Anthropoid Origins

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Recent fossil discoveries have greatly increased our knowledge of the morphology and diversity of early Anthropoidea, the suborder to which humans belong. Phylogenetic analysis of Recent and fossil taxa supports the hypotheses that a haplorhine-strepsirrhine dichotomy existed at least at the time of the earliest record of fossil primates (earliest Eocene) and that eosimiids (middle Eocene, China) are primitive anthropoids. Functional analysis suggests that stem haplorhines were small, nocturnal, arboreal, visually oriented insectivore-frugivores with a scurrying-leaping locomotion. A change from nocturnality to diurnality was the fundamental adaptive shift that occurred at the base of the tarsier-eosimiid-anthropoid clade. Stem anthropoids remained small diurnal arborealists but adopted locomotor patterns with more arboreal quadrupedalism and less leaping. A shift to a more herbivorous diet occurred in several anthropoid lineages.

More than a century of studies in embryology, anatomy, and genetics have resolved the phylogeny of living Primates (Fig. 1). Two great clades of living primates exist, the Strepsirrhini (Lemuriformes) and the Haplorhini (*Tarsius* and Anthropoidea). Within the Anthropoidea are two clades: Catarrhini (the Old World monkeys, apes, and humans) and Platyrrhini (the New World monkeys). Paradoxically, however, the problem of anthropoid origins is still among the most hotly contested in the literature of primate evolution; no consensus has yet emerged regarding the relationships of several groups of Paleogene fossil primates to living strepsirrhines and haplorhines. This lack of consensus has stemmed principally from an absence of morphologically transitional taxa between anthropoids and any of the better known Paleogene primate groups. Here we review the fossil discoveries of the past decade, especially those that begin to close the morphological gap between anthropoids and other primates, and apply cladistic methodology to the assessment of all available fossil evidence in an effort to produce a better resolved phylogeny of primates. Building on comparative studies of primate adaptation, we propose an outline of anthropoid evolution from an adaptive perspective and review the adaptive significance of several peculiar anthropoid features.

The Fossil Record

To avoid confusion in what follows, clarification is needed concerning the usage of several taxonomic names. The taxa Strepsirrhini, Haplorhini, and Anthropoidea, as we use them, refer to "closed descent communities" or stem-based clades (*1*). Anthropoidea is the clade of all species, living or extinct, that are more closely related to living platyrrhines and catarrhines than to *Tarsius*. Similarly, Haplorhini is the clade of all species that are more closely related to Anthropoidea plus *Tarsius* than to living strepsirrhines. (Fig. 1).

Fossil finds in North Africa have now pushed back the fossil record of Anthropoidea from the Oligocene into the Eocene (*2–4*) (Fig. 2), but no taxon yet described from the late Eocene of Africa documents an intermediate morphology between anthropoids and either tarsiers or strepsirrhines. The oldest well-known anthropoids (Parapithecidae and Oligopithecidae) come from the late Eocene of Egypt [about 37 million years ago (Ma)] (*4, 5*). Although somewhat more primitive morphologically than any living anthropoid, the parapithecids and oligopithecids possessed a platyrrhine grade of morphological organization that was substantially identical to that of living platyrrhines (*6–10*).

Early fossil tarsiers and possible lemuriforms are so poorly known that they likewise contribute nothing to narrowing the morphological gap between Anthropoidea and other primates. The fossil record of Lemuriformes remains a virtual blank before the Miocene; just a few doubtful records are recorded in the African Paleogene (*7, 11*). Recent finds have now pushed back the earliest occurrence of tarsiers to the late middle Eocene of Asia (about 45 Ma), establishing a much greater minimum age for the differentiation of the haplorhine crown group from other primates (*12, 13*). However, this material is known only from dental remains.

Two Paleogene groups often have been identified as possible sister taxa for Anthropoidea. The Eocene-Oligocene Adapidae, from North America, Asia, Europe, and Africa, is commonly considered to be the group from which Lemuriformes arose. However, some researchers have also identified them as anthropoid relatives (*14–16*). Another Paleogene group, the Omomyidae of North America, Asia, Europe, and possibly Africa, is often considered to have given rise to tarsiers and to anthropoids, either via separate omomyid stocks (*17*) or via a common stem lineage (*18*). Omomyids and adapids are now much better represented by skulls and limb bones, allowing a fuller phylogenetic assessment of the possibilities than was possible only a decade ago. A third view is that the anthropoid lineage, although sister to omomyids, goes back before the earliest known omomyid (*19*).

The discovery of remains of a new family of Eocene primates in Asia, the Eosimiidae (*12, 13*), has prompted interest in the possibility that eosimiids were ancient primitive anthropoids.

Phylogenetic Models of Anthropoid Origins

To evaluate all of the conflicting hypotheses about anthropoid relationships, we undertook a cladistic analysis of the evidence from dental, cranial, and postcranial skeletons. A total of 256 dental, cranial, and postcranial characters were assessed for 50 taxa (Table 1), including platyrrhines, lemuriforms, the best known ancient fossil catarrhine *Aegyptopithecus*, *Tarsius*, the better known adapids and omomyids (including those cited by various authors as close anthropoid or tarsier relatives), several Eocene-Oligocene African anthropoids, and *Eosimias* dental remains, plus recently reported eosimiid cranial and postcranial material.

Our results (Fig. 3) support these major conclusions: (i) The primary dichotomy in living primates is between haplorhines (*Tarsius* and Anthropoidea) and strepsirrhines (Lemuriformes). (ii) Adapidae is the sister group of Lemuriformes and therefore should be assigned to the strepsirrhine side of the dichotomy. As a consequence, Adapidae are not the sister group of Anthropoidea. (iii) Omomyidae should be assigned to the haplorhine side of the dichotomy. (iv) Eosimiidae is the sister group of Anthropoidea. (v) *Tarsius* is either the sister group of the *Eosimias*-Anthropoidea clade or nested within the omomyids; its exact phyletic position is uncertain and is contingent on the allocation of cranial material of *Eosimias*.

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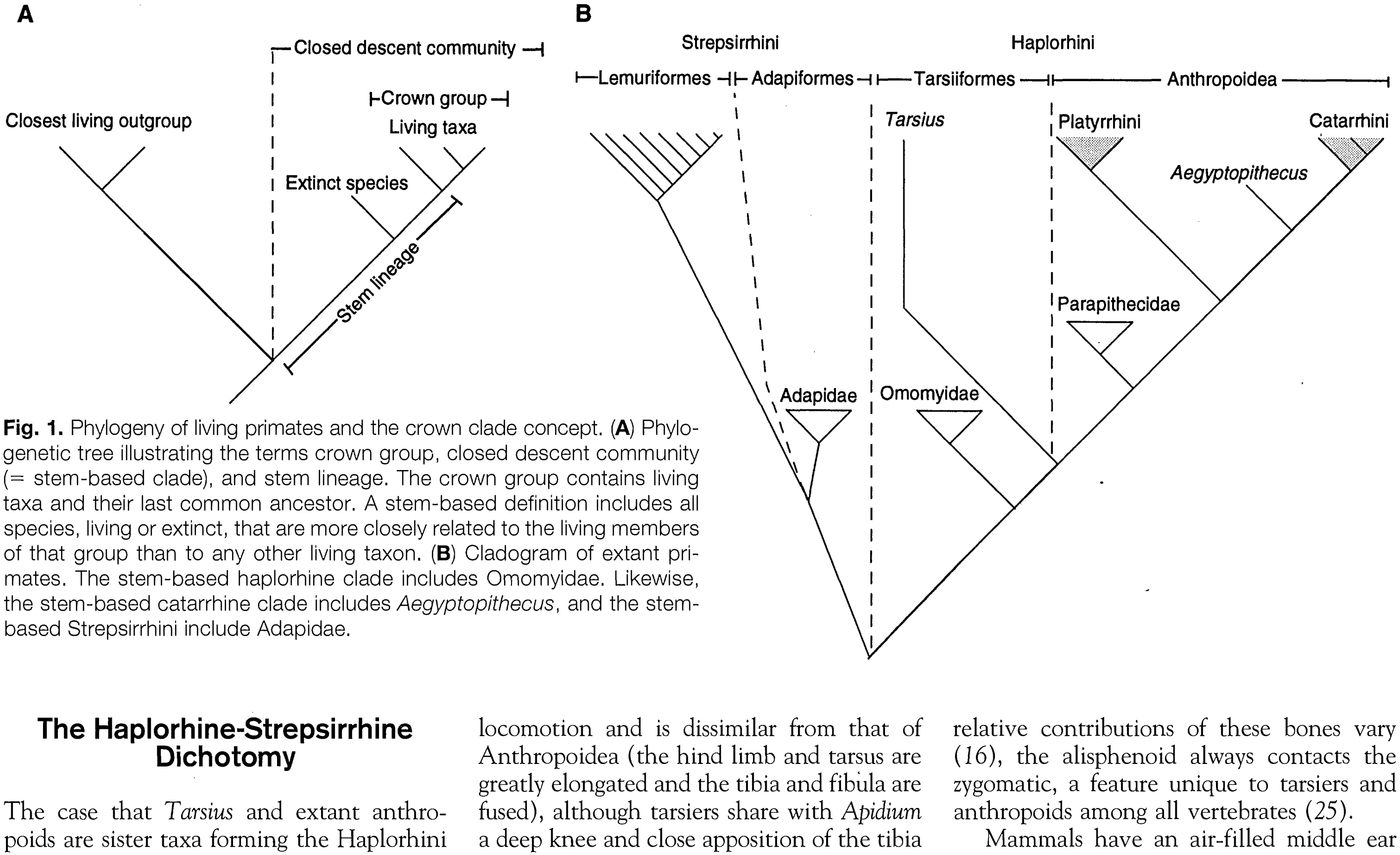

Fig. 1. Phylogeny of living primates and the crown clade concept. (**A**) Phylogenetic tree illustrating the terms crown group, closed descent community (= stem-based clade), and stem lineage. The crown group contains living taxa and their last common ancestor. A stem-based definition includes all species, living or extinct, that are more closely related to the living members of that group than to any other living taxon. (**B**) Cladogram of extant primates. The stem-based haplorhine clade includes Omomyidae. Likewise, the stem-based catarrhine clade includes *Aegyptopithecus*, and the stem-based Strepsirrhini include Adapidae.

The Haplorhine-Strepsirrhine Dichotomy

The case that *Tarsius* and extant anthropoids are sister taxa forming the Haplorhini was first formalized by Pocock and is supported by synapomorphies of soft tissues, by genetics, including DNA sequence data, and by placentation (*20*). A number of dental and, especially, cranial synapomorphies are also known for living Haplorhini (*21–23*). These characters support the hypothesis of crown haplorhine monophyly and are useful guides to the allocation of extinct species for which only morphological data are available.

Tarsiers share only a few dental synapomorphies with anthropoids [orientation of the cristid obliqua and depth of the hypoflexid of M_1 (*21*)]. The postcranial anatomy of tarsiers is very specialized for saltatory locomotion and is dissimilar from that of Anthropoidea (the hind limb and tarsus are greatly elongated and the tibia and fibula are fused), although tarsiers share with *Apidium* a deep knee and close apposition of the tibia and fibula (fused in *Tarsius*) (*24*). In contrast, a number of tarsier-anthropoid synapomorphies unique among primates and all other Mammalia are found in the orbit and middle ear. Among the more important are the following: All primates have a bony lateral orbital bar running from the braincase to the zygomatic arch, but anthropoids and tarsiers are distinguished from other primates (and all other Mammalia) by the expansion of this bar into a postorbital septum—a thin wall of bone separating the orbit from the temporal fossa (Fig. 4). The postorbital septum is composed of the same bones in both tarsiers and anthropoids, and although the relative contributions of these bones vary (*16*), the alisphenoid always contacts the zygomatic, a feature unique to tarsiers and anthropoids among all vertebrates (*25*).

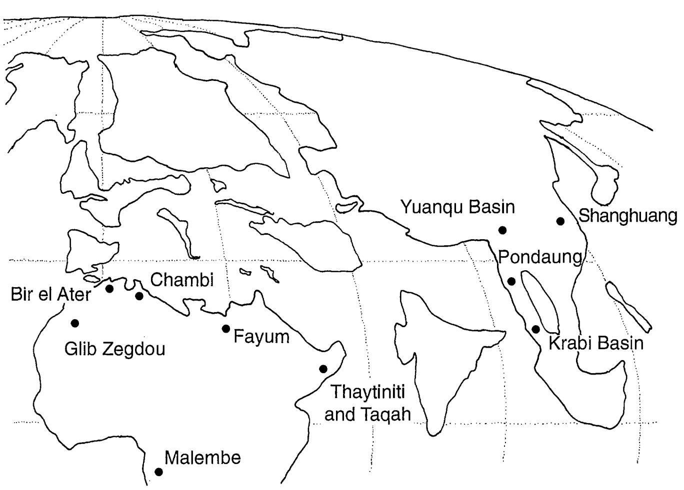

Fig. 2. Distribution of important fossil sites yielding taxa discussed in the text. The map reconstructs the estimated continental positions and coastlines in the late Eocene (about 37 Ma), after (*84*). The sites are the Yuanqu Basin and Shanghuang, China; Pondaung, Burma; the Krabi Basin (Wai Lek), Thailand; Thaytiniti and Taqah, Oman; Fayum, Egypt; Chambi, Tunisia; Glib Zegdou and Bir el Ater, Algeria; and Malembe, Angola.

Mammals have an air-filled middle ear chamber, the tympanic cavity, which houses the ear ossicles and communicates with the pharynx via the auditory tube. In all primates, the tympanic cavity is floored by the petrosal bone, forming an auditory "bulla." In tarsiers and anthropoids, a unique chamber, the anterior accessory chamber, develops as a diverticulum from the auditory tube, with which it remains connected via a narrow opening in adult life (*18, 26*) (Fig. 5).

The internal carotid artery of primates (the artery that in most species supplies the majority of blood to the cerebral arterial circle) courses through the middle ear via a bony canal (*27*). In tarsiers and anthropoids, the internal carotid canal lies wholly within a septum separating the tympanic cavity from the anterior accessory chamber. In addition, tarsiers and anthropoids lack a functional stapedial branch of the internal carotid artery and have a ventrally placed posterior carotid foramen that lies rostral to the fenestra cochleae (*18, 22*).

Adapidae Are Strepsirrhines

Since the turn of this century a hypothesis has existed that an extinct group of the Adapidae is the sister group to Anthropoidea (*28*). Its current advocates (*11, 14, 15, 29*) single out the adapid subfamily Cercamoniinae as the most likely group. Our analysis supports a different view: Cercamoniines are adapids and adapids as a whole are sister to Lemuriformes. This in turn means that proposed dental similarities between adapids and anthropoids must either be symplesiomorphies or homoplasies.

Considerable evidence supports allocation of adapids to strepsirrhines. Similarities of the ear region shared by adapids and Lemuriformes are well known (*8*, *22*, *30*). Most salient are the ring-shaped tympanic bone enclosed within the tympanic cavity, and the posterolateral and dorsal position of the posterior carotid foramen. Adapids and Lemuriformes also share a number of synapomorphies in the bones of the hand and foot. These include a well-developed posterior trochlear shelf of the talus, anterolateral orientation of the medial malleolus, and lateral positioning of the groove for the flexor fibularis of the tibia (*31*, *32*). Allocation of Adapidae to Strepsirrhini presents a substantial impediment to derivation of anthropoids from adapids because, if the basic haplorhine-strepsirhine dichotomy is to be preserved, adapids cannot be both strepsirrhines and anthropoid ancestors. Therefore, proposed evidence of an adapid-anthropoid link must be reevaluated.

Adapids lack the derived cranial features of the orbit and ear region shared by tarsiers and anthropoids (*33*). Recently, new evidence about the cranial anatomy of *Catopithecus* (*6*) shows that it possesses most of the synapomorphies of crown haplorhines or crown anthropoids and differs only in having a more pronounced development of the premaxilla, an unexpanded occipital region, a relatively small brain, relatively small olfactory lobes, and incomplete fusion of the metopic suture in a late juvenile–stage specimen. None of these features could be considered as possible synapomorphies with adapids.

The closest similarities between adapids and anthropoids occur in the dentition and jaws, but there are several serious difficulties with the use of these features to infer phylogeny. First, no single adapid species possesses all the features claimed to link them to early anthropoids, and some of the features may not characterize early anthropoids at all. For example, fusion of the mandibular symphysis characterizes all living anthropoids and is found in some species of each clade of adapids, including advanced cercamoniines. However, the late Eocene anthropoids *Arsinoea* and *Catopithecus* had unfused symphyses (*11*, *21*), which shows that this adapid-anthropoid similarity evolved independently.

Other features in which adapids resemble anthropoids were probably present in the stem lineage of all primates and cannot therefore be synapomorphies of an adapid-anthropoid clade. The most important of these features are the size, proportions, and shape of the incisors. Late Eocene anthro-

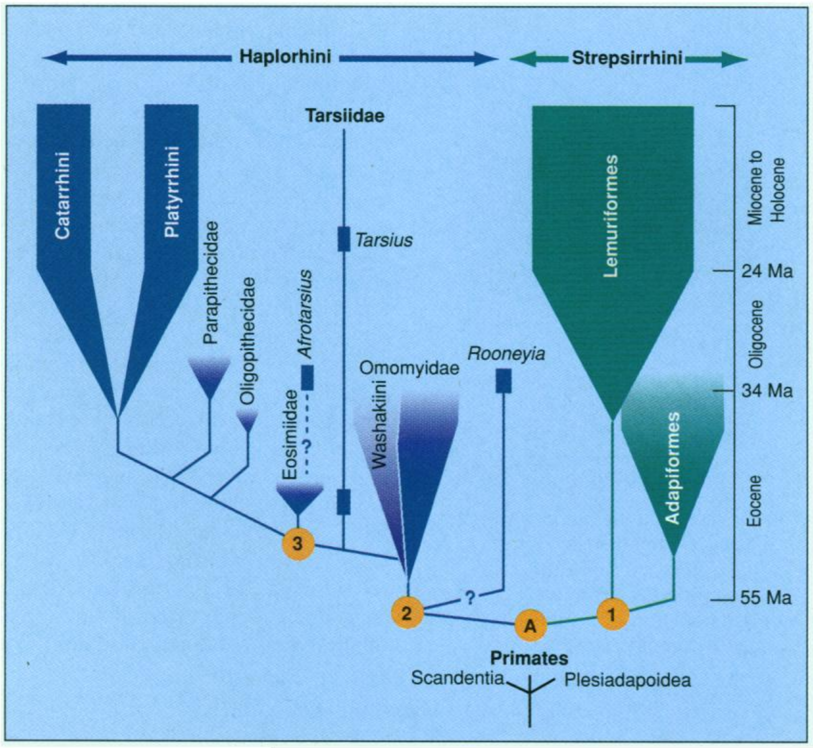

Fig. 3. Phylogenetic relationships of the better known taxa of Eocene and Oligocene primates [as well as extant haplorhines and strepsirrhines; data from (*8, 10, 13, 21, 31, 41, 44, 45, 48, 80, 81, 85, 86*)], updated with personal observations. Taxa used in the analysis are listed in Table 1. Extant Scandentia (*Tupaia glis* and *Ptilocercus lowii*) and Paleocene Plesiadapiformes (*Purgatorius unio* and *Plesiolestes problematicus*) were designated as outgroups. *Afrotarsius* is fit post hoc onto the constrained tree topography. For in-group taxa, the Consistency Index = 0.425 and the Retention Index = 0.595. (Character states and a character-taxon matrix are available at http://www.sciencemag.org/feature/data/kay.shl.) The most important synapomorphies of the numbered clades are discussed in the text. Separate analyses of cranial, postcranial, and dental characters reveal that the phylogenetic signal is not uniformly distributed in the data. For example, when the cranial data are analyzed alone, *Tarsius* is the sister taxon of a monophyletic Anthropoidea, with *Eosimias* (known only from a petrosal) falling out among the omomyids, whereas analysis of the dental data set alone supports a *Tarsius-Eosimias* clade. The postcranial evidence most strongly supports adapid-lemuriform monophyly, an anthropoid-Eosimias clade, and a close relationship between *Tarsius* and the omomyid tribe Washakiini. Temporal calibration of this cladogram suggests that haplorhine-strepsirrhine cladogenesis was pre-Eocene. Symbols at the nodes are as follows: A, Order Primates; 1, Strepsirrhini; 2, Haplorhini; 3, Anthropoidea. Cladogenesis within Anthropoidea is justified in (*21*).

Table 1. The classification followed in the text. Genera shown are only those used in the cladistic analyses. All genera are represented by dental data; * indicates postcranial data and † indicates cranial data. We follow Jenkins in the spelling of Strepsirrhini (*87*).

Order Primates
Semiorder Strepsirrhini
  Suborder Lemuriformes
    *Galago**†, *Nycticebus**†, *Microcebus**†, *Lemur**†
  Suborder Adapiformes
    Family Adapidae: *Adapis**†, *Leptadapis**†, *Afromonius*, *Mahgarita*†, *Protoadapis*, *Cantius* (includes some cranial and postcranial data from *Notharctus**†), *Pronycticebus*†, *Donrussellia*
Semiorder Haplorhini
  Suborder Tarsiiformes
    Family Omomyidae: *Omomys**, *Uintanius*, *Absarokius**, *Tetonius*†, *Anaptomorphus*, *Aycrossia*, *Strigorhysis*, *Anemorhysis*, *Microchoerus**, *Necrolemur**†, *Pseudoloris*, *Trogolemur*, *Arapahovius**, *Tetonoides*, *Dyseolemur*, *Loveina*, *Shoshonius*†, *Hemiacodon**, *Macrotarsius*, *Teilhardina americana**, *Teilhardina belgica*, *Steinius*, *Nannopithex**, *Washakius*
    Family Tarsiidae: *Tarsius**†
    Family *incertae sedis*: *Rooneyia*†
  Suborder Anthropoidea
    Infraorder Platyrrhini
      Family Cebidae: *Dolichocebus*, *Saimiri**†, *Aotus**†, *Callicebus**†
    Infraorder Catarrhini
      Family Propliopithecidae: *Aegyptopithecus**†
    Infraorder Parapithecoidea
      Family Parapithecidae: *Apidium**†, *Parapithecus*, *Simonsius*, *Serapia*, *Arsinoea*
    Infraorder *incertae sedis*
      Family Oligopithecidae: *Catopithecus**
      Family Eosimiidae: *Eosimias**†

poids, like crown anthropoids, have small lower incisors with $I_1 < I_2$. The lower central incisor is spatulate, and the lower lateral incisor is asymmetric, having a flattened mesial edge and a sloping distal edge. The upper central incisor is spatulate, and the upper lateral is pointed or wedge-shaped (*6, 21*).

Adapids resemble anthropoids in having small lower incisors with $I_1 < I_2$, whereas many omomyids have an enlarged I_1 relative to I_2. This apparent distinction between adapids and omomyids is one of the most often cited resemblances between adapids and anthropoids to the exclusion of omomyids (*11, 15*). Significantly, however, some omomyids resemble adapids and anthropoids in incisor morphology: *Washakius* and several other omomyid taxa, including *Teilhardina belgica* (considered by many to be the most primitive known omomyid), have lower incisor proportions resembling those of adapids (*34*). Some omomyids (*Macrotarsius*) have spatulate upper central incisors, and others (*Tetonius* and *Arapahovius*) have a semispatulate I^1 with a pointed tip (*35*). It is probable that the similarities in incisor morphology between adapids and anthropoids are actually primitive for primates (*34, 36*). The lower incisor morphology of *Eosimias* resembles this proposed ancestral morphology (*13*).

In sum, an adapid-anthropoid relationship is unlikely because many of the putative synapomorphies linking the two groups are homoplasies and others are symplesiomorphies, and because postcranial and cranial evidence suggests that adapids are more closely related to extant strepsirrhines than to anthropoids.

Omomyids Are Haplorhines

Cranial and postcranial similarities between omomyids and tarsiers have led many to suggest that Anthropoidea and *Tarsius* may have arisen from separate omomyid ancestors (*37–39*). This proposal is unlikely for two reasons. First, as noted, the above-mentioned synapomorphies of *Tarsius* and Anthropoidea are more numerous and trenchant than those between *Tarsius* and any omomyid. Second, many proposed synapomorphies of a tarsier-omomyid clade (which would exclude Anthropoidea) are more widely distributed among omomyids, leaving open the possibility that they are characters of a more inclusive haplorhine clade including tarsiers, Anthropoidea, and omomyids.

Necrolemur (Microchoerinae, middle Eocene, Europe) and *Shoshonius* (Washakiini, Omomyidae, early Eocene, North America), representing two different subfamilies of Omomyidae, have been independently proposed as close tarsier relatives, based on cranial synapomorphies (*37, 40, 41*). The proposed synapomorphies shared by *Tarsius* on one hand and *Necrolemur* and *Shoshonius* (as well as other less well-known omomyids) on the other include orbits that are large relative to skull length (associated with peaked nasal choanae), a lateral pterygoid plate overlapping the lateral wall of the auditory bulla, a flange of the basioccipital that laps onto the medial wall of the auditory bulla, and origin of the stapedius muscle outside the auditory bulla (*38*). However, the only feature that *Tarsius* shares with one of these taxa (*Shoshonius*) to the exclusion of other omomyids is greatly enlarged orbits (*8*). The presence of all the foregoing features in representatives of several omomyid subfamilies suggests that they are synapomorphies of omomyids as a whole; if so, such resemblances cannot be counted as evidence of a close relationship between tarsiers and any one omomyid lineage.

It has recently been suggested that the morphology of the anterior dentition supports a *Tarsius-Dyseolemur* (Washakiini, late Eocene, North America) sister group relationship (*39*). *Tarsius* has a specialized, daggerlike, upper central incisor and a smaller, pointed lateral incisor. Together

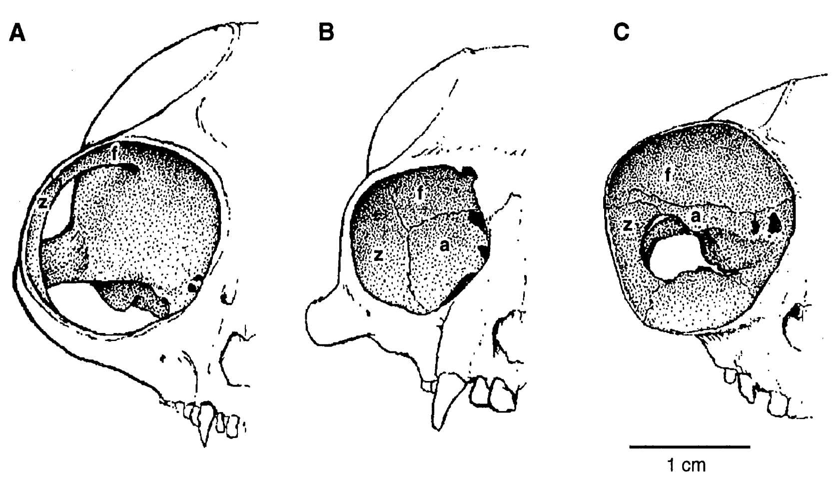

Fig. 4. The orbit of representative primates shown in frontal view, illustrating the composition of the lateral orbital wall. (**A**) *Nycticebus coucang* (Loroidea). (**B**) *Saguinus* sp. (Anthropoidea, Platyrrhini). (**C**) *Tarsius* sp. (Tarsiidae). All primates have some degree of postorbital closure. In strepsirrhines [see (A)], there is a postorbital bar formed by contact between the frontal (f) and zygomatic (z) bones. Anthropoids and tarsiers are the only mammals with a postorbital septum formed from frontal, alisphenoid (a), and zygomatic bones, and the only vertebrates with a zygomatic-alisphenoid contact.

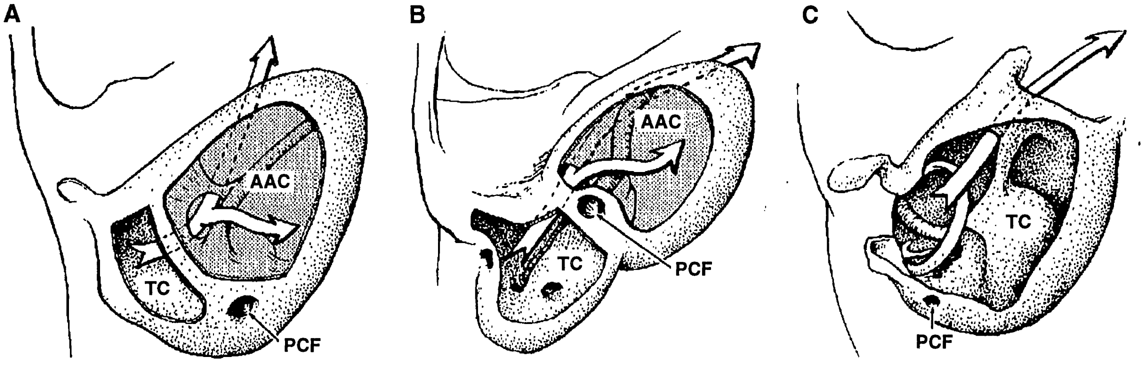

Fig. 5. The ear region of representative primates. (**A**) Basal catarrhine, *Aegyptopithecus zeuxis*. (**B**) *Tarsius* sp. (**C**) A lemuroid. The right ear region is shown in basal view with the auditory bulla opened to reveal the tympanic cavity (TC) and the anterior accessory cavity (AAC) (the latter is only present in tarsiers and anthropoids). Lateral is to the left, rostral to the top. The position of the posterior carotid foramen (PCF), where the internal carotid artery enters the skull, is also shown. Tarsiers and anthropoids share the possession of an AAC and the internal carotid artery running at the base of the septum separating AAC and TC. Arrows show continuity between the air-filled tympanic cavity into the auditory tube (in all three animals) and into an aditus connecting the auditory tube and AAC (in tarsiers and anthropoids).

with the large upper canine, these incisors have interlocking occlusion with a single lower incisor, probably I_1, and a large lower canine. This arrangement presumably is important for puncturing and subduing prey. *Dyseolemur* resembles *Tarsius* in having a pointed I^1 and I^2 and a somewhat enlarged upper and lower canine. However, *Dyseolemur* differs from *Tarsius* in having a lower central incisor that, although pointed, is not greatly enlarged. Thus, although the anterior dentition of *Dyseolemur* shows substantial functional resemblance to that of *Tarsius*, it is as likely to be due to convergence as to shared ancestry.

Postcranial evidence has been used to support a sister group relationship between *Tarsius* and *Necrolemur*. Most omomyids have moderately elongated tarsals and an unfused tibia-fibula, but *Tarsius* and *Necrolemur* share dramatic anterior elongation of the calcaneus and fusion of the distal tibia and fibula (*30, 42*). Although tibiofibular fusion is uncommon among primates, close approximation of the tiba and fibula with a syndesmotic joint (presumed in fossils) is widespread, including the extant *Galagoides* (Galagidae) and the fossils *Absarokius* (Omomyidae) and *Apidium* (Parapithecidae). Moreover, *Necrolemur*'s closest relative *Nannopithex* does not exhibit tibiofibular fusion. It seems more likely that *Absarokius*, *Apidium*, *Necrolemur*, and *Tarsius* evolved their postcranial similarities convergently, possibly as adaptations to specialized leaping. In further support of this conclusion, as noted above, no known cranial synapomorphies link *Necrolemur* with tarsiers to the exclusion of other omomyids (*9*).

In sum, numerous cranial, dental, and postcranial synapomorphies between *Tarsius* and omomyids are compelling evidence for the inclusion of omomyids within the Haplorhini. Most of the apparent tarsier-omomyid synapomorphies are actually haplorhine synapomorphies. Cranial synapomorphies link tarsiers and anthropoids into a monophyletic group that evolved from one omomyid lineage, possibly that leading to washakiins. Nevertheless, the possibility cannot be excluded that *Tarsius* and Anthropoidea arose from separate clades of omomyids—*Tarsius* from washakiins and anthropoids from some as yet unknown group.

Eosimias and the *Tarsius*-Anthropoid Clade

It has been suggested that the Eosimiidae from the late middle Eocene Shanghuang fissures of China (*12, 13, 43*) are stem anthropoids, and the dental evidence supports this view. *Eosimias* possesses several dental and gnathic features that closely approximate our concept of the primate ancestral morphology (an unfused mandibular symphysis, large canines, and $I_1 < I_2$) as well as several stem haplorhine features (single-rooted P_2; $P_{3\text{-}4}$ mesiodistally short, and cheek teeth slightly exodaenodont), all of which are still retained in undoubted anthropoids of the late Eocene. Still other traits ($P_{3\text{-}4}$ roots obliquely oriented, vertically implanted lower incisors, and mandibular symphysis oriented rather vertically) may be synapomorphies of an eosimiid-anthropoid clade, although none of these possible synapomorphies is unique to these taxa.

An isolated petrosal bone from the same locality as the type specimen of *Eosimias sinensis* is attributed to the Eosimiidae (*43*). It is important because it resembles the petrosals of omomyids but lacks the features of the middle ear region linking anthropoids to tarsiers (*8, 22*). If this petrosal is indeed that of an eosimiid, it weakens the case for a tarsier-anthropoid clade to the exclusion of omomyids. However, the petrosal may not actually be eosimiid; it is associated with eosimiids only by size and comes from the same fissure-filling as teeth of omomyids (*43*). If this petrosal is not that of an eosimiid, then *Tarsius* is most parsimoniously interpreted as the sister taxon of an eosimiid-anthropoid clade. Alternatively, although less parsimoniously, eosimiids may have retained the primitive haplorhine (and omomyid) ear region and and are phyletically sister to a *Tarsius*-anthropoid clade.

Limb bones, also from the Shanghuang fissures, allocated to eosimiids on the basis of size and abundance, show a combination of haplorhine and anthropoid features (*44, 45*). Haplorhine features of the tali are a centrally positioned flexor hallucis groove and steep-sided talo-fibular facet; haplorhine humeral features are a mesiodistally angled trochlea, a small capitular tail, and a moderately deep dorsoepitrochlear fossa. Some apparent anthropoid synapomorphies are also reported: The talar tibial facet is distally extended and dorsally elevated, with its medial margin flattened in profile, and the trochlear shelf is reduced. Further, a hallucal metatarsal has a short, rounded peroneal tubercle greatly resembling that of anthropoids but unlike that of Lemuriformes, *Tarsius*, omomyids, or adapids (*46*). Taken together, limb bone anatomy greatly strengthens the case that eosimiids are not only haplorhines but early anthropoids.

In summary, the distribution of cranial, dental, and postcranial synapomorphies definitely establishes eosimiids as haplorhines. Furthermore, dental and postcranial resemblances support an anthropoid assignment of this family and are compatible with the hypothesis of a *Tarsius*-*Eosimias*-anthropoid clade exclusive of omomyids. If *Eosimias* is an anthropoid, the evidence of the petrosal anatomy raises the possibility that primitive anthropoids lacked the features of the ear region linking *Tarsius* and Anthropoidea, making a *Tarsius*-washakiin clade more parsimonious. Choosing between these hypotheses will require better associated material of eosimiid dental and cranial remains.

Poorly Known Possible Anthropoids

Fragmentary material from the African Paleogene suggests the great antiquity and phylogenetic breadth of Primates on that continent, and some of these species have been championed as early anthropoids. *Djebelemur* (early Eocene, Tunisia) and *Shizarodon* and *Omanodon* (Oligocene, Oman) seem to be adapids, as *Aframonius* (late Eocene, Egypt) certainly is (*47, 48*). *Altiatlasius koulchii* (Paleocene, Morocco), known from a few teeth, may be an omomyid (*49*). *Plesiopithecus teras* (late Eocene, Egypt), known from a skull and mandible, has a greatly enlarged lower incisor and reduced premolar dentition. The skull shows that it is not an anthropoid (*11*).

Afrotarsius chatrathi (early Oligocene, Africa), based on a mandible with molars and a broken premolar, was originally described as an African tarsiid (*50*) but was subsequently placed in its own family, Afrotarsiidae, and suggested as a possible sister taxon of Anthropoidea (*21, 51, 52*). The lower molars of *Afrotarsius* share several apparent synapomorphies with *Eosimias*, *Tarsius*, and Anthropoidea: The M_1 cristid obliqua is oriented mesiodistally toward the protoconid, its metaconid is transverse to the protoconid, and there are small molar hypoconulids; and M_2 is larger than M_3. The P_4 anterior root is buccally positioned like that of *Eosimias*. More complete material may demonstrate that eosimiids are actually Asian afrotarsiids.

Algeripithecus minutus (middle Eocene, Algeria) is known from a few upper molars and lower premolars (*53*). The extremely bunodont structure and sloping sides of the upper molars are reminiscent of parapithecids and propliopithecids. The lower premolars lack metaconids, however, unlike oligopithecids or crown anthropoids but similar to parapithecids, in which premolar metaconids are small (*21*).

Proteopithecus sylviae (late Eocene, Africa) is known from a maxilla with P^2 and P^4 through M^2 (*5*). Overall, the best fit of the available data places *Proteopithecus* with *Catopithecus* outside the clade consisting of crown anthropoids and parapithecids.

Several Eocene primates from China and Thailand—*Rencunius*, *Hoanghonius*, and *Wailekia*—are best allocated to cercamoniine Adapidae [based on personal observations and (54)] and are therefore unlikely to have anthropoid affinities. The Asian fossil primates *Pondaungia cotteri* (middle Eocene, Burma) and *Amphipithecus mogaungensis* (late Eocene, Burma) are of less certain affinities, having been variously interpreted as early anthropoids (*30*, *55*) or adapids (*56*). The critical features of the skeleton that are diagnostic of anthropoid status are unknown at present.

Anthropoid Adaptations

Most living anthropoids share a distinctive, although not unique, combination of behavioral traits in diet, activity pattern, sociality, and locomotion. Accompanying these behaviors are a number of anatomical specializations in the masticatory apparatus, visual system, and limb structure that can serve to establish the adaptations of extinct species.

Diet and body size. The diets of fossil mammals can be inferred from dental morphology and body size (*57*). Because insects have tough exoskeletons and leaves consist of large amounts of fiber, both insectivorous and folivorous primates have relatively long cheek-tooth shearing crests. However, insectivores can be distinguished from folivores on the basis of body size. Purely insectivorous primates usually weigh less than 500 g because only small-bodied animals are able to acquire enough insects to fuel their high metabolisms. On the other hand, purely folivorous primates never weigh less than 700 g because the high metabolic demands of small body size are not compatible with the lengthy digestion time required for plant fiber. Thus, small fossil primates with comparatively well-developed cheek-tooth shearing crests were probably insectivores, and large fossil primates with well-developed shearing crests were probably folivores. In contrast to folivores and insectivores, purely frugivorous and gummivorous primates occur at all body sizes and tend to have relatively poorly developed cheek-tooth crests because their foods lack substantial fiber content.

Living platyrrhine primates range in size from 50 to 10,000 g, although it appears that the ancestral platyrrhine was probably no smaller than about 300 g, substantial size reduction having occurred in marmosets and tamarins (*58*). The earliest catarrhines from the early Oligocene fall within the size range of modern platyrrhines. Late Eocene–early Oligocene stem anthropoids ranged from about 300 to 1000 g (*51*, *59*), and Algerian middle Eocene *Algeripithecus* was even smaller (*3*). On the basis of tooth dimensions, Chinese Eocene tarsiids did not exceed living *Tarsius* in size (≃100 g), whereas most omomyids ranged between 50 and 400 g. Adapids were much larger animals that barely overlapped omomyids in body size. *Eosimias centennicus* was small (*13*). Thus, omomyids, eosimiids, and early anthropoids were too small to have been leaf eaters and must have been insectivorous, frugivorous, or both.

Living anthropoids are primarily herbivorous, eating leaves, fruit, and gum. However, most anthropoids eat at least some insects, and the smaller platyrrhine species eat substantial amounts of insects. Leaf eating first occurs late in anthropoid evolution and evolved independently in catarrhines and platyrrhines: early anthropoids of the late Eocene and early Oligocene of Africa have low-crowned molars with either reduced shearing, which suggests that they were predominantly frugivorous (parapithecids and propliopithecids), or moderate shear, which suggests a combination of insectivory and frugivory (oligopithecids) (*6*, *11*, *59*). The dental evidence suggests that omomyids had a mixed frugivorous and insectivorous diet (*60*), whereas the larger bodied adapids were mainly frugivorous and folivorous (*40*). *Tarsius* eats small vertebrates and insects (*61*). Judging from its size (*13*) and high degree of molar shearing (based on personal observations), *Eosimias* was insectivorous.

Thus, evidence from body size and dental morphology suggests that the divergence of the anthropoid stem lineage from their nonanthropoid ancestors may not have been associated with a significant increase in body size or a significant change in diet—the earliest anthropoids were probably small and insectivorous, possibly with some degree of frugivory. However, by the time parapithecids and propliopithecids appeared in the late Eocene, at least some early anthropoids had undergone a shift from insect eating to low-fiber herbivorous diets. If *Eosimias* is an anthropoid, then this dietary shift occurred after the separation of *Eosimias* from the anthropoid stem lineage.

Orbit size and convergence. Extant anthropoids have relatively smaller orbits than do tarsiers or many strepsirrhines. This is attributable to their diurnal activity patterns. At a body size of <1300 g, relative orbit size is correlated with activity pattern (*62*): Small, visually oriented nocturnal mammals have relatively larger eyes and orbits than do diurnal ones. At body sizes above ~1300 g, differences in activity pattern are not reflected in differences in relative orbit size. As a result, activity patterns cannot be inferred for most adapids, because they were too large. However, the orbits of most omomyids such as *Necrolemur*, *Pseudoloris*, *Tetonius*, and *Shoshonius* suggest nocturnal habits (*38*, *62*), and anthropoid diurnality can be traced back at least to the late Eocene, being inferred for *Apidium*, *Simonsius*, and *Catopithecus* (*6*, *11*). *Tarsius* has enormous orbits, much larger than would be expected even for a nocturnal primate. Tarsiers have hypertrophied eyes because, despite being nocturnal, they lack a reflecting tapetum lucidum behind the photoreceptors in the retina. In combination with their possession of a retinal fovea, the absence of a tapetum suggests that tarsiers are descended from diurnal ancestors (*63*). A similar argument might be made for *Shoshonius*, which also has large orbits.

Thus, it appears that the last common ancestor of *Tarsius* and anthropoids was diurnal and descended from a nocturnal ancestor. The relative orbit size in *Eosimias* is unknown. Either way, however, diurnality was not an anthropoid autapomorphy; it occurred earlier in the tarsier-anthropoid stem group.

Extant anthropoids have orbits that are more forward-facing than those of other primates. The orientation of the orbits (and eyes) provides important information about adaptation, although among primates, allometric factors also influence orbital convergence (the degree to which the orbits face in the same direction) and frontation (the degree of verticality of the orbital margins) (*64*). Small-bodied animals have proportionately larger orbits that are less convergent than those of large-bodied animals (*64*, *65*). Moreover, among small-bodied primates, nocturnal animals have relatively larger and less convergent orbits than do diurnal animals. When these allometric effects are taken into account, tarsiers, lorises, and anthropoids all have unexpectedly high degrees of orbital convergence (*65*, *66*). In tarsiers and lorises, this is part of an adaptation for nocturnal visual predation (*66*, *67*), but this explanation cannot be applied to diurnal anthropoids.

Ross (*65*) proposed recently that if the anthropoid stem lineage adopted diurnality at small body size (<1300 g), the resulting decrease in relative orbit size would have been accompanied by an increase in orbital convergence. Subsequent increases in body size would then have produced further decreases in relative orbit diameter and increases in convergence, resulting in the highly convergent orbits of extant and extinct large-bodied anthropoids (such as *Aegyptopithecus*). However, if diurnality had evolved in an animal larger than 1300 g, there would not have been an associated change in relative orbit diameter (nor, hence, in orbital convergence), and the orbits would not be so convergent in extant large-bodied anthropoids. Thus, the stem lineage of anthropoids must have adopted diurnality at a body size less than ~1300 g (*65*). All known omomyids and eosimiids are much smaller than this minimum, whereas adapids are often much larger.

Retinal fovea. Retinal foveae occur in many vertebrates, but tarsiers and anthropoids are the only mammals with a fovea. A fovea is an area on the retina with a high density of photoreceptors, a low ratio of photoreceptors to ganglion cells, and, in tarsiers and anthropoids, an area where the blood vessels are deflected away from the underlying retina. The fovea improves visual acuity. Among vertebrates, foveae are found in fishes, reptiles, and birds that are diurnal visual predators (68), which suggests that the haplorhine fovea evolved to increase visual acuity to facilitate diurnal visual predation (69). Many small-bodied anthropoids (such as squirrel monkeys and callitrichids) spend substantial amounts of time searching for insects and other small invertebrates (*70, 71*). *Tarsius* is a nocturnal visual predator, but the lack of a tapetum lucidum suggests that tarsiers are descended from a diurnal ancestor (63). Thus, it can be hypothesized that the haplorhine fovea evolved to facilitate visual predation of insects in small-bodied diurnal animals (69).

Postorbital closure. As noted above, anthropoids and tarsiers are distinguished from other mammals by their postorbital septum or lateral orbital wall. Various functions have been attributed to this septum, including muscle attachment (*72*), insulation of the foveate eye against movements in the temporal fossa (63), and reinforcement of the face against masticatory forces (*73*). Recent work suggests that the septum is not better at resisting the forces to which it is subjected than is the postorbital bar from which it evolved (*74*) and does not give attachment to muscle fibers in tarsiers and most platyrrhines. However, the anterior temporal muscles do curve around the postorbital septum between origin and insertion (*75*), so if the postorbital septum were not present, the eyes would indeed be bounced around during mastication (*63, 75*). The problem of extraneous eye movement exists in tarsiers and anthropoids because their high degrees of orbital convergence and frontation drag the anterior temporal muscles rostrally, causing the muscles to impinge on the orbit from behind. Increased orbital convergence was explained above. Vertically oriented orbits may be due to the enlarged brains of anthropoids (*75*). In any event, as the ancestors of *Tarsius* and anthropoids evolved their unique orbit orientation, they probably evolved a postorbital septum to protect the orbital contents against masticatory movements in the temporal fossa.

Sexual dimorphism. Extant strepsirrhines and tarsiers show little or no canine or body-size dimorphism. However, many living anthropoid species exhibit substantial sexual dimorphism—males are larger bodied and have larger canines than do females. Other anthropoids are less dimorphic in canine size or body size, or both. Larger, diurnal, more terrestrial primates and species that exhibit more male-male competition for access to mates often have greater dimorphism than do their close relatives that are smaller, nocturnal, and more arboreal, and compete less frequently for access to mates (*76*). Low dimorphism in primates is associated with a variety of social organizations, including monogamy and solitary dwelling, but the presence of greater dimorphism usually is associated with greater complexity in social organization. Therefore, the presence of sexual dimorphism in an extinct species should signal increased social complexity. Canine dimorphism is found among adapids and at least three late Eocene—early Oligocene anthropoid families (parapithecids, oligopithecids, and propliopithecids), and group living may be inferred for some of these animals (*6, 77*). No greater antiquity for sociality is found among haplorhines: Extant *Tarsius* is solitary and monogamous, and omomyids were not dimorphic.

Brain enlargement. With few exceptions, extant anthropoids have relatively larger brains and smaller olfactory lobes than do tarsiers or Lemuriformes, but this difference does not extend to the brain sizes of early fossil anthropoids. The stem anthropoids *Apidium* and *Catopithecus* and the early catarrhine *Aegyptopithecus* had comparatively smaller brains and larger olfactory lobes than do most extant anthropoids (*51, 59*). Compared with living strepsirrhines, known omomyid and adapid olfactory lobes were similarly sized and endocranial volumes were even smaller than those of living strepsirrhines. Only the relative endocranial volume of *Rooneyia* (?Omomyidae) may have been within the size range of lemuriforms and *Tarsius*. Thus, brain size enlargement and olfactory reduction were achieved recently in anthropoid evolution, possibly independently in platyrrhines and catarrhines.

Locomotion. Eocene primates show a substantial range of apparent locomotor habits in an arboreal context. All had grasping feet with a long and retroflexed peroneal tubercle on the first metatarsal. European *Adapis* was a slow-moving arboreal quadruped like a living potto (*Perodicticus potto*) (*78*). The North American adapids *Smilodectes* and *Notharctus* had longer hindlimbs than forelimbs and other features reminiscent of specialized arboreal leaping strepsirrhines such as *Hapalemur* or *Propithecus*, but were more robustly built (*40*).

North American omomyids are known mostly from isolated foot and limb bones (*Hemiacodon*, *Omomys*, and *Absarokius*, although limb proportions are known for *Shoshonius*). These taxa exhibit a moderate degree of tarsal elongation. The talocrural joint was adapted for lateral stability, and the distal femoral condyles (where known) are deep anteroposteriorly. All these traits are similar to those of extant dwarf and mouse lemurs (*Cheirogaleus* and *Microcebus*) and of scurrying-leaping galagos (such as *Galagoides demidovii*) and indicate less specialized vertical clinging or saltation than in *Galago senegalensis* or *Tarsius* (*79*). The limb proportions of *Shoshonius* suggest a similar locomotor profile (*80*). European *Necrolemur* shows several extreme anatomical modifications (an elongate tarsus and distal tibiofibular fusion), suggesting that it was a more habitual leaper (*81, 82*).

Possible eosimiid limb bones are omomyid-like in most ways, which suggests that eosimiids had a cheirogaleid-like locomotion. But a few traits suggest an advance toward a more anthropoid-like condition, with reduced reliance on strong or frequent leaping (for example, the tarsus is shortened as in anthropoids) and less powerful foot grasping (a reduced peroneal tubercle of the hallucial metatarsal).

Eocene-Oligocene African anthropoids show some locomotor diversity. The parapithecid *Apidium* (9) possesses a mixture of features indicating some active quadrupedalism and frequent leaping from a quadrupedal posture. Leaping features include relative hindlimb dominance, tibiofibular syndesmosis (but not fusion), and deep femoral condyles. However, *Apidium* also exhibits a rounded femoral head, less tarsal elongation, and reduced power in the grasping hallux as compared with omomyids. Postcranially less well known oligopithecids may have been more deliberate arboreal quadrupeds (*10*) whose locomotion resembled that of the early catarrhine *Aegyptopithecus* (*83*).

A Scenario for Anthropoid Origins

There is strong evidence for a clade consisting of adapids and Lemuriformes. The hitherto proposed relationship of cercamoniine adapids to anthropoids is not supported by the weight of cranial, dental, and postcranial evidence. A haplorhine group consisting of omomyids, tarsiers, and anthropoids is also strongly supported. Placement of eosimiids in the haplorhine clade is strongly indicated; a sister-group position of the family with anthropoids is favored by dental and postcranial evidence. If an isolated omomyid-like petrosal is correctly allocated to *Eosimias*, *Tarsius* may yet turn out to be more closely related to some omomyid than to anthropoids, but there is compelling evidence from the cranial anatomy to favor tarsiers as the sister taxon of anthropoids.

Whether stem Anthropoidea arose in Africa or Asia is not clear, given the equivalent antiquity of anthropoids in Asia (eosimiids) and in Africa (*Algeripithecus*). The Eocene species that gave rise to the tarsier-anthropoid clade must have resembled omomyids in behavior: It was a small-bodied, partially insectivorous, primarily leaping, and active, arboreal quadrupedal animal, and possibly solitary. However, it departed from typical omomyids by having diurnal rather than nocturnal habits. *Tarsius* diverged from this ancestor by increasing its committment to leaping locomotion, becoming more carnivorous, and returning to a nocturnal way of life. Stem Anthropoidea remained small and diurnal. They shifted to a more herbivorous diet, and adopted locomotor patterns with more arboreal quadrupedalism, less leaping, and less powerful grasping with the hind foot. Some stem anthropoids also show dimorphism, which suggests that some or all were social animals. Brain enlargement and reduction of the olfactory apparatus, as well as increased body size, occurred after the Eocene.

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