (2000) New skeletal remains of *Omomyx* (Primates, Omomyidae): functional morphology of the hindlimb and locomotor behavior of a middle Eocene primate. *J Hum Evol* 38: 300–328
- Beard KC (1989). Postcranial anatomy, locomotor adaptations, and paleoecology of Early Cenozoic Plesiadapidae, Paromomyidae, and Micromomyidae (Eutheria, Dermoptera). Ph.D. dissertation, Johns Hopkins University School of Medicine, Baltimore Maryland
- Beard KC (1990) Gliding behavior and palaeoecology of the alleged primate family Paromomyidae (Mammalia, Dermoptera). *Nature* 345: 340–341
- Beard KC (1993a) Phylogenetic systematics of the Primatomorpha, with special reference to Dermoptera. In: Szalay FS, Novacek MJ, McKenna MC (eds) *Mammal phylogeny: placentals*. Springer-Verlag, New York, pp 129–150
- Beard KC (1993b) Origin and evolution of gliding in Early Cenozoic Dermoptera (Mammalia, Primatomorpha). In: MacPhee RDE (ed) *Primates and their relatives in phylogenetic perspective*. Plenum Press, New York, pp 63–90
- Beard KC (1998) East of Eden: Asia as an important center of taxonomic origination in mammalian evolution. In: Beard KC, Dawson MR (eds) *Dawn of the age of mammals in Asia*. *Bull Carnegie Mus Nat Hist* 34: 5–39
- Beard KC, Wang J (1995) The first Asian plesiadapoids (Mammalia: Primatomorpha). *Ann Carnegie Mus* 64: 1–33
- Biknevicius AR (1986) Dental function and diet in the Carpolestidae (Primates, Plesiadapiformes). *Am J Phys Anthropol* 71: 157–171
- Bloch JJ, Boyer DM (2002) Grasping primate origins. *Science* 298: 1606–1610
- Bloch JJ, Boyer DM (2003) Response to comment on “Grasping primate origins”. *Science* 300: 741c
- Bloch JJ, Boyer DM (in press) New skeletons of Paleocene-Eocene Plesiadapiformes: a diversity of arboreal positional behaviors in early primates. In: Ravosa MJ, Dagosto M (eds)

- Primate origins and adaptations: a multidisciplinary perspective. Plenum Press, New York
- Bloch JI, Silcox MT (2001) New basicrania of Paleocene-Eocene *Ignacius*: re-evaluation of the plesiadapiform-dermopteran link. *Am J Phys Anthropol* 116: 184–198
- Bloch JI, Silcox MT (2003) Comparative cranial anatomy and cladistic analysis of Paleocene primate *Carpolestes simpsoni* using ultra high resolution X-ray computed tomography. *Am J Phys Anthropol* 120(S1): 68
- Bloch JI, Silcox MT (2006) Cranial anatomy and relationships of Paleocene plesiadapiform *Carpolestes simpsoni* (Mammalia, Primates) using ultra high-resolution X-ray computed tomography. *J Hum Evol* 50: 1–35
- Bloch JI, Silcox MT, Sargis EJ (2002) Origin and relationships of Archonta (Mammalia, Eutheria): re-evaluation of Eudermoptera and Primatomorpha. *J Vert Paleontol* 22(Suppl. to 3): 37A
- Bloch JI, Boyer DM, Houde P (2003) New skeletons of Paleocene-Eocene micromomyids (Mammalia, Primates): functional morphology and implications for euarchontan relationships. *J Vert Paleontol* 23(Suppl. to 3): 35A
- Bloch JI, Silcox MT, Boyer DM, Sargis EJ (submitted) New Palaeocene skeletons root the primate tree
- Boyer DM, Bloch JI, Gingerich PD (2001) New skeletons of Paleocene paromomyids (Mammalia, ?Primates): were they mitten gliders? *J Vert Paleontol* 21(Suppl. to 3): 35A
- Boyer DM, Bloch JI, Silcox MT, Gingerich PD (2004) New observations on the anatomy of *Nannodectes* (Mammalia, Primates) from the Paleocene of Montana and Colorado. *J Vert Paleontol* 24(Suppl. to 3): 40A
- Butler PM (1972) The problem of insectivore classification. In: Joysey KA, Kemp TS (eds) *Studies in vertebrate evolution*. Oliver and Boyd, Edinburgh, pp 253–265
- Carlsson A (1922) Über die Tupaiidae und ihre Beziehungen zu den Insectivora und den Prosimiae. *Acta Zool* 3: 227–270
- Cartmill M (1970) The orbits of arboreal mammals: a reassessment of the arboreal theory of primate evolution. Ph.D. dissertation. University of Chicago, Chicago Illinois
- Cartmill M (1972) Arboreal adaptations and the origin of the order Primates. In: Tuttle R (ed) *The functional and evolutionary biology of primates*. Aldine-Atherton, Chicago, pp 97–122
- Cartmill M (1974) Rethinking primate origins. *Science* 184: 436–443
- Cartmill M (1992) New views on primate origins. *Evol Anthropol* 1: 105–111
- Cartmill M (1993) A view to a death in the morning: hunting and nature through history. Harvard University Press, Cambridge
- Crompton RH (1995) “Visual predation,” habitat structure, and the ancestral primate niche. In: Alterman L, Doyle GA, Izard MK (eds) *Creatures of the dark: the nocturnal prosimians*. Plenum Press, New York, pp 11–30
- Dagosto M (1988) Implications of postcranial evidence for the origin of euprimates. *J Hum Evol* 17: 35–56
- De Queiroz K, Gauthier J (1990) Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. *Syst Zool* 39: 307–322
- Ducrocq S, Buffetaut E, Buffetaut-Tong H, Jaeger J-J, Jongkanjanasoontorn Y, Suteethorn Y (1992) First fossil flying lemur: a dermopteran from the Late Eocene of Thailand. *Palaeontol* 35: 373–380
- Fleagle JG (1999) *Primate adaptation and evolution*, vol. 2. Academic Press, San Diego
- Fox RC (1991) *Saxonella* (Plesiadapiformes: ? Primates) in North America: *S. naylori*, sp. nov., from the late Paleocene of Alberta, Canada. *J Vert Paleontol* 11: 334–349
- Franzen JL, Wilde V (2003) First gut content of a fossil primate. *J Hum Evol* 44: 373–378
- Fu J-F, Wang J-W, Tong Y-S (2002) The new discovery of the Plesiadapiformes from the early Eocene of Wutu Basin, Shandong Province. *Vert Palasiat* 40: 219–227
- Garber P (1980) Locomotor behavior and feeding ecology of the Panamanian tamarin (*Saguinus oedipus geoffroyi*, Callitrichidae, Primates). *Int J Primatol* 1: 185–201
- Gheerbrant E, Sudre J, Sen S, Abrial C, Marandat B, Sigé B, Vianey-Liaud M (1998)

- Nouvelles données sur les mammifères du Thanétien et de l'Yprésien du Bassin d'Ouarzazate (Maroc) et leur contexte stratigraphique. *Palaeovertebrata* 27: 155–202
- Gidley JW (1923) Paleocene primates of the Fort Union, with discussion of relationships of Eocene primates. *Proc US Natl Mus* 63: 1–38
- Gingerich PD (1976) Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). *Univ Mich Pap Palaeontol* 15: 1–141
- Gingerich PD, Gunnell GF (1992) A new skeleton of *Plesiadapis cookei*. *The Display Case* 6: 1–2
- Gregory WK (1910) The orders of mammals. *Bull Am Mus Nat Hist* 27: 1–524
- Gunnell GF, Morgan ME, Maas MC, Gingerich PD (1995) Comparative paleoecology of Paleogene and Neogene mammalian faunas: trophic structure and composition. *Palaeogeogr Palaeoclimatol Palaeoecol* 115: 265–286
- Hamrick MW, Rosenman BA, Brush JA (1999) Phalangeal morphology of the Paromomyidae (?Primates, Plesiadapiformes): the evidence for gliding behavior reconsidered. *Am J Phys Anthropol* 109: 397–413
- Heesy C, Ross C (2004) The nocturnal origin of the Order Primates. *J Vert Paleontol* 24 (Suppl. to 3): 69A
- Hoffstetter R (1977) Phylogénie des primates. *Bull Mém Soc Anthropol Paris* t4, série XIII: 327–346
- Hooker JJ (2001) Tarsals of the extinct insectivoran family Nyctitheriidae (Mammalia): evidence for archontan relationships. *Zool J Linn Soc* 132: 501–529
- Johnston PA, Fox RC (1984) Paleocene and late Cretaceous mammals from Saskatchewan, Canada. *Palaeontographica Abt A* 186: 163–222
- Kay RF (2003) The primate fossil record. *Am J Hum Biol* 15: 839–840
- Kay RF, Cartmill M (1977) Cranial morphology and adaptations of *Palaechthon nacimienti* and other Paromomyidae (Plesiadapoidea, ? Primates), with a description of a new genus and species. *J Hum Evol* 6: 19–53
- Kay RF, Thorington RW Jr, Houde P (1990) Eocene plesiadapiform shows affinities with flying lemurs not primates. *Nature* 345: 342–344
- Kay RF, Thewissen JGM, Yoder AD (1992) Cranial anatomy of *Ignacius graybullianus* and the affinities of the Plesiadapiformes. *Am J Phys Anthropol* 89: 477–498
- Kirk EC, Cartmill M, Kay RF, Lemelin P (2003) Comment on “Grasping Primate Origins”. *Science* 300: 741
- Krause DW (1991) Were paromomyids gliders? Maybe, maybe not. *J Hum Evol* 21: 177–188
- Le Gros Clark WE (1925) On the skull of *Tupaia*. *Proc Zool Soc Lond* 1925: 559–567
- Le Gros Clark WE (1926) On the anatomy of the pen-tailed tree shrew (*Ptilocercus lowii*). *Proc Zool Soc Lond* 1926: 1179–1309
- Le Gros Clark WE (1959) *The antecedents of Man*. Quadrangle Books, Chicago
- Lewin R (1987) *Bones of contention*. Simon and Schuster, New York
- Liu F-GR, Miyamoto MM, Freire NP, Ong PQ, Tennant MR, Young TS, Gugel KF (2001) Molecular and morphological supertrees for eutherian (placental) mammals. *Science* 291: 1786–1789
- Lofgren DL (1995) The Bug Creek problem and the Cretaceous-Tertiary boundary at McGuire Creek, Montana. *Univ Calif Publ Geol Sci* 140: 1–185
- MacPhee RDE, Cartmill M, Gingerich PD (1983) New Paleogene primate basicrania and the definition of the order Primates. *Nature* 301: 509–511
- Martin RD (1968) Towards a new definition of Primates. *Man* 3: 377–401
- Martin RD (1986) Primates: a definition. In: Wood B, Martin L, Andrews P (eds) *Major topics in primate and human evolution*. Cambridge University Press, Cambridge, pp 1–31
- Martin RD (1990) Primate origins and evolution: a phylogenetic reconstruction. Princeton University Press, Princeton NJ
- Martin RM (2004) Chinese lantern for early primates. *Nature* 427: 22–23
- Matthew WD, Granger W (1921) New genera of Paleocene mammals. *Am Mus Novit* 13: 1–7

- McHenry HM, Coffing K (2000) *Australopithecus* to *Homo*: transformations in body and mind. *Annu Rev Anthropol* 29: 125–146
- McKenna MC (1966) Paleontology and the origin of the Primates. *Folia Primatol* 4: 1–25
- McKenna MC (1975) Toward a phylogenetic classification of the Mammalia. In: Lockett WP, Szalay FS (eds) *Phylogeny of the Primates*. Plenum Press, New York, pp 21–46
- McKenna MC, Bell SK (1997) *Classification of mammals above the species level*. Columbia University Press, New York
- Mivart St G (1873) On *Lepilemur* and *Cheirogaleus*, and on the zoological rank of the Lemuroidea. *Proc Zool Soc Lond* 1873: 484–510
- Miyamoto MM, Porter CA, Goodman M (2000) c-Myc gene sequences and the phylogeny of bats and other eutherian mammals. *Syst Biol* 49: 501–514
- Murphy WJ, Eizirik E, Johnson WE, Zhang YP, Ryder OA, O'Brien SJ (2001a) Molecular phylogenetics and the origins of placental mammals. *Nature* 409: 614–618
- Murphy WJ, Eizirik E, O'Brien SJ, Madsen O, Scally M, Douady CJ, Teeling EC, Ryder OA, Stanhope MJ, de Jong WW, Springer ML (2001b) Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science* 294: 2348–2351
- Napier JR, Napier PH (1967) *A handbook of living primates*. Academic Press, London
- Niemitz C (1979) Outline of the behavior of *Tarsius bancanus*. In: Doyle GA, Martin RD (eds) *The study of prosimian behavior*. Academic Press, New York, pp 631–660
- Ni X, Wang Y, Hu Y, Li C (2004) A euprimate skull from the early Eocene of China. *Nature* 427: 65–68
- Novacek MJ (1992) Mammalian phylogeny: shaking the tree. *Nature* 356: 121–125
- Novacek MJ, Wyss AR (1986) Higher-level relationships of the recent eutherian orders: morphological evidence. *Cladistics* 2: 257–287
- Olson LE, Sargis EJ, Martin RD (2004) Phylogenetic relationships among tree shrews (Scandentia): a review and critique of the morphological evidence. *J Mamm Evol* 11: 49–71
- Olson LE, Sargis EJ, Martin RD (2005) Intraordinal phylogenetics of tree shrews (Mammalia: Scandentia) based on evidence from the mitochondrial 12S rRNA gene. *Mol Phylogenet Evol* 35: 656–673
- Pumo DE, Finamore PS, Franek WR, Phillips CJ, Tarzami S, Balzarano D (1998) Complete mitochondrial genome of a neotropical fruit bat, *Artibeus jamaicensis* and a new hypothesis of the relationships of bats to other eutherian mammals. *J Mol Evol* 47: 709–717
- Rasmussen DT (1990) Primate origins: lessons from a neotropical marsupial. *Am J Primatol* 22: 263–277
- Ravosa MJ, Savakova DG (2004) Euprimate origins: the eyes have it. *J Hum Evol* 46: 355–362
- Rose KD (1981) The Clarkforkian Land-Mammal Age and mammalian faunal composition across the Paleocene-Eocene boundary. *Univ Mich Mus Pap Paleontol* 26: 1–197
- Rose KD (1995) The earliest primates. *Evol Anthropol* 3: 159–173
- Rose KD, Walker AC (1985) The skeleton of early Eocene *Cantius*, oldest lemuriform primate. *Am J Phys Anthropol* 66: 73–89
- Rowe T (1987) Definition and diagnosis in the phylogenetic system. *Syst Zool* 36: 208–211
- Runestad JA, Ruff CB (1995) Structural adaptations for gliding in mammals with implications for locomotor behavior in paromomyids. *Am J Phys Anthropol* 98: 101–119
- Russell DE (1964) Les mammifères Paléocène d'Europe. *Mém Mus Hist nat nouvelle série* 13: 1–324
- Sargis EJ (2001a) A preliminary qualitative analysis of the axial skeleton of tupaiids (Mammalia, Scandentia): functional morphology and phylogenetic implications. *J Zool Lond* 253: 473–483
- Sargis EJ (2001b) The grasping behaviour, locomotion and substrate use of the tree shrews *Tupaia minor* and *T. tana* (Mammalia, Scandentia). *J Zool Lond* 253: 485–490
- Sargis EJ (2002a) Functional morphology of the forelimb of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. *J Morphol* 253: 10–42

- Sargis EJ (2002b) Functional morphology of the hindlimb of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. *J Morphol* 254: 149–185
- Sargis EJ (2002c) A multivariate analysis of the postcranium of tree shrews (Scandentia, Tupaiidae) and its taxonomic implications. *Mammalia* 66: 579–598
- Sargis EJ (2002d) The postcranial morphology of *Ptilocercus lowii* (Scandentia, Tupaiidae): an analysis of primatomorphan and volitanian characters. *J Mamm Evol* 9: 137–160
- Sargis EJ (2002e) Primate origins nailed. *Science* 298: 1564–1565
- Sargis EJ (2004) New views on tree shrews: the role of tupaiids in primate supraordinal relationships. *Evol Anthropol* 13: 56–66
- Sargis EJ (in press) The postcranial morphology of *Ptilocercus lowii* (Scandentia, Tupaiidae) and its implications for primate supraordinal relationships. In: Ravosa MJ, Dagosto M (eds) *Primate origins and adaptations: a multidisciplinary perspective*. Plenum Press, New York
- Sigé B, Jaeger J-J, Sudre J, Vianey-Liaud M (1990) *Altiatlasius koulchii* n. gen et sp., primate omomyidé du paléocène supérieur du Maroc, et les origines des euprimates. *Palaeontographica* 212: 1–24
- Silcox MT (2001) A phylogenetic analysis of Plesiadapiformes and their relationship to Euprimates and other archontans. Ph.D. dissertation, Johns Hopkins School of Medicine, Baltimore Maryland
- Silcox MT (2003) New discoveries on the middle ear anatomy of *Ignacius graybullianus* (Paromomyidae, Primates) from ultra high resolution X-ray computed tomography. *J Hum Evol* 44: 73–86
- Silcox MT (in press) Primate taxonomy, plesiadapiforms, and approaches to primate origins. In: Ravosa MJ, Dagosto M (eds) *Primate origins and adaptations: a multidisciplinary perspective*. Plenum Press, New York
- Silcox MT, Gunnell GF (in press) Plesiadapiformes. In: Janis CM, Gunnell GF, Uhen MD (eds) *Evolution of tertiary mammals of North America. Vol 2: Marine mammals and smaller terrestrial mammals*. Cambridge University Press, Cambridge
- Silcox MT, Bloch JL, Sargis EJ, Boyer DM (2005) Euarchonta (Dermoptera, Scandentia, Primates). In: Rose KD, Archibald JD (eds) *The rise of placental mammals: origins and relationships of the major extant clades*. Johns Hopkins University Press, Baltimore
- Simmons NB (1994) The case for chiropteran monophyly. *Am Mus Novit* 3103: 1–54
- Smith T, Van Itterbeeck J, Missiaen P (2004) Oldest plesiadapiform (Mammalia, Primates) from Asia and its palaeobiogeographical implications for faunal interchange with North America. *CR Palevol* 3: 43–52
- Springer MS, Murphy WJ, Eizirik E, O'Brien SJ (2003) Placental mammal diversification and the Cretaceous–Tertiary boundary. *Proc Natl Acad Sci USA* 100: 1056–1061
- Springer MS, Stanhope MJ, Madsen O, de Jong WW (2004) Molecules consolidate the placental mammal tree. *Trends Ecol Evol* 19: 430–438
- Stafford BJ, Thorington RW Jr (1998) Carpal development and morphology in archontan mammals. *J Morphol* 235: 135–155
- Stafford BJ, Szalay FS (2000) Craniodental functional morphology and taxonomy of dermopterans. *J Mammal* 81: 360–385
- Storch G, Richter G (1994) Zur Paläobiologie Messeler Igel. *Natur u. Museum* 124: 81–90
- Strait SG (2001) Dietary reconstruction of small-bodied omomyoid primates. *J Vert Palaeontol* 21: 322–334
- Sussman RW (1991) Primate origins and the evolution of angiosperms. *Am J Primatol* 23: 209–223
- Sussman RW, Raven RH (1978) Pollination of flowering plants by lemurs and marsupials: a surviving archaic coevolutionary system. *Science* 200: 731–736
- Szalay FS (1968) The beginnings of primates. *Evolution* 22: 19–36
- Szalay FS (1969) Mixodectidae, Microsypidae, and the insectivore-primate transition. *Bull Am Mus Nat Hist* 140: 195–330
- Szalay FS (1972) Paleobiology of the earliest primates. In: Tuttle RH (ed) *The functional and evolutionary biology of primates*. Aldine-Atherton, Chicago, pp 3–35

- Szalay FS (1975) Where to draw the nonprimate-primate taxonomic boundary. *Folia Primatol* 23: 158–163
- Szalay FS (1977) Phylogenetic relationships and a classification of the eutherian Mammalia. In: Hecht MK, Goody PC, Hecht BM (eds) Major patterns in vertebrate evolution. Plenum Press, New York, pp 315–374
- Szalay FS (1981) Phylogeny and the problem of adaptive significance: the case of the earliest primates. *Folia Primatol* 36: 157–182
- Szalay FS, Dagosto M (1980) Locomotor adaptations as reflected on the humerus of Paleogene Primates. *Folia Primatol* 34: 1–45
- Szalay FS, Dagosto M (1988) Evolution of hallucial grasping in primates. *J Hum Evol* 17: 1–33
- Szalay FS, Decker RL (1974) Origins, evolution, and function of the tarsus in late Cretaceous Eutheria and paleocene primates. In: Jenkins FA Jr (ed) Primate locomotion. Academic Press, New York, pp 223–359
- Szalay FS, Delson E (1979) Evolutionary history of the primates. Academic Press, New York
- Szalay FS, Drawhorn G (1980) Evolution and diversification of the Archonta in an arboreal milieu. In: Lockett WP (ed) Comparative biology and evolutionary relationships of tree shrews. Plenum Press, New York, pp 133–169
- Szalay FS, Lucas SG (1993) Cranioskeletal morphology of archontans, and diagnoses of Chiroptera, Volitantia, and Archonta. In: MacPhee RDE (ed) Primates and their relatives in phylogenetic perspective. Plenum Press, New York, pp 187–226
- Szalay FS, Lucas SG (1996) The postcranial morphology of Paleocene *Chriacus* and *Mixodectes* and the phylogenetic relationships of archontan mammals. *Bull New Mex Mus Nat Hist Sci* 7: 1–47
- Szalay FS, Tattersall I, Decker RL (1975) Phylogenetic relationships of *Plesiadapis*: postcranial evidence. In: Szalay FS (ed) Approaches to primate paleobiology. Karger, Basel, pp 136–166
- Szalay FS, Rosenberger AL, Dagosto M (1987) Diagnosis and differentiation of the order Primates. *Yrbk Phys Anthropol* 30: 75–105
- Tabuce R, Mahboubi M, Tafforeau P, Sudre J (2004) Discovery of a highly-specialized plesiadapiform primate in the early-middle Eocene of northwestern Africa. *J Hum Evol* 47: 305–321
- Tong Y (1988) Fossil tree shrews from the Eocene Hetaoyuan formation of Xichuan, Henan. *Vert Palasiat* 26: 214–220
- Van Valen LM (1994) The origin of the plesiadapid primates and the nature of Purgatorius. *Evol Monogr* 15: 1–79
- Van Valen LM, Sloan RE (1965) The earliest primates. *Science* 150: 743–745
- Waddell PJ, Okada N, Hasegawa M (1999) Towards resolving the interordinal relationships of placental mammals. *Syst Biol* 48: 1–5
- Wible JR (1993) Cranial circulation and relationships of the colugo *Cynocephalus* (Dermoptera, Mammalia). *Am Mus Novit* 3072: 1–27
- Wible JR, Covert HH (1987) Primates: cladistic diagnosis and relationships. *J Hum Evol* 16: 1–22
- Wible JR, Martin JR (1993) Ontogeny of the tympanic floor and roof in archontans. In: MacPhee RDE (ed) Primates and their relatives in phylogenetic perspective. Plenum Press, New York, pp 111–146

2007

SPRINGER
REFERENCE

Winfried Henke
Ian Tattersall
Editors

VOLUME 2

Handbook of Paleoanthropology

Primate Evolution and Human Origins

 Springer