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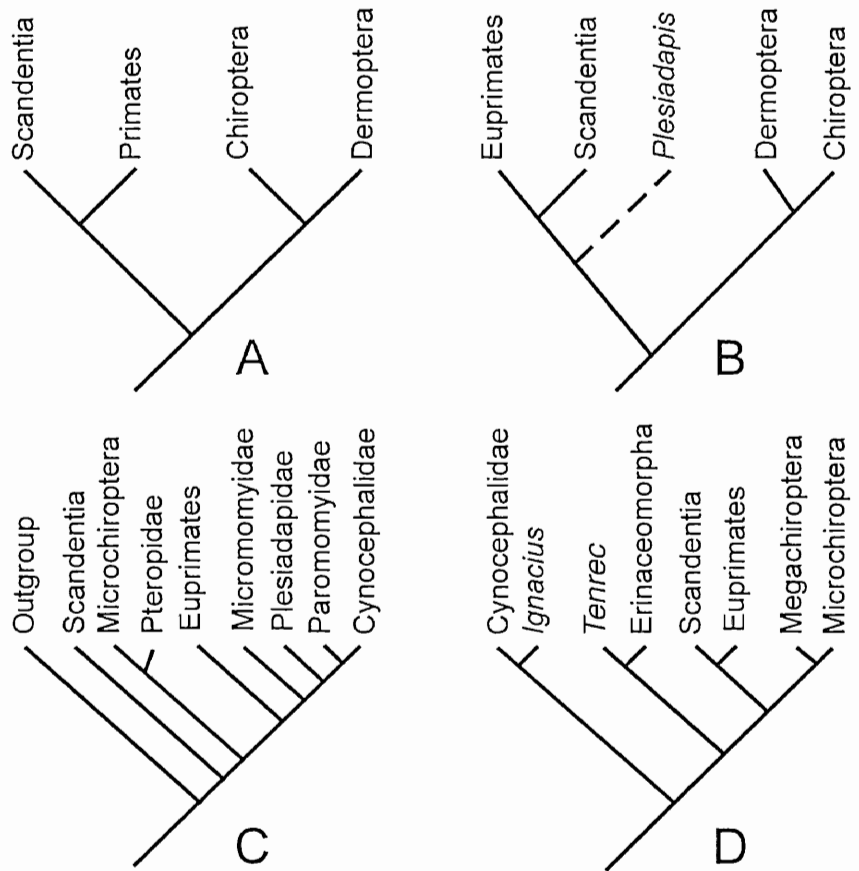
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EUARCHONTA (DERMOPTERA, SCANDENTIA, PRIMATES)

GREGORY (1910) NAMED ARCHONTA (DERIVED from the Greek for chief: *ἄρχων*) for a supraordinal group composed of Menotyphla (Tupaïidae + Macroscelididae), Dermoptera, Chiroptera, and Primates. Gregory suggested an origin for these taxa from a common ancestor in the Upper Cretaceous that may have resembled a tree shrew in form. A monophyletic Archonta was not immediately widely accepted. For example, Simpson (1945) considered Archonta to be an unnatural group and did not include it in his landmark classification of mammals. Later, however, support began to grow for a modified version of Archonta, excluding macroscelidids (e.g., McKenna, 1975; Szalay, 1977; Novacek and Wyss, 1986). A key component of archontan monophyly was the proposed relationship between dermopterans and chiropterans, referred to as Volitantia Illiger, 1811. Morphological support suggested for the monophyly of Volitantia (e.g., Novacek and Wyss, 1986; Wible and Novacek, 1988; Szalay and Lucas, 1993, 1996; Simmons and Geisler, 1998; Shoshani and McKenna, 1998; Stafford and Thorington, 1998) includes a substantial number of features such as the elongation of the forelimbs; the fusion of the distal part of the ulna to the radius; and the presence of the humeropatagialis muscles, a scaphocentralunate, and a tendon-locking mechanism on the digits of the feet (see Simmons and Geisler, 1998: table 4, for a more complete list).

Starting with Carlsson (1922) and continuing into the 1960s, tupaiids were often included in the order Primates—a classification that received particular support from the work of Le Gros Clark (1925, 1926). Van Valen (1965) and McKenna (1966) advocated removing tupaiids from the order, based on the premise that many of the

Fig. 9.1. Competing hypotheses of relationships among archontans. (A) Modified after Novacek (1992: fig. 1). (B) Modified after Wible and Covert (1987: fig. 7a). (C) Modified after Beard (1993a: fig. 10.1). (D) Modified after Kay et al. (1992: fig. 11).



features that they were supposed to share with Euprimates (=primates of “modern aspect”; i.e., Primates not including plesiadapiforms; see Hoffstetter, 1977) were mis-characterizations, convergences, or symplesiomorphies. Butler (1972) grouped tupaiids in their own order, Scandentia Wagner, 1855, and this classification has since been followed by most mammal systematists. In spite of their removal from Primates, a euprimate-scandentian relationship was still supported by some authors (e.g., Wible and Covert, 1987; Kay et al., 1992). Novacek (1992; Fig. 9.1A) supported a monophyletic Archonta with sister taxon relationships between Primates and Scandentia, and between Dermoptera and Chiroptera. Subsequent morphological debates about the intraordinal relationships of living archontans have largely focused on conflicts between these phylogenetic hypotheses and apparently inconsistent evidence from the fossil record (see reviews in Szalay and Lucas, 1996; Sargis, 2002c).

Even though phylogenetic analyses of morphological data often result in hypotheses with a monophyletic Archonta and Volitanti, these particular relationships have consistently not been supported by molecular analyses. In fact, no phylogenetic hypothesis based strictly on molecular data has ever supported a close relationship between chiropterans and other archontans—instead, chiropterans have generally fallen out with carnivores and ungulates (e.g., Miyamoto et al., 2000; Liu et al., 2001; Murphy et al., 2001a,b; Springer et al., 2003, 2004). Although results of early mo-

lecular studies provided conflicting hypotheses regarding the monophyly of a version of Archonta that excludes bats (Allard et al., 1996), a consensus now appears to be developing in support of a clade composed of Scandentia, Dermoptera, and Primates (Adkins and Honeycutt, 1991; Waddell et al., 1999; Liu et al., 2001; Murphy et al., 2001a,b; Springer et al., 2003, 2004). Waddell et al. (1999) proposed the name Euarchonta for this group.

Within Euarchonta, there have been various hypothesized interordinal relationships based on molecular studies, although a clade including Dermoptera and Scandentia has appeared in several recent results (Liu et al., 2001; Murphy et al., 2001a,b; Springer et al., 2003, 2004). Euarchonta has recently been grouped in several molecular analyses with Glires (rodents + lagomorphs; e.g., Waddell et al., 1999; Murphy et al., 2001a,b; Springer et al., 2003, 2004) in a clade that Murphy et al. (2001b) named Euarchontoglires.

Our purpose in this chapter is to review the morphological evidence, particularly the fossil material, that is central to debates about the origins and relationships of Euarchonta and to discuss recent viewpoints about these issues.

INSTITUTIONAL ABBREVIATIONS

UM, University of Michigan, Museum of Paleontology
(Ann Arbor, Michigan)

TF, Collections of the Palaeontological Section, Department of Mineral Resources, Bangkok (Ducrocq et al., 1992)

DISTINCTIVE MORPHOLOGICAL FEATURES AND FOSSIL REPRESENTATIVES OF EXTANT EUARCHONTAN GROUPS

Euarchonta

A list of hypothesized synapomorphies for Archonta or Euarchonta is given in Table 9.1 and illustrated in Figs. 9.2–9.3 (see also Figs. 9.4, 9.5). A recent reconstruction of the euarchontan morphotype (Bloch et al., 2003) suggests that the common ancestor of this group was a small-bodied arboreal form similar to the living scandentian *Ptilocercus* (Sargis, 2002c). This common ancestor may have frequently adopted vertical postures on large-diameter supports—this is suggested, for example, by the presence of an elliptical acetabulum (see Fig. 9.5A) and deep, narrow unguals (see Fig. 9.5D,E). Of the other features listed in Table 9.1, only a few (characters 1 and 6) are thought to be present in all living archontans. If bats are excluded, then characters 5 and 2 can also be added to this list. It is worth noting that of these four characters, only two features of the ankle (characters 5 and 6) are potentially identifiable in fossils. Although the variability in these features in modern archontans does create some methodological difficulties, if they were all present in the ancestral archontan or euarchontan, then more re-

cent modifications to these traits do not eliminate them as support for the monophyly of Archonta or Euarchonta.

Dermoptera

Living dermopterans are nocturnal gliders that are found only on a group of islands in Southeast Asia (Stafford and Szalay, 2000). Stafford and Szalay (2000) argued convincingly for a separation of living members into two monospecific genera, *Cynocephalus volans* and *Galeopterus variegatus*, although most other recent authors have included both extant species in the genus *Cynocephalus*. Stafford and Szalay's (2000) argument was based on the presence of more robust masticatory features in *C. volans* than are found in *G. variegatus*.

Overall, modern dermopterans are profoundly odd animals, with many very unusual morphological characteristics. One of the most distinctive features of living dermopterans is their patagium, which is more extensive than in other extant gliding mammals, extending between the digits of the hand (interdigital patagium; the reason for the common name “mitten gliders”), between the limbs, and even between the hindlimb and the tail (uropatagium). Dermopterans have numerous unusual postcranial features that are possibly associated with this structure, including a distinctive lengthening of the intermediate phalanges of the hand (Beard, 1989, 1990). Dentally, dermopterans are unusual in having multi-tined, pectinate lower incisors that may be used in certain grooming behaviors (Aimi and Inagaki, 1988). The first upper incisor is lost, and there is a central gap in the upper dental arcade, so that i1 and i2 articulate

Table 9.1 Hypothesized synapomorphies of Archonta and Euarchonta

Number	Character	Number	Character
1	Pendulous penis suspended by a reduced sheath between the genital pouch and abdomen (Smith and Madkour, 1980)	9	Robust, medially protruding lesser tuberosity (missing in tupaiines; Sargis, 2002c)
2	Tectopetal connections to the superior or anterior colliculus of one side with progressively more projections from the ipsilateral retina (absent in microchiropterans; Johnson and Kirsch, 1993)	10	Spheroidal capitulum of the humerus (missing in chiropterans and tupaiines), circular and excavated radial central fossa (missing in chiropterans and tupaiines; Szalay and Lucas, 1996; Sargis, 2002c)
3	Presence of at least one entotympanic element, with a close proximity to the tubal cartilage, tegmen tympani, internal carotid artery and nerve, and the greater petrosal nerve (missing in euprimates; Wible and Martin, 1993)	11	Acetabulum elliptical in shape with buttressing cranially (missing in tupaiines; Sargis, 2002c)
4	Epitympanic wing of the petrosal absent (missing in euprimates and tupaiines; Wible and Martin, 1993)	12	Enlarged, flattened triangular areas for attachment of quadratus femoris (missing in tupaiines, plesiadapids, and chiropterans; Sargis, 2002c)
5	Sustentacular facet of the astragalus in distinct medial contact with the navicular facet of the astragalus (missing in microchiropterans; Szalay and Drawhorn, 1980; Novacek and Wyss, 1986)	13	Short, shallow patellar groove (missing in euprimates; Szalay and Lucas, 1996; Sargis, 2002c)
6	Large distal sustentacular facet of the calcaneum articulating with a ventral extension of the navicular facet of the astragalus (Hooker, 2001)	14	Synovial distal tibiofibular joint (missing in some euprimates, tupaiines, and chiropterans; Sargis, 2002c)
7	Craniocaudal expansion of the ribs (missing in primates and tupaiines; Sargis, 2002c)	15	Concave cuboid facet on the calcaneus (missing in tupaiines and chiropterans; Szalay and Lucas, 1996; Sargis, 2002c)
8	“Weak” or absent spinous processes on C3–C7 (missing in euprimates and tupaiines; Sargis, 2002c)	16	Wide distal facet on the entocuneiform (missing in tupaiines and chiropterans; Szalay and Lucas, 1996; Sargis, 2002c)
		17	Deep, narrow unguals (missing in euprimates; Sargis, 2002c)

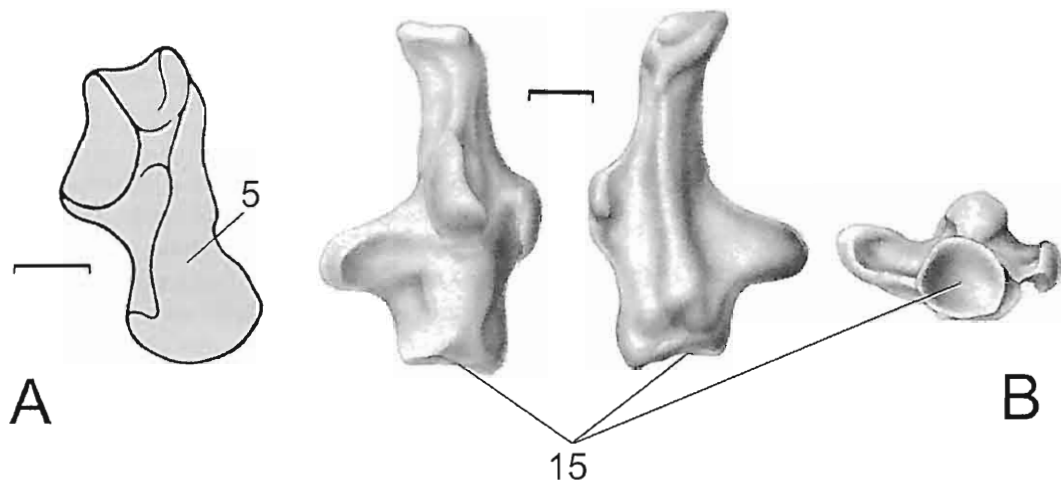


Fig. 9.2. Tarsal bones of *Ptilocercus lowii*, demonstrating characteristic archontan features. Numbers refer to characters in Table 9.1. (A) Left astragalus in plantar view. The sustentacular facet is in distinct medial contact with the navicular facets. Redrawn after Szalay and Drawhorn (1980: fig. 2). (B) Left calcaneus in dorsal (left), plantar (middle), and distal (right) views. This specimen has a round and concave cuboid facet. Redrawn after Szalay and Drawhorn (1980: fig. 9). Scale bar = 1 mm.

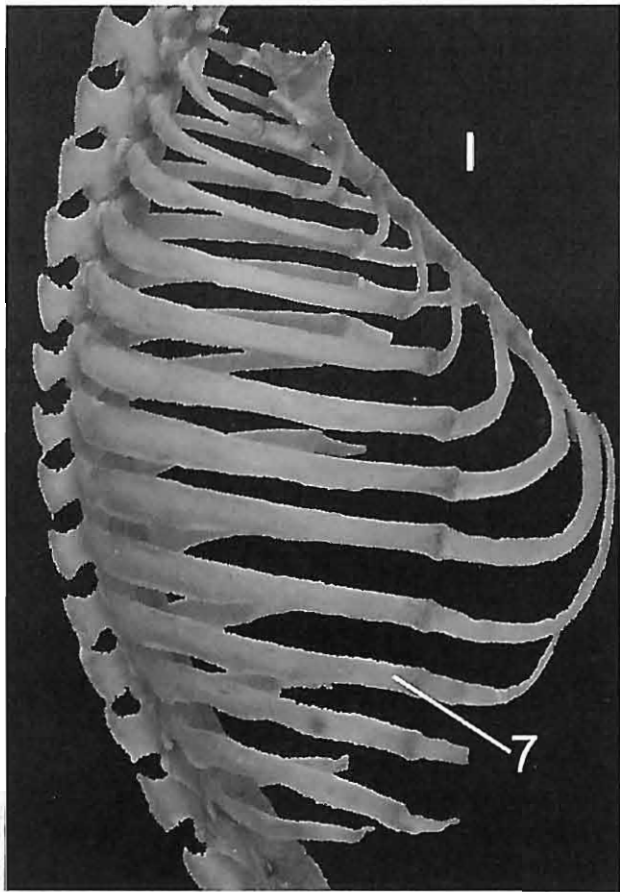


Fig. 9.3. Thorax of *Cynocephalus volans* in lateral view, demonstrating the characteristic euarchontan feature of craniocaudally expanded ribs (Table 9.1, character 7). Scale bar = 5 mm.

with an edentulous premaxillary pad (Stafford and Szalay, 2000). *Galeopterus variegatus* also has multi-tined canines, although these teeth are more typically caniniform in *C. volans* (Stafford and Szalay, 2000). The upper and lower premolars are enlarged and extensively molarized in both species. The upper molars exhibit very large conules, no hypocones, and a transverse valley running buccolingually between the paracone/paraconule and metacone/metaconule (MacPhee et al., 1989). The lower molars (and p4) have a distinctly crestiform paracristid that is well separated from the protoconid and metaconid, and strong shearing crests. In the cranium, the majority of the auditory bulla is formed by the ectotympanic, plus one or two small entotympanic elements associated with the auditory tube (Wible and Martin, 1993). The ear region is extensively pneumatized, and the orientation of the eardrum is unusual in remaining nearly horizontal into adulthood (Hunt and Korth, 1980). The internal carotid artery involutes in ontogeny, and the brain is supplied with blood by the vertebral arteries (Hunt and Korth, 1980).

The fossil record of dermopterans that are clearly related to modern Cynocephalidae (not including the more questionably assigned dermopterans, e.g., Plagiomenidae, Paromomyidae) consists of only one specimen, a poorly preserved mandibular fragment from late Eocene sediments from the Krabi Basin, southern Thailand. This specimen (TF 2580) is the holotype of *Dermotherium major* (Ducrocq et al., 1992) and is classified in the same family as modern dermopterans (Cynocephalidae; often referred to as Galeopithecidae, but Stafford and Szalay, 2000, argue that because *Cynocephalus* is the type genus, the valid family name is Cynocephalidae).

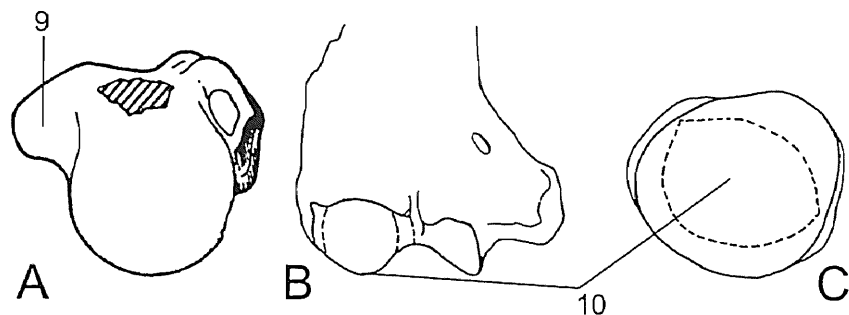


Fig. 9.4. Characteristic archontan features. Numbers refer to characters in Table 9.1. (A) Right humerus of *Phenacolemur simonsi* in proximal view, demonstrating a robust, medially protruding lesser tuberosity. Redrawn after Beard (1989: fig. 67). (B) Right distal humerus (anterior view) and (C) proximal radius (proximal view) of a characteristic euarchontan. Redrawn after Beard (1989: fig. 69). Panels (B) and (C) illustrate a spheroidal capitulum and corresponding circular and deeply excavated central fossa of the radius.

Stafford and Szalay (2000) disputed the hypothesized relationship between *Dermotherium major* and Cynocephalidae based on inconsistencies in the description of the specimen, an inadequate accounting for the differences between the two genera of modern dermopterans, and the widespread distribution in Eutheria of the traits supposedly linking *Dermotherium* to Dermoptera. To deal with these criticisms, new comparisons of a cast of TF 2580 were made to both *Galeopterus variegatus* and *Cynocephalus volans*. In these comparisons, the differences between the two modern species were taken into account, and any inconsistencies in the description were rendered irrelevant by fresh observations (Silcox, 2001). These comparisons show that *Dermotherium major* is remarkably similar in most comparable aspects of morphology to the modern taxa, in ways that are more distinctive and unique than Stafford and Szalay (2000) imply. The morphology of the molar talonid basin, for example, is identical. This similarity includes not only the (admittedly widespread) close approach of the hypoconulid to the entoconid, but the manner in which this occurs (i.e., both cusps are distinct, pointed, and are not developed along a clear postcristid). Like modern dermopterans, the talonid in *Dermotherium* is extremely broad relative to the trigonid. Although these breadth relationships are found in some other mammals (e.g., primates), the wide gap between the hypoconulid and hypoconid and the deepening of the basin to a “pit” along the midline just behind the postvallid is more distinctive and less commonly found (e.g., these features are generally missing in primates). Modern cynocephalids share with *Dermotherium* an indistinct, lingually shifted paraconid. Again, this feature is found in other mammals (e.g., paromomyids), but the similarities are not as detailed. In modern cynocephalids and *Dermotherium*, this trigonid morphology is associated with a paracristid that extends mesiolingually as a relatively straight crest. The mesial orientation of the paracristid makes the trigonid basin relatively long and the front of the tooth triangular (rather than rectangular) in shape. This configuration differs, for example, from paromomyids, in which the lingual shift of the paraconid is associated with a shortening of the trigonid and a less mesially inclined paracristid. Overall, then, the similarities between *Dermotherium* and modern dermopterans do not consist of vague similarities in broadly distributed features, but rather to very detailed and narrowly distributed character complexes. This impression is

not contradicted by including both modern genera in the assessment.

Based on these comparisons, it seems that the fossil record of definitive Dermoptera does extend back to the late Eocene. As a result of the damage to TF 2580 and the similarity of its preserved morphology to that in modern cynocephalids, the specimen does not add much new information regarding the primitive morphology of Cynocephalidae or its close relatives. It does, however, demonstrate that the divergence of Dermoptera from other mammals must have predated the late Eocene. The location of this specimen, near the modern distribution of dermopterans, could suggest that the group has never existed outside of Southeast Asia, although this view is invalidated if plagiomenids were dermopterans (see below).

Scandentia

Although extant scandentians are more speciose and extensively distributed than dermopterans, they are also found only in Southern Asia. Extant members of this order are typically included in one family, Tupaiidae, with two subfamilies, Tupaiinae and Ptilocercinae. The latter of the two subfamilies is represented by only a single species, *Ptilocercus lowii*, which is the most arboreal and likely the most primitive member of the group (Sargis, 2002a–c). Distinctive features of Scandentia include the presence of a post-orbital bar and divergent orbits. A list of possible scandentian synapomorphies is given in Table 9.2.

The fossil record of Scandentia is very limited. The only records of the order before the Miocene are fragments of teeth from the Middle Eocene of China that, although placed in a new species and genus (*Eodendrogale parvum*), differ only in relatively minor details from the modern genus *Dendrogale* (Tong, 1988). The Miocene material is also quite limited, including a few skull fragments and various isolated teeth, all of which are closely comparable to modern scandentians (Dutta, 1975; Chopra and Vasishat, 1979; Chopra et al., 1979; Jacobs, 1980; Qiu et al., 1985; Qiu, 1986; Mein and Ginsburg, 1997; Ni and Qiu, 2002). The only possible postcranial specimen known for a fossil scandentian is a rib cage from Pliocene deposits of the Upper Siwaliks of India, attributed to *Tupaia* (Dutta, 1975). As such, the fossil record of scandentians is of limited value in providing information on the early events in the evolution of the group or the likely

Table 9.2 Hypothesized synapomorphies of Scandentia

Number	Character
1	Enclosure of the intratympanic portion of the internal carotid artery in a bony canal floored proximally and distally by the entotympanic, and by the petrosal in between (Wible and Zeller, 1994)
2	Enclosure of the intratympanic portion of the stapedial artery by the petrosal in a canal on the promontorium, and within the epitympanic crest beneath the tympanic roof (Wible and Zeller, 1994)
3	Absence of an exit for arteria diploëtica magna (Wible and Zeller, 1994)
4	Alisphenoid canal present (Wible and Zeller, 1994)
5	Maxillary artery passes medial to the mandibular nerve, beneath the foramen ovale (Wible and Zeller, 1994)
6	Laryngeopharyngeal artery present (Wible and Zeller, 1994)
7	Scaphoid and lunate fused into scapholunate (Sargis, 2002a)
8	Articular facet for the medial malleolus on the posterior side of the sustentaculum (Szalay and Lucas, 1996; Sargis, 2002c)

form of ancestors to the order, beyond indicating that such ancestors must have predated the middle Eocene. As with definitive dermopterans, the fossil record of scandentians is entirely Asian in distribution.

Euprimates

Cartmill (1992: 105) recognized five adaptive complexes that he identified as the “chief primate peculiarities” found in most modern members of the order: grasping extremities, claw loss, optical convergence and orbital approximation (including the presence of a postorbital bar), enhanced vision, and brain enlargement. To this list, we can add the presence of a petrosal bulla (Cartmill, 1972) and dental features that are associated with increased omnivory (e.g., low-crowned molars with broad talonid basins; Szalay, 1968b).

Compared to the other euarchontan groups, the fossil record of Euprimates is better sampled. Several reviews of the fossil record of primates exist (e.g., Szalay and Delson, 1979; Hartwig, 2002) and our discussion focuses only on those forms most relevant to debates about the origins and supraordinal relationships of the group.

Many fossils traditionally grouped in two families, Adapidae and Omomyidae (sometimes raised to superfamilial or infraordinal rank), have been recovered from early Eocene sediments in North America and Europe. The earliest and most primitive representatives of these two families are the adapids *Cantius* and *Donrussellia* (Godinot, 1978, 1992; Godinot et al., 1987; Gingerich et al., 1991) and the omomyids *Teilhardina* and *Steinius* (Simpson, 1940; Bown, 1976; Rose and Bown, 1991; Rose, 1995). These basal taxa are dentally very similar to one another, with a recent study (Rose and Bown, 1991) identifying only a single known, derived trait of omomyids that separates them from primitive adapids (a single-rooted, rather than double-rooted, p2). A

few other subtle dental features have been found that distinguish the most primitive adapids from omomyids, including the loss of the postmetaconule crista and the buccal position of the hypoconulid (Godinot, 1992). The implication of these dental similarities may be that we are approaching, in the early Eocene, the common root for euprimates, or at least for Adapidae + Omomyidae.

The fossil record of primitive euprimates in Africa and Asia is much more limited. Although some of this material can be confidently attributed to Adapidae or Omomyidae, other specimens remain more controversial. Of particular importance to issues of euprimate, primate, and archontan (or euarchontan) origins are *Petrolemur brevirostre* (late Paleocene), *Decoredon anhuiensis* (early Paleocene), and *Altianius orlovi* (early Eocene) from Asia, and *Altiatlasius koulchii* (late Paleocene) from Africa. It has been suggested that *Petrolemur brevirostre* and *Decoredon anhuiensis* are not primates (Rose, 1995; Wang et al., 1998). *Petrolemur* was classified by McKenna and Bell (1997) as an oxyclaenid ungulate, and this seems a more likely attribution than Primates (see also Szalay, 1982). Although McKenna and Bell (1997) included *Decoredon* in Primates, it lacks distinguishing primate features (Rose, 1995) and is more likely to be a condylarth than a primate.

That leaves *Altiatlasius* from the Late Paleocene of Morocco as the oldest known possible euprimate. The systematic position of *Altiatlasius* has also been a subject of debate. Although *Altiatlasius* was originally described as an omomyid, Sigé et al. (1990) also suggested a possible relationship to basal “simiiforms” (i.e., anthropoids), a view supported by Godinot (1994). Gingerich (1990) suggested a plesiadapiform attribution, and Hooker et al. (1999) argued for assignment to the family Toliapinidae in the Plesiadapiformes. Silcox (2001) disagreed—her cladistic analysis supported a basal euprimate position for *Altiatlasius*. Neither Silcox (2001) nor Hooker et al. (1999) analyzed any anthropoids, however, and thus the anthropoid hypothesis has not been tested. Although the affinities of this taxon remain somewhat uncertain, it appears to be a euprimate, making it the oldest known for that group.

Altianius is likely not as old as *Altiatlasius* (coming from the Bumbanian of Mongolia; although Bowen et al., 2002, suggest that the Bumbanian may straddle the Paleocene-Eocene boundary), but may be equally important to an understanding of the earliest part of the euprimate fossil record. Dashzeveg and McKenna (1977), in describing the initial material of *Altianius*, likened it to anaptomorphine omomyids. These authors also noted similarities to carpolestid plesiadapiforms, and Rose and Krause (1984) expanded on these comparisons, arguing that there were at least as many similarities to carpolestids as to omomyids. Gingerich et al. (1991) retained *Altianius* in the Omomyidae, based on overall similarity, including small size. They also documented some important new anatomical findings, including a 2.1.4.3 lower dental formula, rendering this taxon more primitive than the derived anaptomorphine omomyids with which it shares the most postcanine simi-

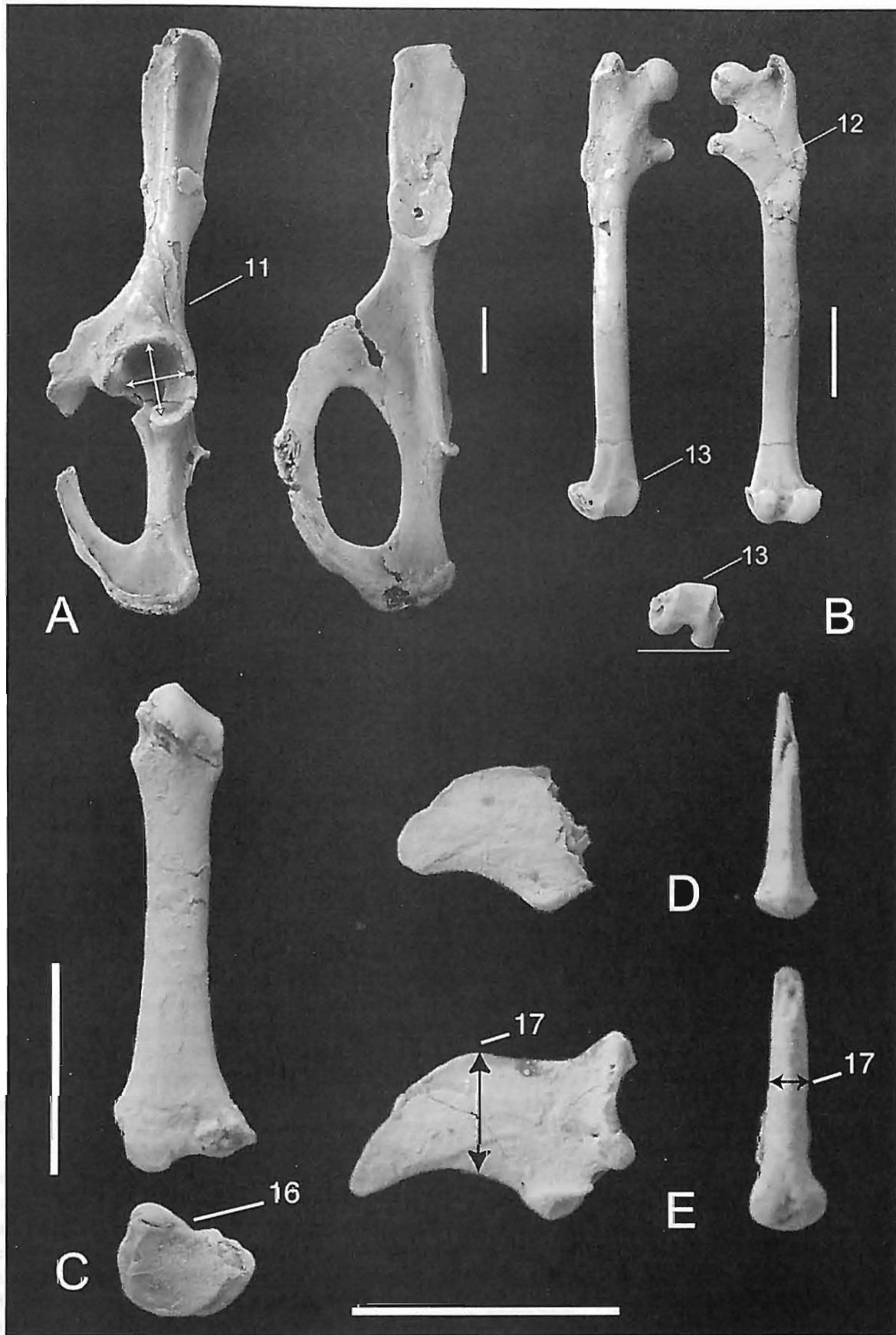


Fig. 9.5. Paromomyid fossils, demonstrating characteristic archontan features. Numbers refer to characters in Table 9.1. (A) Clarkforkian *Ignacius* sp. (UM 82606), left innominate. This specimen illustrates cranial buttressing above an elliptically shaped acetabulum. Scale bar = 5 mm. (B) Clarkforkian *Ignacius* sp. (UM 82606), right femur. Lines point to the short, shallow patellar groove, and the enlarged attachment area for quadratus femoris. Scale bar = 10 mm. (C) Clarkforkian *Ignacius* sp. (UM 82606), right metatarsal I. The broad proximal facet on the first metatarsal reflects the wide distal facet on the entocuneiform. Scale bar = 5 mm. (D) *Acidomomys hebeticus* (UM 08209), distal phalanx is both deep and narrow. (E) Clarkforkian *Ignacius* sp. (UM 82606), distal phalanx is both deep and narrow. Scale bar = 5 mm.

larities. This observation suggests that such similarities are likely to be homoplasies. Beard (1998) hypothesized that *Altanius* was a basal euprimate, a position also supported by Silcox (2001).

Both *Altiatlasius koulchii* and *Altanius orlovi* can be plausibly interpreted as basal euprimates outside Adapidae and Omomyidae. Interestingly, these two taxa are very different morphologically (Rose, 1995; Silcox, 2001). *Altanius orlovi* has a relatively sharp-cusped, high-crowned dentition, with a well-demarcated postprotocingulum and hypocone. *Altiatlasius koulchii*, however, lacks a postprotocingulum and a hypocone and has a wide stylar shelf, which are likely to be primitive characteristics. This taxon also has very bunodont cusps and is quite low-crowned, which might not be expected in a basal euprimate based on the taller, more acute cusps of the most primitive adapids and omomyids (*Donrussellia* and *Teilhardina*). In sum, these two taxa give a rather different picture of dental morphology at the base of the euprimate clade, and suggest that we may be missing a significant portion of the Old World diversity at the base of the euprimate radiation. The age of *Altiatlasius* indicates that euprimates, and by extension Euarchonta, must have already diverged by the late Paleocene.

PALEOCENE POSSIBLE ARCHONTANS

Apart from *Altiatlasius* and possibly *Altanius*, there are currently no known Paleocene members of Euprimates, Dermoptera, or Scandentia. There are, however, a number of Paleocene groups that have been considered possible archontan, euarchontan, or euprimate relatives that may provide additional information about the origin and evolution of these groups.

Plesiadapiformes

Plesiadapiforms are Paleocene-Eocene fossil mammals known from North America, Europe, and Asia. Currently, 11 distinct families are recognized (Purgatoriidae, Microsomyidae, Microsyopidae, Palaechthonidae, Paromomyidae, Plesiadapidae, Carpolestidae, Saxonellidae, Picrodontidae, Picromomyidae, and Toliapinidae; Silcox, 2001). The term "Plesiadapiformes" is not included as a formal taxonomic label in Table 9.3 because it seems likely that it is not a monophyletic group (see Fig. 9.6). Nonetheless, these 11 families do generally share a suite of characteristics that include enlarged, procumbent upper and lower central incisors, low-crowned molars with wide talonid basins, an enlarged m3 hypoconulid, and a P4 with a postprotocingulum. Many plesiadapiforms also exhibit enlargement and elaboration of the premolars (or m1, in the case of picrodontids) and substantial dental reduction. Postcranially, the group shares features for non-leaping arboreality (Szalay et al., 1975, 1987; Szalay and Drawhorn, 1980; Bloch and Boyer, 2002, 2003, in press).

Table 9.3 Classification of Euarchonta

Cohort Euarchonta
Family Mixodectidae
Order Scandentia
Family Tupaiidae
Subfamily Ptilocercinae
Subfamily Tupaiinae
Order Dermoptera
Family Cynocephalidae
Family Plagiomenidae
Order Primates
Family Microsyopidae
Family Purgatoriidae
Family Picromomyidae
Family Micromomyidae
Family Toliapinidae
Superfamily Paromomyoidea
Family Palaechthonidae
Family Paromomyidae
Family Picrodontidae
Superfamily Plesiadapoidea
<i>Chronolestes simul</i>
Family Plesiadapidae
Family Carpolestidae
Family Saxonellidae
Semiorder Euprimates
<i>Altiatlasius koulchii</i>
<i>Altanius orlovi</i>
Family Adapidae
Family Omomyidae
Many other families

Note: The classification given here is that used in this chapter.

As plesiadapiform fossils from North America began to be discovered and described in the early part of the twentieth century, they were generally included in Primates, often specifically in Tarsiidae (e.g., Matthew and Granger, 1921; Gidley, 1923), largely based on dental similarities. Martin (1968) and Cartmill (1972) were among the first to seriously call this ordinal placement into question. Both Martin and Cartmill emphasized only the formation of a clearer definition of the order Primates based on the presence of characters relating to the unique ecological adaptations of modern members of the group. Neither offered any substantively new views on the broader relationships of plesiadapiforms to other archontans. More compelling arguments for the exclusion of plesiadapiforms from primates were made by authors who argued that they were not the sister group of euprimates and/or may be more closely related to some other group. Wible and Covert (1987) argued that Scandentia was a more likely sister taxon to Euprimates than Plesiadapiformes, based on characters derived entirely from the basicranium. They published a "preferred" cladogram, not backed up by a data matrix, which positioned *Plesiadapis* as the sister taxon to Scandentia + Euprimates (their "Primates"), with Dermoptera + Chiroptera being the sister group to that clade (see Fig. 9.1B). They argued that the dental evidence linking plesiadapiforms to eu-

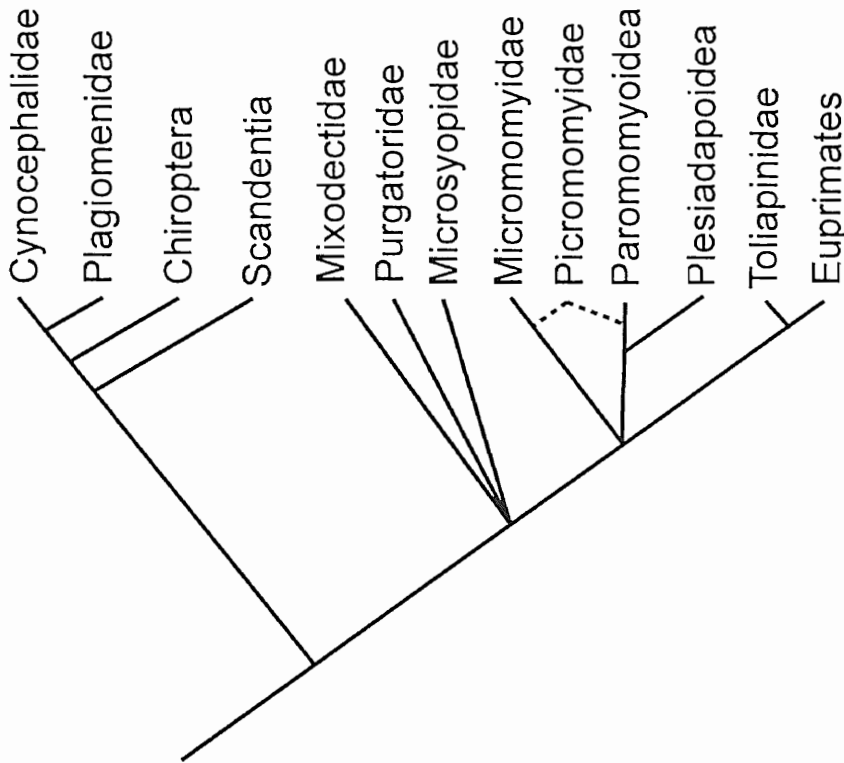


Fig. 9.6. Hypothesis of phylogenetic relationships among euarchontans. This tree is based on a parsimony analysis run in PAUP 4.0^β (Swofford, 2003) using 181 dental, cranial, and postcranial characters (Silcox, 2001). This is a simplified version of the Adams consensus tree, calculated from 20 equally parsimonious trees of length = 788 steps, CI = 0.490, RI = 0.521, and RC = 0.255. On this tree, Plesiadapoidea includes (*Chronolestes simul* (Saxonelellidae (Plesiadapidae + Carpolestidae))). Paromomyoidea includes (Picrodontidae (Paromomyidae + "Palaechthonidae")). Toliapinidae on this tree includes only *Toliapina* and *Avenius*. These results support the inclusion of plesiadapiforms in Primates and plagiomenids in Dermoptera. Also supported are the monophyly of Volitania (Dermoptera + Chiroptera) and a clade including Volitania and Scandentia. Removal of Chiroptera from the analysis does not substantively change the other relationships on the tree, but a Dermoptera + Scandentia clade is supported. A more comprehensive analysis, including new data for extant taxa (e.g., *Ptilocercus lowii*) and undescribed fossil specimens is currently being undertaken. Preliminary results (Bloch et al., 2002, 2003; Bloch and Boyer, 2003) are basically in agreement with the findings of Silcox (2001), although a more basal position within primates is supported for Micromomyidae, as is a sister-group relationship between Plesiadapoidea and Euprimates.

primates consisted only of ill-defined "trends" (1987:9) rather than well-documented synapomorphies. This conclusion was not based on a cladistic analysis that included dental data, however, and amounts to an unfounded dismissal of an entire partition of morphological data. This is particularly problematic, as the euprimate-plesiadapiform relationship had always been based largely on dental evidence. Furthermore, one of the critical basicranial features that they cited in support of a Scandentia-Euprimate clade has since been found in a paromomyid plesiadapiform (a bony tube for the internal carotid nerves and/or artery; Silcox, 2003).

Two papers published in the same issue of *Nature* in 1990 suggested different possible relationships for plesiadapiforms. These two papers documented new cranial (Kay et al., 1990) and postcranial (Beard, 1990) material of paromomyid plesiadapiforms, which was interpreted to support a closer relationship between some plesiadapiforms and Dermoptera. Subsequent, more detailed cladistic analyses (Kay et al., 1992; Beard, 1993a) supported this interpretation, and in both cases the results did not support a monophyletic Volitania. Instead, at least some plesiadapiforms were found to be sister taxa to Dermoptera, to the exclusion of Chiroptera.

Although Beard (1990, 1993a,b) and Kay and coauthors (1990, 1992) did form some similar conclusions about paromomyids and dermopterans, their results are actually incongruent regarding broader relationships within Archonta.

Kay et al. (1992) failed to support archontan or euarchontan monophyly, with paromomyids, plesiadapids, and dermopterans falling outside of erinaceomorph and tenrecoid insectivores, and presumably far distant from bats, primates, and tree shrews (see Fig. 9.1D). Like Wible and Covert (1987), these authors did not include dental data in their analysis and obtained results that supported a sister-group relationship between scandentians and euprimates. Kay et al. (1992) also presented evidence that paromomyids and plesiadapids form a monophyletic clade to the exclusion of dermopterans. Beard (1993a; see Fig. 9.1C), however, argued for a paraphyletic Plesiadapiformes, with paromomyids being more closely related to modern dermopterans than to any other plesiadapiforms, including plesiadapids. Beard recognized this relationship by including plesiadapiforms with cynocephalids (=his galeopithecids; see above) in Dermoptera and proposing a new group name, Eudermoptera, for modern dermopterans + paromomyids. In a subsequent paper, Beard (1993b) expanded Eudermoptera to include Micromomyidae, based on the hypothesis that gliding had already evolved in this group. A key element of this argument was the presence of relatively long, thin intermediate manual phalanges in Paromomyidae and Micromomyidae. This morphology was interpreted to reflect the presence of the uniquely dermopteran interdigital patagium, based on the same functional argument that alleged a relationship between this feature and improved control of the patagium in modern cynocephalids. In contrast to Kay

et al. (1992), Beard (1993a,b) argued that it was this reconstituted Dermoptera (*sensu lato*) that was the sister taxon to euprimates, proposing the name Primatomorpha for Dermoptera (including plesiadapiforms) + Primates. The sister group to this clade in Beard's (1993a) analysis was Chiroptera, with Scandentia falling out as the basalmost group of archontans. By excluding nonarchontan mammals, Beard's (1993a) analysis did not test the monophyly of Archonta as a whole.

Both the results of Beard (1990, 1993a,b) and Kay et al. (1990, 1992) suggested alternatives not only to the systematic position of plesiadapiforms, but also to the relationships of archontans in general. An implication of these papers is that an understanding of the systematic position of plesiadapiforms is central to an understanding of archontan relationships. In particular, these hypotheses represent competing viewpoints as to the monophyly of Volitantia. Some authors have tried to reconcile these views by simply classifying some plesiadapiforms in Dermoptera (e.g., Thewissen and Babcock, 1992; Simmons and Quinn, 1994). These implied phylogenetic hypotheses are not based on cladistic analysis, however, and are directly at odds with the results of Beard (1990, 1993a,b) and Kay et al. (1990, 1992).

The hypotheses of Kay et al. (1990, 1992) and Beard (1990, 1993a,b) have not gone unchallenged, with many papers questioning elements of both the systematic and functional conclusions reached by these authors (e.g., 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; Bloch and Silcox, 2001; Boyer et al., 2001; Bloch and Boyer, 2002, 2003; Bloch et al., 2002; Sargis, 2002c; Silcox, 2003). The issues raised by these authors include problems with the identification of some of the phalanges attributed to paromomyids and micromomyids, demonstrating that these taxa do not have the unusual hand proportions found in dermopterans (Krause, 1991; Boyer et al., 2001; Hamrick, 2001; Bloch and Boyer, 2002). Moreover, the discovery of "primatomorphan" features in the most plesiomorphic extant scandentian greatly weakens the postcranial support for the monophyly of Primatomorpha (Sargis, 2002c). New discoveries, and new interpretations of the cranial material have also called into question the degree of similarity between dermopterans and paromomyids in the ear region (Wible, 1993; Wible and Martin, 1993; Bloch and Silcox, 2001; Silcox, 2003).

New phylogenetic analyses and new fossil finds have suggested a return to earlier views (e.g., Szalay and Delson, 1979; Szalay et al., 1987) that Primates should be defined in such a way that plesiadapiforms are included. For example, the first associated skeletal material ever recovered for a carpolestid has revealed the presence of a divergent, opposable hallux with a nail, a feature previously thought to be limited to euprimates (Bloch and Boyer, 2002). A cladistic analysis of plesiadapiforms and other archontans, incorporating cranial, dental, and postcranial features, also failed to support the Eudermoptera or Primatomorpha hypotheses. Instead,

it supports a sister-group relationship between Euprimates and a paraphyletic Plesiadapiformes (Fig. 9.6; Silcox, 2001; see also Bloch and Boyer, 2002, 2003; Bloch et al., 2002). Although the results of this analysis support Volitantia, contrary to the molecular results mentioned above, the inclusion of bats is not critical to the overall topology, as no substantive changes in the other relationships on the tree occur when the analysis is run without Chiroptera. In particular, a relationship between Dermoptera and Scandentia was maintained, which matches the findings of some recent molecular work (e.g., Liu et al., 2001; Murphy et al., 2001a,b; Springer et al., 2003, 2004). In light of the exclusion of ungulates and carnivorans from this dataset (taxa that are supposed to be closer to bats than are euarchontans, according to molecular results), this analysis cannot yet be seen as a test of the monophyly of either Volitantia or Archonta, leaving the systematic position of Chiroptera equivocal.

Plesiadapiforms include the oldest known archontans (or euarchontans), in the family Purgatoriidae. The earliest possible member of this family, *Purgatorius ceratops*, dates from the latest Cretaceous (Van Valen and Sloan, 1965; Van Valen, 1994) or earliest Paleocene (Lofgren, 1995; Clemens, in press) and comes from North America.

Plagiomenidae

Plagiomenidae is known from the Paleocene and Eocene of North America. The dental similarities between Plagiomenidae and modern dermopterans have been recognized ever since *Plagiomene* was first described in 1918 (Matthew, 1918), and until recently, most authors treated members of this group as the earliest representatives of that order (e.g., Rose, 1973). MacPhee et al. (1989) provided the first description of cranial material of a plagiomenid. The specimen they described was heavily damaged, but their reconstruction hypothesized some profound differences from modern dermopterans. In particular, they reconstructed the auditory bulla as a highly complex, composite structure quite unlike the bulla of extant dermopterans.

Although not providing any additional evidence for a plagiomenid-dermopteran relationship, this basicranial evidence also did not convincingly support any other set of relationships—it only demonstrated the morphology to be oddly autapomorphic. As such, the ear morphology does not necessarily detract from the phylogenetic signal of the dentition. New results from an analysis including both dental and cranial traits (Silcox, 2001; Fig. 9.6) support the traditional alliance of plagiomenids with modern dermopterans, suggesting again that this family may be the earliest representation of Dermoptera known in the fossil record.

Mixodectidae

Mixodectidae, from the Torrejonian (early Paleocene) of North America, has often been linked to Plesiadapiformes, based on dental similarities between this group and Micro-

syopidae (see the historical review in Szalay, 1969). Szalay (1969) argued against such an association, and also rejected a mixodectid-plagiomenid link. Gunnell (1989) performed a cladistic analysis of plagiomenids and mixodectids. Although this analysis might seem to support a sister-group relationship between these families, failure to include other taxa means that other possibilities were not tested. Gunnell (1989: 67) concluded that mixodectids were “difficult to evaluate systematically or functionally.” Szalay and Lucas (1996) published the first postcranial material attributed to the group, and documented a number of similarities to plesiadapiforms, *Ptilocercus*, and their reconstruction of the “protoeuprimate,” suggesting that Mixodectidae is referable to Archonta (or Euarchonta). Where preserved, this postcranial material suggests that mixodectids are an aberrant group of basal archontans, but does not provide evidence of supposed volitantian features (Silcox, 2001). This argues weakly against a special relationship with plagiomenids if Volitania is monophyletic, although plagiomenids are unknown from the postcranium.

Nyctitheriidae

Nyctitheriidae is a family of insectivores from the Paleocene and Eocene of North America and Asia, and the Paleocene-Oligocene of Europe (McKenna and Bell, 1997). Dental similarities between nyctitheriids and chiropterans have long been recognized. For example, *Wyonycteris*, a taxon that was initially described as the earliest bat (Gingerich, 1987) is now generally included in Nyctitheriidae (e.g., McKenna and Bell, 1997), following challenges to its chiropteran status (Hand et al., 1994; Hooker, 1996).

Recently, postcranial material has been described for the family (Bloch and Boyer, 2001; Hooker, 2001; Bloch et al., 2003). The tarsal elements studied by Hooker (2001) revealed some surprising similarities to archontans. When Hooker included these features—along with cranial and dental traits—in a cladistic analysis, he found a sister-group relationship between nyctitheriids and a Euarchonta clade that included a plesiadapiform, a euprimate, a dermopteran, a scandentian, and *Mixodectes*. Hooker also supported a close relationship between Nyctitheriidae + Euarchonta and a late Cretaceous primitive mammal from Asia, *Deccanolestes*, with microchiropterans lying outside of this clade. *Deccanolestes* was included in Hooker’s analysis, based on a hypothesized relationship with Archonta from tarsal evidence (Prasad and Godinot, 1994), which, if upheld, would make it the earliest known archontan. Although Hooker’s analysis included relatively little taxonomic diversity, his findings suggest that nyctitheriids warrant additional consideration as possible primitive archontans or euarchontans.

Apatemyidae

Apatemyidae is a broadly dispersed and long-lived family of odd fossil mammals from the Paleocene and Eocene of

Europe and the Paleocene-Oligocene of North America (McKenna and Bell, 1997). Apatemyids exhibit some general dental similarities to plesiadapiforms, including a set of enlarged upper and lower central incisors. Gingerich (1989) suggested that the family could belong in the same taxonomic assemblage as plesiadapiforms (“Proprimates”), and MacPhee et al. (1983) placed apatemyids as one of several groups possibly related to the origin of Primates. Other authors, however, have questioned a close association of this family with early primates (e.g., McKenna, 1963, 1966; Szalay, 1968a; Silcox, 2001). In their recent classification of mammals, McKenna and Bell (1997) classified Apatemyidae in the order Cimolesta with several other primitive mammalian groups (e.g., palaeoryctids), under the grandorder Ferae, indicating a closer relationship to carnivorans than to primates.

A cladistic analysis capable of assessing a possible apatemyid-primate relationship has never been performed. The recent discovery of relatively complete material for apatemyids, including well-preserved crania and postcrania, (e.g., Koenigswald, 1990; Bloch and Boyer, 2001) suggests that a reassessment of possible archontan or euarchontan affinities for this group may be warranted (Godinot, pers. comm.). The material from Messel that has been described indicates arboreality, and presumably convergent adaptive similarities to the euprimate *Daubentonia*. The very long fingers of apatemyids are also seen in many archontans (part of the gliding/flying complex in dermopterans and chiropterans, and associated with grasping in euprimates and non-plesiadapid plesiadapiforms; Simmons and Geisler, 1998; Hamrick, 2001; Bloch and Boyer, 2002, 2003). Although a tie with Archonta remains tentative at the current time, further analysis of undescribed specimens is warranted to more fully assess this possibility.

TIMES OF ORIGIN

Various studies have attempted to estimate the time of origin of Primates using molecular data. These estimates have generally produced dates for the divergence of primates that extend well into the Cretaceous (e.g., Hedges et al., 1996; Árnason et al., 1998; Eizirik et al., 2001), averaging around 90 million years ago (Tavaré et al., 2002) and implying an even earlier divergence date for Archonta or Euarchonta. The most recent molecular estimates, from an analysis that controls for many of the problems that have plagued previous studies, indicate somewhat later divergences. Springer et al. (2003) support late Cretaceous dates for the major events in euarchontan diversification (including origination of the group from a common ancestor with Glires), with all such branching events likely postdating the 90 million year mark, but predating the K/T boundary. These estimates are closer to the age of the oldest euarchontan fossils.

The very limited paleontological record for scandentians and crown-clade dermopterans makes it impossible to

formulate a plausible fossil-based hypothesis for a time of origin for these groups, as it seems clear that they have very long ghost lineages. The oldest possible dermopteran, however, is the early Paleocene (Torrejonian) plagiomenid *Elpidophorus*, indicating that Dermoptera had likely arisen by that time. The oldest known clear archontans (or euarchontans; i.e., not including the poorly known *Deccanolestes*) are plesiadapiform primates. The earliest proposed date for a plesiadapiform is the latest Cretaceous age suggested for *Purgatorius ceratops* (Van Valen and Sloan, 1965; Van Valen, 1994), based on a single tooth of questionable identity. This date has been the source of considerable debate. The only known specimen of the species comes from a time-averaged Cretaceous-Paleocene (Lancian/Puercan-1) deposit, making its proposed Cretaceous age questionable (Lofgren, 1995; Clemens, in press). The next oldest euarchontan material consists of isolated teeth of *Purgatorius* from Rav-W1 (Pu-1; earliest Paleocene; Johnston and Fox, 1984). This material is better constrained geologically, and the one well-preserved upper molar exhibits features that support its interpretation as the most primitive known member of the genus (Silcox, 2001). The fossil record thus indicates that primates diverged by at least the earliest Paleocene. The earliest euprimate is *Altiatlasius*, which is late Paleocene in age (Sigé et al., 1990; Gheerbrant et al., 1998), implying that euprimates had arisen by that time.

The date of the earliest recognized fossils indicates only a minimum age for the divergence of a given clade. Various approaches have been attempted to estimate the length of the gap between the earliest fossils and the actual point of divergence for Euprimates. Gingerich and Uhen (1994) used a probability model to evaluate Cretaceous ages for the origin of euprimates (their "Primates"), concluding that it was improbable that this group arose before 63 million years ago. This analysis was based, however, on an earliest date for euprimates of 55 million years ago. Such an estimate would need to be recalculated with a late Paleocene date (based on *Altiatlasius*) for Euprimates, and an earliest Paleocene date for Primates that includes *Purgatorius*, which would likely push both of these divergences (as well as the origin of Archonta or Euarchonta) into the late Cretaceous.

Tavaré et al. (2002) reached a very different conclusion from that of Gingerich and Uhen (1994). They estimated the last common ancestor of living primates at 81.5 million years ago, which they suggested is in better agreement with molecular estimates than are other fossil-based approaches. There are several fundamental problems with the techniques applied by Tavaré et al., however, which reduce confidence in their results and in their assertion of a close agreement with molecular dates. Molecular estimates are generally based on a divergence point—that is, the date at which the stem lineage leading to some modern group branched off. Tavaré et al. dealt only with the origination time of the last common ancestor of living primates (i.e., euprimates), not taking into account the length of the stem separating divergence from origination. This is particularly problematic if plesiadapiforms are stem primates (Fig. 9.6),

as they include a broad radiation of forms, classified into more than 120 different species. These stem taxa sit in the gap between the point of divergence of the earliest primate and the point of origination of the group including all living primates. To be truly comparable with molecular estimates, their analysis would have to take these forms into consideration. In light of the speciose nature of the plesiadapiform radiation, doing so would likely push their estimated date back in time significantly, to a point even earlier than that given by molecular estimates.

Furthermore, there are some fundamental problems with the model used by Tavaré et al. (2002). By assuming a logistic diversification model, these authors do not account for two key issues in estimating early primate evolutionary rates. First, it seems likely from the relatively sudden appearance of so many plesiadapiforms and euprimates that a very rapid diversification accompanied each of these adaptive radiations. These diversifications likely resulted from the opening up of niches following the extinction of the dinosaurs, and the creation of new niches by a major radiation of angiosperms (Sussman, 1991). Second, primates, as tropical, forest-living animals, are heavily influenced by climate and the distribution of tropical forests. Consequently, rates of diversification have likely varied considerably over the history of the group. This provides an additional reason why very rapid diversification during the late Paleocene and early Eocene—the warmest period in the Cenozoic—is plausible. Tavaré et al. do not allow for such large rate variations, and particularly for unusually rapid rates at the base of the tree. When these issues are taken into consideration, it seems quite plausible that the speciose Eocene euprimate fossil record could have arisen very quickly, and did not require some 25 million years to accrue.

What can be said with some confidence is that the fossil record demonstrates that primates (and by extension Archonta or Euarchonta) had diverged by the earliest Paleocene or possibly the latest Cretaceous. There is currently no concrete paleontological support for an earlier origin for Archonta, particularly in light of the primitive nature of *Purgatorius*. Thus, the discrepancy between even the more recent molecular divergence estimates of Springer et al. (2003, 2004) and the evidence from the fossil record is still significant and must be reconciled. Future collecting may fill this gap, or it may indicate that the earliest archontans were not much separated from *Purgatorius* in either time or morphology.

PLACES OF ORIGIN

The place of origin of Archonta (or Euarchonta) remains unclear in the absence of definitive fossil stem taxa or a consensus on the group's sister taxon. If recent molecular results supporting Euarchontoglires (e.g., Waddell et al., 1999; Murphy et al., 2001a,b; Springer et al., 2003, 2004) are correct, they may be supportive of an Asian origin for Euarchonta, based on the Asian distribution of most proposed

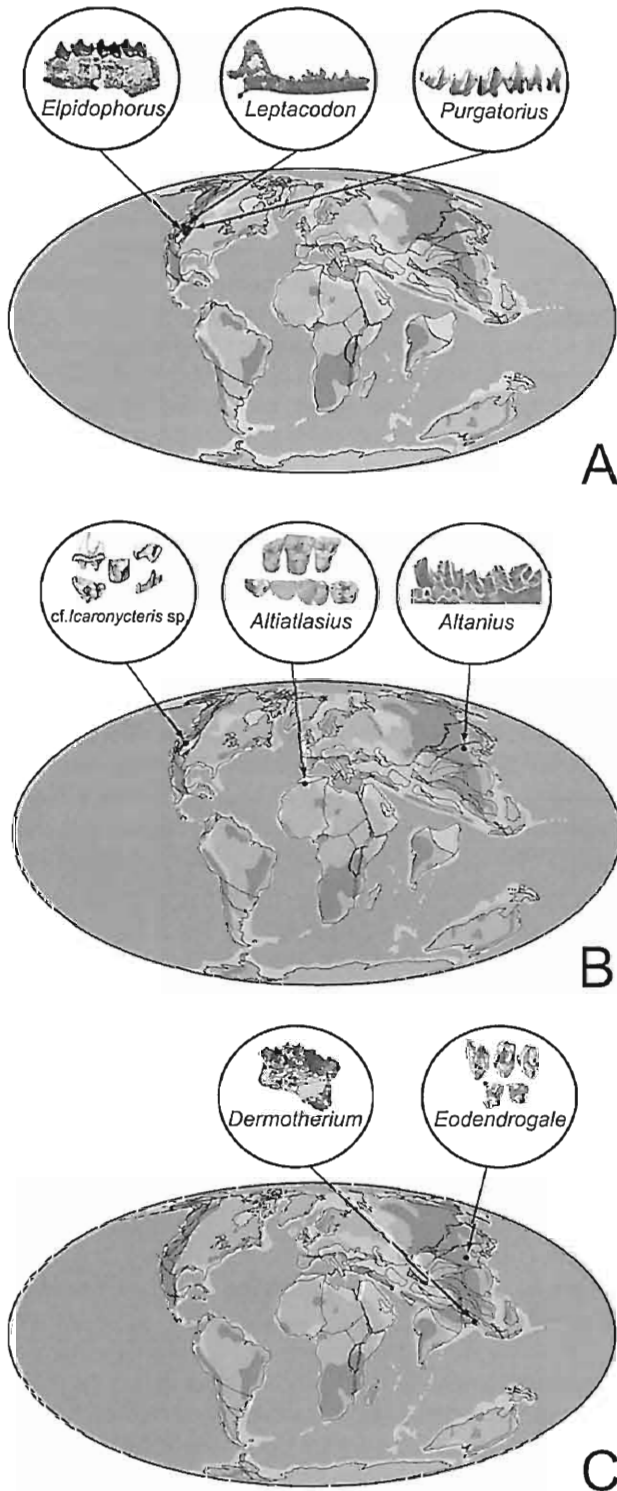


Fig. 9.7. Geographic and temporal distribution of fossils key to archontan or euarchontan origins and relationships. All maps are from Scotese (2001). (A) Early Paleocene. The only euarchontans known from the early Paleocene are the plagiomenid dermopteran *Elpidophorus* and the plesiadapiform primate *Purgatorius*, both from North America. If nyctitheriids are archontans (as suggested by Hooker, 2001), Paleocene *Leptacodon* from North America may prove key to issues of archontan (or euarchontan) origins. *Elpidophorus*: left mandible of *E. minor*, modified from Szalay (1969: plate 24 [4]); *Leptacodon*: right mandible of *L. tener*, modified from McKenna (1968: fig. 4); *Purgatorius*: right mandible of *P. janisae*, modified from Clemens (1974: fig. 2). (B) Late Paleocene. The earliest euprimate (*Altiatlasius*) and earliest chiropteran (cf. *Icaronycteris* sp.; Gingerich, 1987) appear in the late Paleocene of Africa and North America, respectively. *Altanius*, from Asia, may be latest Paleocene or earliest Eocene in age (Bowen et al., 2002). cf. *Icaronycteris*: isolated teeth of cf. *Icaronycteris* sp., modified from Gingerich (1987: fig. 23); *Altiatlasius*: isolated teeth of *A. koulichii*, modified from Sigé et al. (1990: plate 4); *Altanius*: left mandible of *A. orlovi*, modified from Rose and Krause (1984: fig. 2c). (C) Eocene. The earliest definitive dermopteran (*Dermotherium*) and scandentian (*Eodendrogale*) do not appear until the Eocene, with both specimens coming from Asia. By this time, Chiroptera and Primates were already broadly distributed across the Northern Hemisphere and, in the case of Chiroptera, Australia. *Dermotherium*: left mandible of *D. major*, modified from Ducrocq et al. (1992: fig. 1A); *Eodendrogale*: isolated teeth of *E. parvum*, modified from Tong (1988: fig. 1).

relatives or ancestors to Glires, including zalambdalestids (Archibald et al., 2001), anagalids, and pseudictopids (McKenna and Bell, 1997). The results of Silcox's analysis (2001; see Fig. 9.6) suggest a North American origin for Archonta, however, based on the North American location (Fig. 9.7) of the earliest plagiomenids (*Elpidophorus*), plesiadapiforms (*Purgatorius*), and chiropterans (*Icaronycteris*). A North American origin would also apply to Euarchonta. If mixodectids, apatemyids, and nyctitheriids are primitive archontans, then the presence of the earliest representatives of these groups in North America adds support to this idea. This pattern may be a result of preservation bias, because the fossil record from North America is more complete than that from other possible source areas, including particularly Africa, which has a very poor Cretaceous and Paleocene mammalian fossil record. If *Deccanolestes* were an archontan, this would strengthen the case for an Asian origin, although this specimen comes from the Indian subcontinent, which was isolated from the rest of Asia until approximately 55 million years ago (Clyde et al., 2003).

As noted above, the fossil record of definitive dermopteran and scandentians is extremely limited and entirely Asian in distribution. Therefore, the existing evidence supports an Asian origin for these clades, although the earliest known fossils likely significantly postdate the origins of these groups (i.e., they have ghost lineages that stretch at least the length of the Paleocene and early Eocene). If plagiomenids were dermopteran, this would substantially reduce the ghost lineage of Dermoptera. The exclusively North American distribution of plagiomenids would then suggest a North American origin for Dermoptera. The earliest record of a fossil bat, cf. *Icaronycteris* sp. (Gingerich, 1987), also comes from North America, implying that if Volitantia is valid, it may have a North American origin.

Primates can also be reconstructed as having a North American origin, based on the exclusively North American distribution of the most primitive members of this group (i.e., Purgatoriidae, Palaechthonidae, and Micromomyidae; Silcox, 2001; Bloch et al., 2003; see Fig. 9.6). Unlike that of Beard (1998), Silcox's (2001) analysis does not support an unequivocal resolution to the place of origin of Euprimates (his "Primates"). Although Asia is one possible place of origin (based largely on the primitive features of *Altanius*; Beard, 1998), the African location of the oldest fossil taxon

(*Altiatlasius*) assigned to Euprimates in Silcox's (2001) analysis makes the latter continent slightly more likely. The predominantly North American distribution of plesiadapiforms might support North America as a place of origin for Euprimates. However, because plesiadapiforms have only been known from Asia since 1995 (Beard and Wang, 1995) and are currently unknown in Africa, it is possible that a more complete record for the group would change that perception. Recent findings (Bowen et al., 2002) indicate that, contrary to previous assertions, euprimates do not occur in the North American record earlier than they do in Asia. The relatively sudden appearance of euprimates in Europe without clear precursors at the beginning of the Eocene might argue against an origin of Euprimates on this continent, in spite of the presence of the most primitive adapid (*Donrussellia*) and omomyid (*Teilhardina*; also known from North America). Silcox (2001; see Fig. 9.6), however, found support for a sister-group relationship between the plesiadapiform family Toliapinidae *sensu stricto* (i.e., including only the European genera *Toliapina* and *Avenius*) and Euprimates. Even though the support for this grouping is extremely weak (largely because Toliapinidae is known only from a handful of isolated teeth), this finding does suggest the possibility that Europe needs to be considered as a possible source area for Euprimates. In sum, the place of origin of Euprimates remains equivocal, and could conceivably be Asia, Africa, Europe, or North America.

CONCLUSIONS

These are exciting times for the study of archontan relationships. The controversy sparked by the bold interpretations by Beard (1990, 1993a) and Kay et al. (1990, 1992) of new fossil specimens has inspired new, detailed morphological descriptions of previously poorly known archontan groups (e.g., Stafford and Szalay, 2000; Sargis, 2002a–c), the introduction of new methods for analyzing and interpreting form and phylogeny (e.g., Runestad and Ruff, 1995; Hamrick et al., 1999), projects to find and study additional fossils (e.g., Bloch and Boyer, 2002; Bloch et al., 2003), and comprehensive cladistic analyses (e.g., Silcox, 2001; Bloch et al., 2002). There are two major issues that remain unresolved about this section of the mammalian evolutionary tree, however. First, stem archontan (or euarchontan) fossil taxa have yet to be convincingly identified. Second, the immediate sister taxon to Archonta (or Euarchonta) also needs to be recognized. Resolving these issues is central to a better understanding of this group, as these identifications are needed to accurately polarize characters.

Recent molecular studies have forced morphologists to query their basic assumptions and to re-evaluate interpretations of paleontological data. There are two major areas of conflict that remain between morphological and molecular results. The first relates to the timing of the origin of the group. Molecular studies conclude that the divergence point is much earlier than the fossil record would suggest. The

second relates to the phylogenetic position of bats, and by extension, to the validity of Archonta vs. Euarchonta. Molecular studies suggest that bats are members of Laurasia-theria (Murphy et al., 2001a) whereas morphology has consistently placed them in Archonta, although the molecular hypothesis has not been explicitly tested with morphological data using cladistics. Understanding and accounting for the reasons behind these divergent results remains a major challenge, which could fundamentally shake up our understanding of the early history of Archonta.

SUMMARY

Morphological evidence is supportive of a supraordinal clade including Scandentia, Dermoptera, Chiroptera, and Primates, which can be referred to as Archonta. Recent molecular studies have supported a modified version of this clade that excludes Chiroptera, called Euarchonta. Molecular estimates of origination times place Euarchonta's origin well into the Cretaceous. Fossil evidence is supportive of a more recent origin—by the latest Cretaceous or earliest Paleocene. The place of origin of Euarchonta is reconstructed as North America, although this may be a product of uneven geographic sampling in the Cretaceous and Paleocene. The fossil record of definitive members of two euarchontan groups, Dermoptera and Scandentia, is very limited. The specimens available are weakly supportive of an Asian origin for both groups and a divergence by the late Eocene. If Plagiomenidae are dermopterans, as we suggest, then this might alter the place of origin for Dermoptera to North America and the age of origin to the early Paleocene. Primates are much better known from the fossil record, and include the earliest euarchontan (*Purgatorius*) from the latest Cretaceous or early Paleocene of North America. The presence of the most primitive primates in North America supports an origin for the group on that continent. The place of origin of Euprimates remains equivocal, and may be Africa, Asia, North America, or even Europe. In light of the age of *Altiatlasius*, Euprimates had already diverged by the late Paleocene.

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