CHAPTER 3

How Close Are the Similarities between *Tarsius* and Other Primates?

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For centuries, the tiny primate *Tarsius* has amazed and frustrated those who study it. Its bizarre attributes make its phylogeny difficult to establish. Still, systematists support tarsier phylogenies based on interpretations of data constrained by assumed phylogenies or reconstructed transformation series. Consequently, retrieving specific details of *Tarsius* anatomy and considering them in light of alternative interpretations is difficult. This situation is an unfortunate legacy of taxonomic practice, whereby the identity (diagnosis) of a new taxon is defined less by the features of the organism than by the ways in which it is thought to be similar to other taxa, which are also defined comparatively.

To rectify this, I present first, a morphological overview and second, a brief account of its systematic history. I use the development of the orbital region as an example of how we might try to delineate primitive retention from shared derivedness. I also discuss features that pertain to *Tarsius*'s potential phylogenetic relationships to other extant primates. Since hypotheses of phylogenetic relatedness of various fossils to lower or higher primates often rely on comparisons with *Tarsius,* I review fossils offered as *Tarsius,* sister taxa of *Tarsius,* and more basal anthropoids.

Extant *Tarsius:* An Overview

The tarsier (genus *Tarsius*)—a small, nocturnal, totally carnivorous, large and bug-eyed, long-ankled, scaly-tailed primate—has been known to the scientific community since Camel's 1706 publication of a new small mammal from the Philippines. The five currently recognized species of *Tarsius* (*T. bancanus, T. syrichta, T. spectrum, T. pumilis,* and *T. dianae*), and two additional unnamed species (Groves, pers. com.) are distributed throughout the tropical evergreen rain forests of much of the southeast Asian archipelago.

Tarsiers are nocturnal, extremely hindlimb dominated, arboreal mammals (Niemitz, 1984b), which, relative to their small body size, perform extraordinary leaps, covering wide spaces in kangaroo style. Some saltatory primates (e.g., *Microcebus* and *Hapalemur*) typically land hands first, but *T. bancanus* usually lands feet first, especially after traversing great distances (Peters and Preuschoft, 1984). *T. bancanus* uses both feet simultaneously in propelling itself, whereas *T. syrichta* takes a step prior to lift-off and upon landing. Only *T. bancanus* displays a preference for vertical rather than horizontal supports for perching and inclined branches for sleeping (Niemitz, 1984b). Like *Galago senegalensis, T. spectrum* exploits varied substrates while *T. dianae* tends toward walking quadrupedally on more horizontal supports.

Tarsius is the only totally carnivorous and insectivorous (animalivorous) primate. It preys on a diversity of insects (including retaliatory red ants), various crustaceans (shrimp, crabs), small vertebrates (bats, birds, fish, and flying frogs), and even snakes (including neurotoxic species) (Niemitz, 1979, 1984a; Jablonski and Crompton, 1994). Tarsiers typically consume the entire prey, even if the prey's mass exceeds its own. In hunting, tarsiers usually prowl noiselessly above ground level and then ambush their prey by pouncing on it, eyes closed, killing it with a series of powerful bites inflicted by their pointed antemolar teeth (Jablonski and Crompton, 1994). As noted in captive *T. bancanus,* for their small size (body weight: 115–150 g), tarsier proclivities toward relatively large prey (lizards of 3–5 g and mice of 5–8 g) results in marked fluctuations in daily body weight (Izard et al., 1985).

Typical of tropical insectivorous mammals of body weights in excess of 35 g, at least *Tarsius syrichta* and *T. bancanus* have low body temperatures and, as calculated for the Philippine tarsier, a low basal metabolic rate (65% of what is expected of an animal of similar body weight) (McNab and Wright, 1987). *T. bancanus* may be torpid during the day (Niemitz et al., 1984), but this condition has not been detected in *T. syrichta*—and would not be expected in mammals living in tropical forests within a 10 degree latitude of the equator (McNab and Wright, 1987). Interscapular brown body fat (the "interscapular hibernating gland"), which is thermoregulatory tissue in neonatal mammals (including humans) that remains active in adult hibernating mammals, also occurs in adult *Tarsius* (Niemitz et al., 1984).

Gestation in captive *Tarsius bancanus* is 178 days (Izard et al., 1985), whereas it is 157 days in *T. spectrum* and 180 in *T. syrichta* (Roberts, 1994). In a comparison to 26 prosimian species (Roberts, 1994), although tarsiers ranked among the smallest (adult *T. bancanus* weighs 130 g, *T. spectrum* weighs 200 g, *T. syrichta* weighs 113 g), tarsiers have long gestation periods (cf. *Microcebus murinus* [adults weigh 84 g and gestate 61 days]). *Galago demidovii* (adults weigh 63 g and gestate 111 days) is most similar to *Tarsius.* In *Loris tardigradus* (298 g) and *G. senegalensis* (201 g), gestation lengths are 166–169 and 141 days, respectively. Izard et al. (1985) suggest that *Tarsius*'s relatively long gestation period is due either to its restricted animalivorous diet and/or its apparently low metabolic rate, the latter of which Niemitz et al. (1984) think correlated with producing only one offspring per year. Also possibly correlated with gestation length, as seen in *T. bancanus* (Roberts, 1994), are (1) prenatal development slowest among mammals; (2) brain at birth largest among mammals relative to body size (60–70% adult size); and (3) neonate approximately 20% maternal body mass.

Tarsius is the only primate with a bicornuate uterus that also develops hemochorial placentation, which it achieves through a unique sequence of events: Rauber's layer is lost prior to implantation, as it is in prosimians, and amniogenesis begins by cavitation with the formation of a primordial amniotic cavity as in anthropoids, but then changes to folding for the duration (Luckett, 1974, 1976; but see Starck, 1984).

The pelage of the large tarsier species is generally grayish buff; the fur of *T. dianae* is somewhat woollier in appearance (Niemitz et al., 1991). The tail is sparsely covered with hair, but the tip bears a distinct tuft, which is densest in *T. bancanus. T. spectrum* and apparently *T. bancanus* develop edentate- and reptile-like scales along the tail and around the areolae (Niemitz, 1979). *T. dianae* is distinguished at least from *T. spectrum* in having a hairless patch at the base of its ear (Niemitz et al., 1991).

Orbital size increases from *T. pumilus* (smallest), *T. spectrum,* and perhaps *T. dianae, T. syrichta,* to *T. bancanus* (largest). In all tarsiers, the orbital enlargement dominates the skull so that the size relationships of the organs of the head are unique among mammals (Starck, 1984). For example, the average volume of a tarsier's eyeball (2.8 cm^3) equals its average cranial capacity (Castenholz, 1984). The unusually spheroidal/ tubular eyeball protrudes more than half its length beyond the margin of the shallow orbit cupping it; the eyeball/orbital volume ratio is 1.79 in *Tarsius,* roughly 1.0 for various lower primates, and 0.32 for *Homo.* With its eyes immobilized in their orbits, *Tarsius* makes visual adjustments not by eyeball movement, but by rotating the entire head through an arc of approximately 180 degrees to either side.

Tarsius also develops a small, triangular, hairless region at the medial border of each nostril that is continuous with the hairless skin of the inside its nostrils (Klauer, 1984). The rest of the oro-nasal region is profusely covered with different kinds of hairs, including thick vibrissal (i.e., sensory or sinus) hairs, which occur everywhere except, perhaps, in the internarial region (Hofer, 1979, 1980; Klauer, 1984). The perimeter of a tarsier's lips bears an unusual arrangement of interdigitating hairs and distinct lateral papillae that cover the gaps between the anterior and most of the cheek teeth. The upper and lower lips bear an abundance of sebaceous and apocrine glands throughout, creating *Tarsius*'s distinctive circum-oral organ.

Systematic History

Tarsius was first described by the missionary J. G. Camel (1706–8), who named it *Cercopithecus luzonis minimus* because he mistakenly thought it was a monkey from the island of Luzon in the Philippines. In the tenth edition of the *Systema Naturae* (in which he replaced Anthropomorpha with primates), Linnaeus (1758) used Camel's description for the binomial *Simia syrichta.* Buffon (1765) described a juvenile mammal of unknown origin; because of the extreme length of the hindlimb (especially the foot and upper tarsals), he coined the name "tarsier" for it. Since Buffon did not realize that his "tarsier" was the same animal as Linnaeus's *Simia syrichta,* he suggested that it might be a jerboa or an opossum, which Linnaeus unwittingly accepted. In 1777, Erxleben argued that the tarsier was a primate most similar to lemurs and coined *Lemur tarsier* to include both of Linnaeus's and Buffon's animals. Ultimately, Storr (1780) created the genus *Tarsius* in order to distinguish this primate from lemurs.

Since Linnaeus's *Simia syrichta* was based on a specimen from the Philippines, the correct designation for this particular primate is *Tarsius syrichta.* In 1778, Pallas recorded the first tarsier of possible Celebesian (i.e., Sulawesian) origin and referred to it as *Lemur spectrum.* Thus, this species name has priority over those subsequently proposed for Sulawesian tarsiers (*T. fuscus, T. fuscomanus,* and *T. fisheri*), and the correct binomial is *T. spectrum.* In 1821, Horsfield described tarsiers from Bangka, which he named *T. bancanus. T. pumilus* was first identified by Miller and Hollister (1921) and rediscovered by Musser and Dagosto (1987). *T. dianae* was recently described by Niemitz et al. (1991).

Because *Tarsius* and *Galago* have similarly distinctive hindlimb morphologies, taxonomists such as Geoffroy-Saint Hilaire and Cuvier (1795) and de Blainville (1839) grouped these taxa together. In 1811, Illiger placed them in their own family, Macrotarsi, and relegated lemurs and lorises to another, Prosimia (Prosimii). Fitzinger (1861) and Gray (1870) kept Illiger's Macrotarsi, as did Brehm (1868), who also added to it the long-footed *Microcebus.* In 1883, as the counterpart to Mivart's (1864) taxon for higher primates, Anthropoidea, Flower proposed the suborder Lemuroidea, which he divided into three families: Lemuridae (lemurs, lorises, bush babies), Chiromyidae (*Daubentonia,* which was then still called *Chiromys*), and Tarsiidae (*Tarsius*). Illiger's suborder Prosimii eventually replaced Flower's Lemuroidea as the taxonomic partner of Anthropoidea. With Hubrecht's (1898) description of a type of hemochorial placentation occurring in *Tarsius* (as well as in *Tupaia*), which he contrasted with the epitheliochorial placentation of bush babies, support for a *Tarsius-Galago* relationship began to erode. In 1918, on the basis of an incorrect assessment of narial morphological types, Pocock (1918) suggested that *Tarsius* should be dissociated from other prosimians—which he relegated to Geoffroy's (1812) suborder Strepsirrhini—and grouped with anthropoids in the suborder Haplorhini.

Pocock's (1918) taxonomic suggestion lay virtually unnoticed until the 1950s, when Hill (1953) devoted one volume of his treatise on comparative primate anatomy to Strepsirrhini and the rest to Haplorhini, the first volume of which dealt solely with *Tarsius* (Hill, 1955). Nevertheless, the suborders Prosimii and Anthropoidea continued to be the favored divisions of Primates until the 1970s and '80s, when studies, especially on placentation, the auditory bulla, carotid circulation, and craniofacial morphology, were seen as indicating a closer relationship between *Tarsius* and anthropoids than between *Tarsius* and lemurs and lorises. There are, however, a number of features that appear to link *Tarsius* closely with the lorisiform group of strepsirhine primates (e.g., Schwartz, 1984, 1986, in press). Recently, the pendulum has begun to swing back toward recognizing the groups Prosimii and Anthropoidea (e.g., see contributions in Fleagle and Kay, 1994; Ankel-Simons, 2000; and Delanty and Ross, 2000).

While eighteenth-century comparative anatomists grouped *Tarsius* with *Galago* and, eventually, also with *Microcebus* on the basis of pedal anatomy, the picture of Prosimii inherited by the twentieth century was not that *Tarsius*'s relationships were within that group, but that it was a lower primate or an evolutionarily intermediate between the lower and higher primates. Superficially, at least, *Tarsius,* with its large eyes, somewhat globular cranium, seemingly short snout, vertical torso, and primitive molar morphology, made a convenient model from which to derive anthropoids, who were seen as progressively evolving these attributes, culminating in *Homo sapiens.* (Jones Wood [1920] even argued that especially *Tarsius*'s upright posture made it a perfect model for the ancestor of the human lineage alone.) *Tarsius* was kept with lemurs and lorises largely because it was seen as a rather primitive primate.

The notion that *Tarsius* is a lower primate, foreshadowing higher primate evolution, was bolstered by interpretations of a diversity of small Eocene fossils. European forms (such as *Necrolemur* and other microchoerines) were taken as the closest potential relatives of tarsiers. North American Eocene fossils were considered both sufficiently similar to modern tarsiers in size, cheektooth morphology, cranial shape, and development of moderate tarsal elongation that they could serve as tarsier predecessors. They were also primitive enough in molar cusp pattern to provide convincing anthropoid ancestors.

Thus, fossil tarsioids or tarsiiforms, as they were variably called, became the link between *Tarsius* and anthropoids. Because fossils could be linked to living tarsiers, which, in turn, were supposedly intermediate between higher and lower primates, primate taxonomists could choose to embrace the subordinal divisions Strepsirrhini and Haplorhini. Whereas in the scheme of dividing primates into the suborders Prosimii and Anthropoidea, fossil tarsioids could be accepted as prosimian because of their primitive molar morphology (in spite of the fact that an animal's primitiveness does not indicate phylogenetic relationship), in the divisions Strepsirrhini-Haplorhini these fossils became de facto haplorhines only because of their association with *Tarsius.* Haplorhini was, and still is, defined largely on the basis of unfossilizable anatomies (e.g., see Beard's [1988] argument for a rhinarium in extinct tarsiiforms).

Before we proceed with evaluating the alternatives—Prosimii and Anthropoidea versus Strepsirrhini and Haplorhini—we must clarify the features that support the competing hypotheses. With this goal in mind, I review the salient morphologies.

Morphology: Comparisons and Interpretation

The Eye and Orbital Region

Various features of the eye—a well-developed central retinal fovea, a macula lutea, and the lack of a tapetum—have been taken as being similar in *Tarsius* and anthropoids. Although *Tarsius* does not develop a tapetum, it also does not consistently develop a retinal fovea (Castenholz, 1984). When a retinal fovea is present, it is relatively quite small and composed entirely of rods. *Galago* also develops a small central fovea (ibid.). The structure identified in *Tarsius* as a "macula lutea" (Woollard, 1926) was an artifact of fixation (Kolmer, 1930). Anthropoids lack a tapetum and develop a large central foveae; only the nocturnal *Aotus*'s retina is composed entirely of rods. Wolin (1974) suggested that, in retinal organization, *Aotus* may be less like other anthropoids than *Tarsius,* and Castenholz (1984: 317) concluded that, because "the eye of *Tarsius* is the most specialized eye found in primates," it is impossible to "decide which one of the specializations [is] of phylogenetic significance."

The perimeter of the enormous bony orbit of *Tarsius* is somewhat lipped; it is most distended superiorly and laterally. The superior orbital rim approaches (and, as in *T. bancanus,* may exceed) the height of the neurocranium; the inferior margin is level with the tooth row. The enormous orbits also add to the illusion that the facial skeleton is hafted low on the cranium (cf. Rosenberger and Szalay, 1980; Beard and MacPhee, 1994; Ross, 1994), as it is in anthropoids (ibid.), but radiographic analysis demonstrates that this is not the case (fig. 3.1). Near-frontal alignment of *Tarsius*'s eyeballs (not the orbits, which, as in *Galago,* retain the primitive orientation

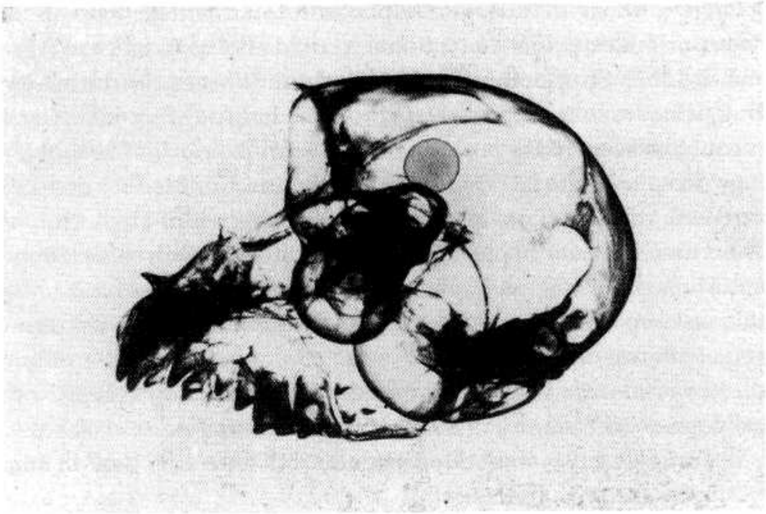

Figure 3.1. Radiograph of a skull of *Tarsius spectrum* (Rijksmuseum van Natuurlijke Historie [RMNH] d, Leiden). Note that the auditory region is vacuous, that the facial skeleton is not hafted low upon the cranium, and that the huge orbit encroaches upon the elongated snout. Arrows point to superior and inferior orbital margins. (© J. Schwartz)

[Schwartz, 1996]) is associated with extreme medial orbital convergence. This is the most pronounced among primates and both compresses the entire nasal region dorsally and reduces the nasal cavity and paranasal sinuses (Starck, 1975, 1984). Anthropoids, however, with their relatively smaller orbits, have absolutely reduced snouts and nasal cavities.

Orbital size and convergence in *Tarsius* appears correlated with its development of a large and extensive (apical) interorbital septum, which is formed by contributions not only from the vomer and an ossified nasal septum, but also and uniquely from the frontal bones and the interorbital lamina of the presphenoid (Starck, 1984). Severe orbital convergence in some specimens results in incomplete ossification of the interorbital septum. *Tarsius* is further unique among mammals in general in that the large rostral portion of its cranial cavity, together with the bulbous chamber of the roof and the small lamina cribrosa of the nasal capsule, is associated with a long olfactory tube formed entirely from the frontal bone (Starck, 1984: 287).

Various authors (e.g., Cartmill, 1978, 1980, 1994; Ross, 1994) have emphasized the orbital region in their arguments for *Tarsius*'s being either intermediate between lower and higher primates or specifically related to anthropoids, because, while all living primates possess a postorbital bar, only *Tarsius* and anthropoids develop some degree of postorbital closure.

However, the bony flanges that contribute to postorbital closure in *Tarsius* hardly impinge upon this region as much as they do in various New World monkeys (even those that achieve only incomplete postorbital closure). Catarrhines essentially have complete postorbital closure. If those extinct "tarsiiforms" for which crania are known are indeed related to *Tarsius* (see below), then postorbital closure would have occurred independently in *Tarsius* and anthropoids because the fossils have only postorbital bars. Indeed, independent attainment of postorbital closure in *Tarsius* and anthropoids through different growth patterns best explains the differences in the relative bony contributions to their respective orbital regions.

Cartmill (e.g., 1978, 1980) suggested that *Tarsius* and anthropoids achieve postorbital closure from the primitive condition of a postorbital bar via varying degrees of enlargement of the same three bones: the zygoma, frontal, and maxilla. As he portrayed it, in *Tarsius* and in anthropoids, the alisphenoid becomes enlarged and the frontal either displaces or overrides the parietal and squamosal. In support of the supposition that *Tarsius* is intermediate between prosimians (with postorbital bars) and anthropoids (with postorbital closure), Cartmill (1980) proposed that a transformation series from *Galago senegalensis* to *Tarsius* to *Saimiri sciureus* illustrates how expansion of the alisphenoid and frontal could have occurred. If the eyeballs of these three primates were the same size, the suggested transformation series from *Galago* to *Tarsius* might be phylogenetically relevant. However, *Tarsius*'s eyeball is huge, which has implications for interpreting orbital morphology.

In spite of *Tarsius*'s extreme degree of orbital hypertrophy, the circumferentially enormous but shallow orbits barely cup its eyeballs (fig. 3.2). In other prosimians and especially in anthropoids, the orbits are deep at birth and remain so in the adult (fig. 3.3). In juvenile and adult anthropoids, the frontal process of the zygoma tapers superiorly in frontal view; it is also deep anteroposteriorly, as is reflected in the long zygomaticofrontal suture (fig. 3.4). Within the orbit of juvenile and adult anthropoids, the sphenoid is generally rectangular in outline and its lateralmost extremity, delineated by the zygomaticosphenoid suture, is contained well within the orbital cone (fig. 3.3). Externally in juvenile and adult anthropoids, the (ali)sphenoid, which lies behind and well away from the lateral orbital rim, faces laterally and contributes to the wall of the temporal fossa (fig. 3.4). The shape of the (ali)sphenoid may differ between anthropoid subclades, but whatever the configuration in the juvenile, it is retained in the adult of that taxon (e.g., fig. 3.4). Thus, the essential features of adult anthropoid postorbital closure are established early in life.

In the reverse of the anthropoid configuration, the zygomatic frontal process of juvenile and adult tarsiers broadens superiorly. Instead of closing

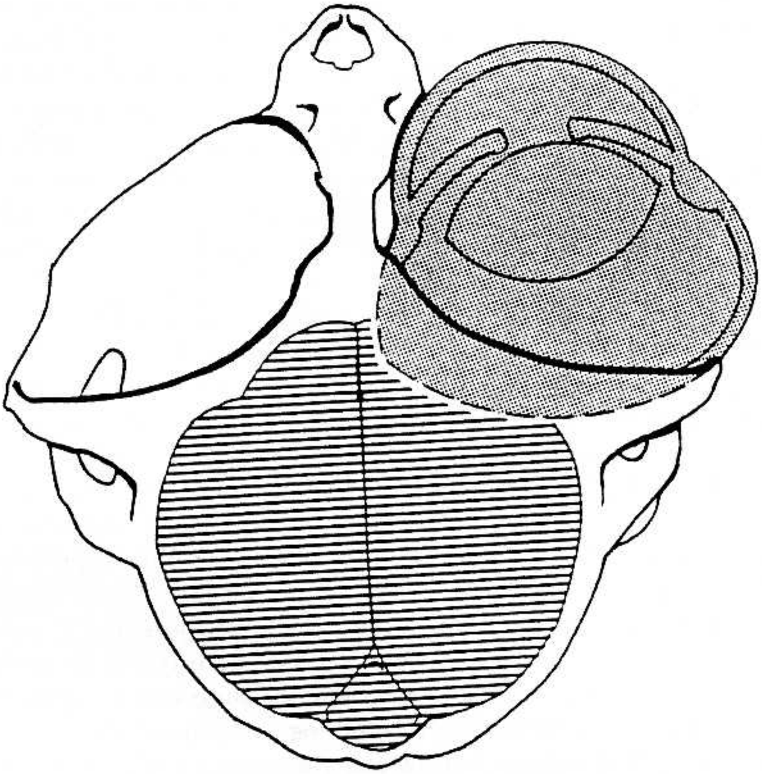

Figure 3.2. Superior view of skull of *Tarsius* illustrating the unusual morphology of the eye, its protrusion from the bony orbit, and its size relative to the brain. (Modified from Castenholz, 1984, and Stephan, 1984. Drawing by J. Anderton.)

off the back of the orbit, this strut of bone is well separated from the lateral wall of the brain case in the juvenile and remains so in the adult. Thus, *Tarsius*'s zygomatic frontal process is always differentiated as part of a postorbital bar. Within the orbit, the medially expanded sphenoid tapers laterally to a thin and short "tail" that nestles in the notch formed by the contact of the zygomatic frontal process and the frontal bone. Externally, the laterally extended sphenoid thus protrudes into the space of the temporal fossa. Also externally, as seen in juveniles, *Tarsius*'s (ali)sphenoid has two surfaces essentially at right angles to each other: one surface faces back upon the temporal fossa and the other faces laterally outward.

It is often difficult to delineate sutures in adults, but it is obvious that the configuration established in juveniles is maintained, if not exaggerated, in adults. *Tarsius* thus differs significantly from anthropoids in that the sphenoid extends from within the orbit to protrude laterally beyond the plane

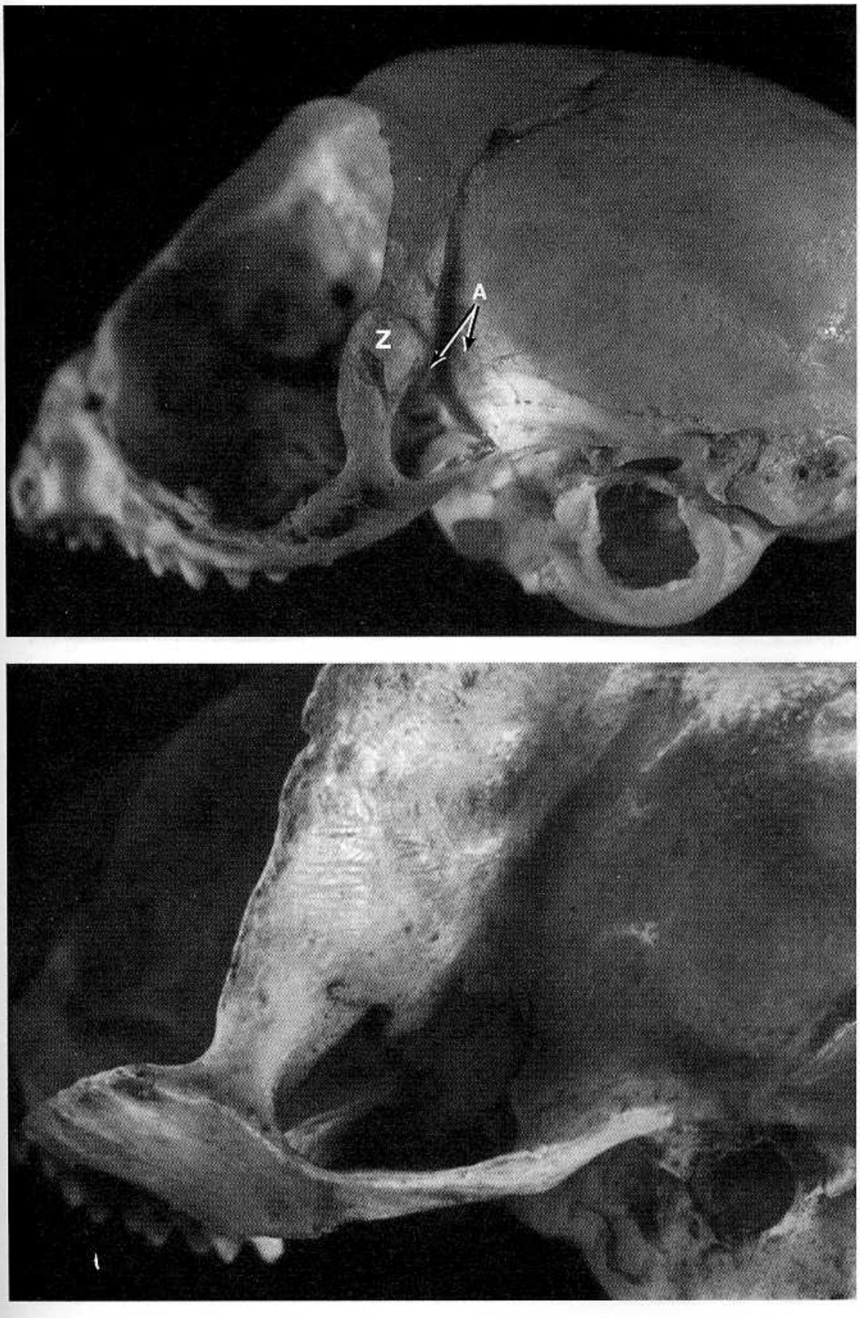

Figure 3.3. Closeup in lateral view of the bony orbital region of two *Tarsius spectrum:* (above RMNH n) a juvenile individual (antemolar deciduous teeth in place, with M2s beginning to erupt) and (below) a fully adult individual (RMNH d). In the juvenile, the superiorly expanded zygoma (Z), which is separated from the cranial vault as is a postorbital bar, is clearly delineated, as is the alisphenoid (A) with its posteriorly and laterally facing surfaces, the former of which contributes to the orbital lip. Although the sutural distinctions are obscured in the adult, it is obvious that the relative dispositions of the zygoma and alisphernoid are not appreciably different from the juvenile state. Not to scale. (© J. Schwartz)

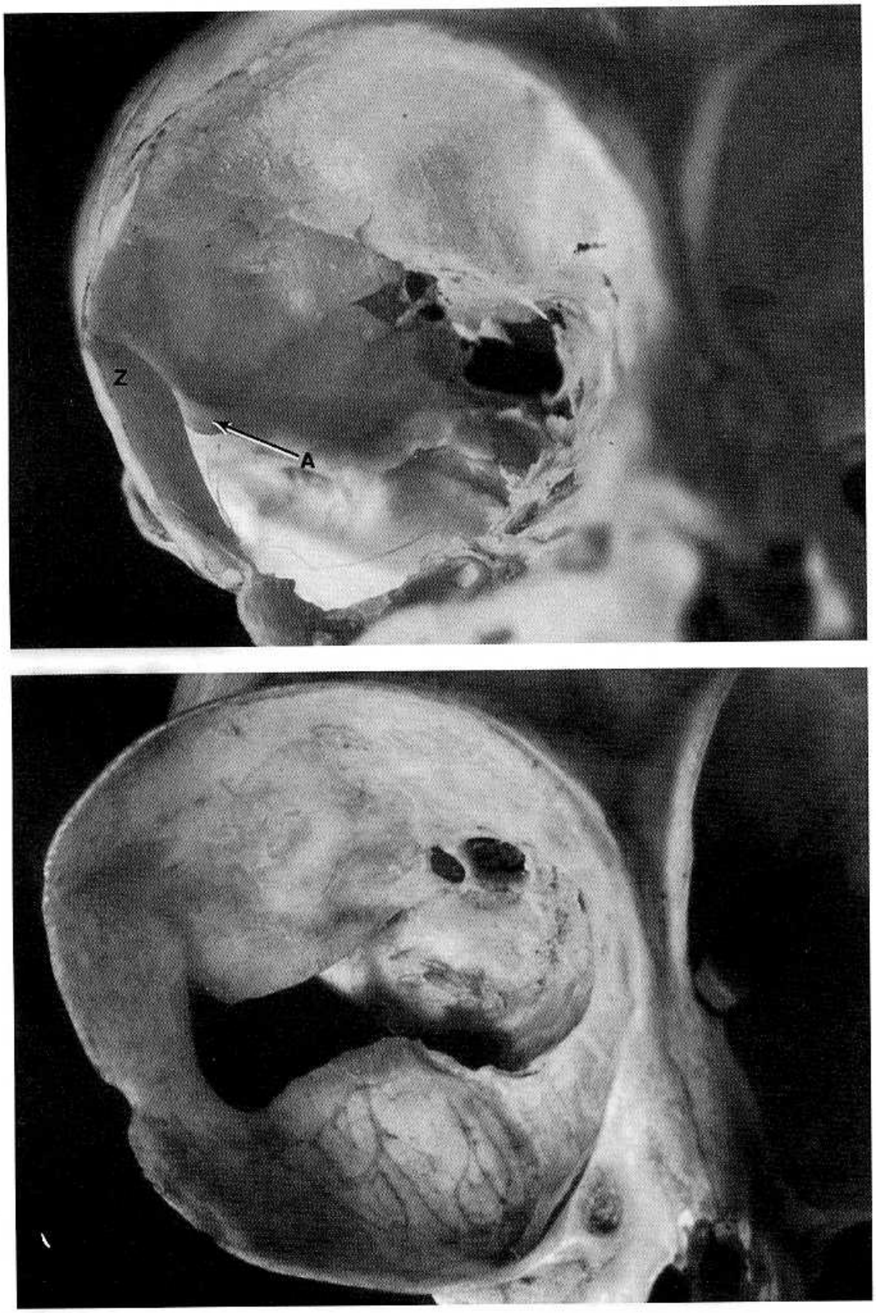

Figure 3.4. Frontal view of same specimens as in fig. 3.3. In the juvenile (above), the superiorly expanded zygoma (Z) is clearly separated from the cranial wall and a thin lateral extension of the otherwise bulbous alisphenoid (A) extends laterally beyond the cranial wall to insert in the notch between the zygoma and frontal. In the adult (below), the outline of the superiorly expanded zygoma is faintly visible and it appears that the lateral extension of the alisphenoid has expanded somewhat in its vertical dimension. The lateral extremity of the alisphenoid has both an orbital and a temporal fossal surface. In the juvenile and the adult alike, the zygoma stands away from the cranial vault as a postorbital bar. Not to scale. (© J. Schwartz)

of the cranial vault wall such that is has both orbital and temporal fossal surfaces. Although, during growth, the lateralmost extremity of the external (ali)sphenoid may expand vertically (in part, perhaps, because of the relation of musculature to bone [cf. Ross, 1995]) and extend a bit farther away from the brain case to face upon the temporal fossa, the configuration of the frontal process of *Tarsius*'s zygoma (being broad superiorly) and its separation from the lateral wall of the brain case remain constant.

Tarsius's large and unusual interorbital septal region also appears correlated with the enlargement and medial convergence of its orbits (Starck, 1975, 1984). Although the presence of an interorbital septum has been used to unite *Tarsius* with anthropoids (e.g., Cartmill, 1978, 1980), not all anthropoids develop one (e.g., *Aegyptopithecus, Alouatta,* hominoids), and, when they do, it is not the same as in *Tarsius* (Simons and Rasmussen, 1989). In addition, not only do some prosimians (*Loris,* various omomyids, *Galago senegalensis,* and *Microcebus murinus*) develop an interorbital septum, but so, too, do most mammals. In general in mammals, in conjunction with orbital enlargement, reduction of the nasal cavity, and changes in craniofacial orientation, the interorbital septum is retained in the adult (Starck, 1975) rather than incorporated into the ethmoid complex, as in *Macaca* (Zingeser and Lozanoff, 1989. Consequently, absence, not presence, of an interorbital septum in any mammal—primates included—is the phylogenetically significant character state.

The point of greatest interorbital constriction in *Tarsius* and anthropoids is supposed to lie below the olfactory lobes, while in strepsirhines it is above. Hence the development of an "apical" interorbital septum has been cited as a derived feature of Haplorhini (e.g. Cartmill, 1978). However, the interorbital septum of *Galago senegalensis* and *Microcebus murinus* lies below the olfactory lobes, as does the region of greatest constriction in *Hapalemur griseus* (Simons and Rasmussen, 1989).

Starck (1975, 1984) suggested that much of *Tarsius*'s craniofacial morphology—e.g., reduction of the nasal cavity and paranasal sinuses, development of an extensive interorbital septum, encasement of the long olfactory nerves in a bony canal derived from the frontal bones, as well as partial postorbital closure—is related to the extreme hypertrophy of its eyeball and orbit. Thus, seemingly favorable comparisons between *Tarsius* and anthropoids are likely superficial.

The Nasal Region

As originally conceived by Pocock, Haplorhini subsumed primates whose nostrils are continuous or aborally rounded along the lateral margin; similar to carnivores and insectivores, the lateral narial margins of strepsirhine primates are creased or slit. Pocock also noted in haplorhine primates the absence of a naked rhinarium and the presence of a narrow internarial region and a continuous upper lip beset with hairs, but it was Hill (1955) who emphasized these features in the definition of Haplorhini. Subsequently, however, Hofer (1980) demonstrated that *Tarsius* and various New World monkeys are morphologically strepsirhine in having laterally creased (not aborally rounded) nostrils (particularly well developed in *T. dianae* [Niemitz et al., 1991]), and also questioned whether features of *Tarsius*'s nasal region were homologous with those of anthropoid primates.

Hofer (1977) pointed out that many nonprimate mammals are haplorhine in lacking a rhinarium and in having mobile and medially fused upper lips that bear hairs. He also demonstrated that, in contrast to catarrhines, which have a smoothly continuous upper lip, various New World monkeys are similar to lorisids in retaining a midline rhinarial groove coursing from the narial region to the lip margin—which suggests a morphocline from a more deeply fissured upper lip (as in lemurs), to a grooved upper lip (as in lorisids and various New World monkeys), to a smoothly continuous upper lip (as in catarrhine primates). Since Anthropoidea appears to be a monophyletic group (and would be even if *Tarsius* were its sister taxon) (e.g., Schwartz, 1986), one would have to hypothesize that the last common ancestor of extant anthropoids had a medially fissured upper lip. As such, total fusion of the upper lip (i.e., complete coalescence of embryonically separate median nasal prominences) would have been independently derived in most species of *Tarsius* as well as in the last common ancestor of extant catarrhines. In fact, the deeply fissured internarial region of *T. dianae* could reflect different ontogenies of median nasal prominence fusion in the species of this primate genus and in catarrhine primates.

Hofer (1976, 1979, 1980) also noted that, in contrast to New World monkeys, *Tarsius* is restrictively similar only to catarrhine primates in having typical body hairs rather sinus hairs (vibrissae, "whiskers") within the internarial region. The conclusion from these data alone is either that *Tarsius* is most closely related to catarrhines or that each taxon independently evolved whiskerless internarial regions.

As in prosimians and New World monkeys, the nasal capsule of *Tarsius* protrudes anteriorly and the nostrils are laterally directed and separated by a wide internarial region (i.e., the nose is platyrrhine) (Hofer, 1980; Klauer, 1984). As in most mammals, including prosimians, New World monkeys, and even some catarrhine primates, adult tarsiers retain a functional vomeronasal organ. In concert with the absence of a rhinarium, *Tarsius*, anthropoids, and various artiodactyls and perissodactyls also have hair (but different kinds in different taxa) distributed across the upper lip and they also lack a philtrum, which, when present, tethers an otherwise mobile upper lip to the gum (Hofer, 1980; Maier, 1981; Klauer, 1984). Rasmussen's (1986) study of the interincisal diastema of various Eocene adapids (i.e., potential fossil relatives of lemurs) indicates that some of these fossil taxa may have lacked a rhinarium and, thus, had an untethered upper lip. Taking the entire oro-nasal region into consideration, *Tarsius* cannot be regarded either as a morphological intermediate between lower and higher primates or as the sister taxon of anthropoids.

The Auditory Region

The auditory region of *Tarsius* is noteworthy (Schwartz, 1984; MacPhee and Cartmill, 1986; Simons and Rasmussen, 1989). In general, the bulla and the anterior accessory cavity are quite inflated and, especially in the larger species, right and left anterior accessory cavities almost meet each other at the midline of the basicranium (Schwartz, in press). Although while still in its ring stage the ectotympanic is encased by and fuses to the inner wall of the ontogenetically expanding petrosal bulla, it subsequently ossifies into a tubular extension that protrudes laterally beyond the lateral margin of the bulla itself (MacPhee and Cartmill, 1986). A mediolaterally oriented bony septum separates the anterior accessory cavity from the tympanic cavity behind it; the promontory lies medially within the anthropoid tympanic cavity and posterior to the septum.

Anthropoids have a septum, but it extends the anteroposterior length of the bulla and over the promontory; consequently, the tympanic cavity lies lateral and the accessory cavity medial to it. In *Tarsius,* the internal carotid artery penetrates the septum laterally and centrally (Schwartz, 1984) and courses anteriorly through the anterior accessory cavity, pursuing a prepromontorial route (Simons and Rasmussen, 1989). In prosimians and anthropoids, the internal carotid artery pierces the bulla posteriorly and takes a transpromontorial course as it proceeds anteriorly. In anthropoids, the internal carotid artery courses within a bony canal that is incorporated into the septum. Thus, although *Tarsius* and anthropoids can be described as having a perbullar course of the internal carotid artery because the artery is associated with the septum (MacPhee and Cartmill, 1986; MacPhee et al., 1995), the details of bullar penetration and the path of the carotid artery relative to the promontorium and the septum are distinctly different (Simons and Rasmussen, 1989).

In various prosimians, the internal carotid artery bifurcates within the bulla into promontory and stapedial branches. In *Tarsius,* anthropoids, and virtually all lorisiforms (including cheirogaleids), the stapedial artery atrophies prenatally. *Tarsius,* anthropoids, and various lorisiforms also develop an anterior accessory cavity in the middle ear, although, in anthropoids, it is primitively quite trabeculated. The anterior accessory cavity become larger from *T. pumilus, T. spectrum,* and perhaps *T. dianae, T. syrichta,* to *T. bancanus* (cf. Musser and Dagosto, 1987).

The medial and lateral pterygoid plates, although involved with muscles of mastication, can be discussed here because of their peculiar association with the auditory region. In *Tarsius,* the strikingly reduced medial pterygoid plates converge at the midline of the basicranium where they fuse together as well as to the basisphenoid (Schwartz, in press). The medial pterygoid plates thus form a somewhat funnel-shaped structure that appears to extend the nasal cavity posteriorly. *Tarsius*'s lateral pterygoid plates are huge and winglike. They fan out from their articulation with the medial pterygoid plates to embrace and partially fuse with the anterior accessory cavities as far laterally at times as the articular fossae (ibid.). *Tarsius* is thus unique among primates because other prosimians and anthropoids develop individually distinct medial and lateral pterygoid plates that are either subequal in length or of unequal length, with the medial plate being moderately shorter than the lateral plate (ibid.).

Cartmill et al. (1981) and MacPhee and Cartmill (1986) suggested that seven features of the auditory region support the monophyly of extant Haplorhini: (1) absence of an annular bridge; (2) small tympanic cavity; (3) entry of the carotid artery into the bulla posteromedially; (4) presence of an anterior accessory cavity; (5) perbullar path of the carotid artery; (6) promontory artery unreduced in size but stapedial artery vestigial or absent; and (7) primary supply of the middle meningeal artery via the maxillary artery. Of these, MacPhee and Cartmill suggested that only features 1, 2, and 4 are identical in *Tarsius* and anthropoids; accepting the other features as potential synapomorphies requires complicated arguments. Although the claim of tarsier-anthropoid similarity might be correct, features 1 and 2 are also characteristic of lorisids and galagids, and feature 4 is found in all lorisiforms, including cheirogaleids. Interestingly, and to the exclusion of *Tarsius,* lorisiforms and anthropoids are similarly unique in having a complex epitympanic recess and a large mastoid cavity.

From the preceding review, the following emerges as being particularly important. In lorisiforms, the tympanic cavity and accessory chamber lie medial to the septum; in anthropoids, the tympanic cavity and accessory chamber lie lateral to the septum; and, in *Tarsius,* the anterior accessory chamber lies anterior, and the tympanic cavity posterior to the septum (Simons and Rasmussen, 1989). The entry of the carotid artery in *Tarsius* is lateral and central with regard to the entire bullar region (but anterior and central if only the true bulla is considered), and variably posteromedial in anthropoids, as it also is in lorisids and galagids. The perbullar course of the carotid artery is transpromontorial in anthropoids but prepromontorial in

Tarsius (ibid.). Cross-taxic comparison leads to the conclusion that possession of an unreduced promontory artery is primitive for primates, whereas a vestigial or totally absent stapedial artery represent derived character states. Since *Tarsius,* anthropoids, and lorisiforms are characterized by the latter state, there is only one feature of the auditory region that supports Haplorhini: the maxillary artery is the primary source of the middle meningeal artery. As noted above, other basicranial features suggest that the relatedness of lorisiforms and anthropoids and others unite *Tarsius,* lorisiforms, and anthropoids.

The Jaws and Teeth

Tarsius's oddly laterally oriented coronoid process, which is most elevated in *T. syrichta,* barely rises above the level of the mandibular condyle, which is so mediolaterally compressed from side to side that, even in the large *T. syrichta,* it is barely wider mediolaterally than the neck of the ramus (Schwartz, 1984). In other primates, and mammals in general, the condyle is mediolaterally broad (Schwartz, 1984). In profile, *Tarsius*'s smooth and slightly domed condyle lies in the same plane as the ramus and is barely delineated from the bone from which it emerges; in the large tarsier species its articular surface extends anteriorly for some distance in the direction of the coronoid process, as well as down the condylar spine of the ramus (Schwartz, in press).

Tarsius's uniquely configured mandibular condyle articulates in a crisply excavated articular fossa that is bounded posteriorly by the tubular ectotympanic, medially by the lateral wall of the anterior accessory cavity, and laterally by the root of the zygomatic portion of the temporal bone (Schwartz, in press). The mandible is thus essentially limited to a hingelike motion during mastication (also see Jablonski and Crompton, 1994). In all other primates, the zygomatic root lies superior to the articular fossa, which, in turn, is never as restricted as in *Tarsius* (Schwartz, in press). Thus, even though lorisids and catarrhines develop to varying degrees a tubular ectotympanic, this structure, in conjunction with the postglenoid plate, present to some extent in all primates, does not impinge significantly on their articular fossae.

The dental formula of adult *Tarsius* is typically given as 2.1.3.3/1.1.3.3. Morphologically, however, none of *Tarsius*'s anterior teeth—upper or lower—is "incisiform." Although differing in size, the first six upper teeth are essentially premolariform in shape, and their bases are ringed with cingulum. They are also pointed and to some extent conical. The first upper tooth is the tallest and most conical in the upper jaw, and it is also more trenchant than the tooth identified as the "canine." The second tooth ("second incisor") is the smallest upper tooth; it and the two teeth behind it (the "canine," which is the second tallest tooth in the upper jaw, and "first premolar") may bear a tiny posterior heel. The fifth and sixth upper teeth (the "second" and "third premolars") bear an additional cusp lingually, which is somewhat larger in the sixth tooth. Although primitive in overall design and transverseness, M^{1-3} possess distinctively compressed and U-shaped protocristae that emanate from a broad and somewhat compressed protocone; M^{1-2} also bear a tiny prehypocone crista. Among primates, prehypocone cristae are found only in extant lorisiforms and various presumed fossil tarsiiforms (Schwartz, 1984, 1986).

Tarsius's first and third lower teeth (the incisor and first premolar) are the smallest lower teeth; the first tooth is relatively very small in the large species and relatively larger in the smaller species (Schwartz, in press). The distal edge of the first mandibular tooth flares laterally and bears a thin margocristid while the mesial edge is essentially straight. The lingual surface bears a variably distinct longitudinal keel, which is rather mesially positioned and thus subdivides the crown quite asymmetrically. These features are most pronounced on the relatively large lower anterior tooth of *T. pumilus* and less pronounced on the relatively smaller lower anterior tooth of the larger species. Although I (e.g., 1984) previously argued that the homologue of the lower anterior tooth of *Tarsius* does not exist in other primates, this appears not to be the case. The features of *Tarsius*'s lower anterior tooth, which are so clearly illustrated in Musser and Dagosto's (1987) scanning electron micrographs of *T. pumilus,* are undeniably present in the lateral tooth of lemur, loris, and indriid toothcombs as well as in the large lower anterior tooth of various fossil tarsiiforms.

Since the lateral tooth of the prosimian toothcomb is usually identified as a canine (the underlying notion being that the canine and incisors became modified into elongate and narrow toothcomb teeth), logic would demand a similar identification of the lower anterior tooth of *Tarsius* (and of relevant fossil primates, as well). However, of greater importance than giving these teeth a name is recognizing that they are morphologically similar, and that, on this basis, they should be identified as homologues of the same tooth.

The second-fifth lower teeth of *Tarsius* (the canine and premolars) are similar morphologically in being premolariform and bearing a small but distinct heel that is incorporated into the cingulid ringing the base of the crown. The heel and cingulid of the second tooth are least pronounced buccally. The second tooth is the tallest, the next tooth behind is the shortest, and the somewhat bulkier fourth and fifth teeth are intermediate in height. As in lorisiforms and various fossil tarsiiforms, the third-fifth lower teeth (the premolars) are basically ovoid in outline. In all species of *Tarsius,* the lower canine and premolars bear a small but distinct heel incorporated into the cingulid surrounding the base of the crown.

M_{1-3} primitively retain distinct paraconids which remain separated from the metaconid throughout the series. M_3 is also primitive in having a moderately enlarged and somewhat centrally emplaced hypoconulid (posterior lobe). M_{1-3} are distinctive in having a sharply angular hypoconid, a well-defined buccal cingulid, and a tall protoconid and metaconid that are connected by a crest and form a steep wall facing the talonid. The latter cusp and crest configurations are also distinctive of lorisiforms and various fossil tarsiiforms (Schwartz, 1984, 1986).

Given the number of autapomorphic features of *Tarsius*'s jaws and teeth, as well as the obvious primitive aspects of molar morphology, few potential synapomorphies can be delineated. Of particular note are similarities with lorisiforms (especially the above-cited lower molar features, a prehypocone crista on M^{1-2}, and ovoid lower premolariform teeth). More broadly, *Tarsius*'s lower anterior tooth (the incisor) is strikingly similar to the lateral tooth of the toothcomb of toothcombed prosimians—which, if synapomorphic, not only unites these taxa as a clade, but also demonstrates that *Tarsius* has the most derived toothcomb among prosimians.

The Postcranial Skeleton

Postcranially, *Tarsius* possesses enlarged digital pads on hands and feet [being least pronounced in the small *T. pumilus* (Musser and Dagosto, 1987)], grooming claws on the second and third pedal digits, fusion of the tibia and fibula, profound elongation of the calcaneus and navicular bone, and relatively short metatarsals (e.g., Hill, 1955; Jouffroy et al., 1984). Degeneration of the nails on nongrooming clawed digits—often claimed as distinctive of tarsiers—is severe only in *T. bancanus* and *T. syrichta,* whereas *T. spectrum, T. dianae,* and especially *T. pumilus* possess nails that are quite well developed, compressed laterally, and strongly keeled centrally, as in *Daubentonia, Euoticus, Galago, Allocebus,* and various marmosets (ibid.; Soligo and Müller, 1999).

Tibiofibular fusion occurs in the smaller mouse lemurs and bush babies (Howell, 1944), which are remarkably similar to *Tarsius* in their degree of tarsal elongation and relative metatarsal truncation (Jouffroy et al., 1984). Marked elongation of the calcaneus and navicular is noted in the East African Miocene galagids *Progalago* and *Komba* (Walker, 1974) as well as in various fossil tarsiiforms (*Necrolemur, Nannopithex, Hemiacodon, Tetonius, Teilhardina, Arapahovius*) (see review in Schwartz, 1986). Galagids, *Microcebus, Phaner,* and *Tarsius* are collectively distinguished among extant primates in having an extremely elongated calcaneus and a much-reduced cuboid; in *Tarsius,* the orientation of the cuboidal trochlear facet prevents lateral deviation of the foot (Jouffroy et al., 1984). *Tarsius,* galagids, and *Microcebus* are the only prosimians, and *Callithrix* and *Pongo* the only anthropoids, in which the foot is longer than either the femur or tibia. The extremely long hindlimb of *Tarsius* and most galagids is reflected in their having the lowest intermembral indices (femur length/humerus length) among primates (ibid.).

Among extant primates, the femora of *Tarsius* and galagids are distinguished in having a cylindrical head, a more anteriorly expanded greater trochanter that extends onto the shaft, a deeper triangular depression at the intersection of the greater trochanter and the proximoanterior margin of the shaft, bowing of the proximal shaft anteriorly, a relatively short neck and high neck angle, and a relatively pronounced posterior projection of the lesser trochanter (Dagosto and Schmid, 1996). *Tarsius* and galagids also have the highest knee index (>100, reflecting a very deep knee). Many of these femoral features are also seen to some extent in various omomyids and microchoerines (ibid.). *Tarsius*'s talus is unique among primates in being extremely compressed superoinferiorly and in exhibiting little articular morphology superiorly (Schwartz, 1992).

Tarsius is outstanding in the great length of its forelimb (e.g., as measured relative to the length of the precaudal portion of its vertebral column) (Schultz, 1984). It also has the relatively longest hand of any living primate. As in anthropoid hands, *Tarsius*'s third finger is the longest, but, as in prosimian feet, its fourth digit is the longest. Thus *Tarsius* is unique among primates in not having structural similarity between its hand and foot in digital proportions. As in prosimians, *Tarsius* primitively retains a prepollex in the carpal region. *Tarsius* is apparently apomorphically similar to various lorisids in having pisiform-radius contact (Schwartz, 1992), but is primitively similar to most prosimians and anthropoids in having a proximally peaked and triangular os centrale (Schwartz and Yamada, 1998). *Tarsius*'s long scapula, together with its scapulohumeral and scapular indices, suggests an animal that should be terrestrial and quadrupedal. This describes *T. dianae* (which preferentially locomotes quadrupedally along horizontal supports), but not the clinging and leaping *T. bancanus* (thus suggesting caution in interpreting the locomotory behavior of extinct taxa).

A survey of various primates reveals that the nails on *Tarsius*'s non-grooming claw pedal digits I and IV (digit V was not analyzed) are similar to at least *Nycticebus, Galago,* and *Microcebus,* among prosimians, and *Cercopithecus aethiops* (but not *C. cephus*), *Papio anubis, Homo,* and *Hylobates,* among anthropoids, in having only one layer (Soligo and Müller, 1999). All other primates studied are (primitively) similar in having pedal digit nails composed of two layers (ibid.), which, therefore, makes this character useless in terms of resolving phylogenetic relationships.

The grooming claw of the second and third pedal digits is large in all species of *Tarsius* and similar in shape and structure (primitively retaining two layers) to the single grooming claw present on only the second pedal digit of extant prosimians (Soligo and Müller, 1999; Spearman, 1985). Although Soligo and Müller (1999) claimed that their data support the grouping of *Tarsius* with anthropoid primates and *Microcebus* with *Lemur* rather than with *Galago* and *Nycticebus,* this is clearly not the case. Synapomorphy at some level of common ancestry would be the more reasonable explanation of why *Microcebus, Galago,* and *Nycticebus* have a single-layered nail not only on digits I and IV, but on digit III as well. Assuming that prosimians and anthropoids are, respectively, monophyletic groups (e.g., see review in Schwartz, 1986)], *Tarsius*'s single-layered nail of nongrooming-clawed pedal digits links it not as the sister taxon of either Prosimii or Anthropoidea, but as a member of a subclade either of lorisiform or catarrhine primates.

Regardless of whether *Tarsius* is more closely related (somehow) to either strepsirhines or anthropoids, one must still deal with the fact that this primate possesses two pedal grooming claws. Thus, the following scenarios emerge. (1) The last common ancestor of all extant primates possessed a grooming claw on the second pedal digit, and this condition was retained in strepsirhine primates and in *Tarsius. Tarsius* either developed a second grooming claw autapomorphically or retained it from a last common ancestor that it shared with anthropoids; and, thus, the last common ancestor of anthropoids would have "lost" one or two grooming claws (and gained nails). (2) The last common ancestor of all extant primates did not possess a grooming claw. The last common ancestor of strepsirhine primates developed a grooming claw on the second pedal digit independently of either *Tarsius* or the last common ancestor of *Tarsius* and anthropoids. *Tarsius* either developed the second grooming claw on the third pedal digit autapomorphically or retained it from a last common ancestor it shared with anthropoids. Thus, the last common ancestor of anthropoids lost one or even two grooming claws (and "gained" nails). Or (3), as recently proposed by Soligo and Müller (1999), the last common ancestor of all extant primates had a grooming claw on the second pedal digit. This was retained in all strepsirhines and the last common ancestor of *Tarsius* and anthropoids. *Tarsius* developed a grooming claw on the third pedal digit, and the last common ancestor of extant anthropoids lost the grooming claw (and gained a nail).

The simplest suggestion is (4) that *Tarsius* and strepsirhines possess a grooming claw on the second pedal digit because they inherited this unique feature from a common ancestor they shared to the exclusion of anthropoids. As for which state—one or two grooming claws—preceded which, since both of *Tarsius*'s grooming claws and the single grooming claw of strepsirhines are (primitively) composed of two layers, while the nail (whether flat or keeled and compressed) on a strepsirhine's third pedal digit is (derivedly) single layered, it would appear that the last common ancestor of all prosimians would have been *Tarsius*-like in possessing two double-layered grooming claws and *Lemur*- and *Daubentonia*-like in having double-layered structures on digits I and IV. Within this hypothesized clade (prosimians), the situation is not as clear cut. Either (1) the last common ancestor of strepsirhine prosimians was characterized by the loss of the grooming claw on the third pedal digit and *Tarsius* and lorisiforms independently developed single-layered nails on digits I and IV, or (2) *Tarsius* and lorisiforms are united by their common development of single-layered nails on digits I and IV, with reduction to a single grooming claw occurring independently in lemuriforms and lorisiforms. Truly, beyond the fact that *Tarsius* and strepsirhine prosimians appear synapomorphic in having a grooming claw on the second pedal digit, the distribution of different nail and claw morphology and histological detail does not lend itself to an easy resolution of other potential phylogenetic relationships.

Placentation

Luckett (e.g., 1974, 1976), essentially following Hubrecht (1898), argued that *Tarsius* and anthropoids are closely related because the end product of their placental development is a hemochorial type, in contrast to the versions of epitheliochorial placentation seen in strepsirhine primates. When faced with such notable differences between *Tarsius* and anthropoids as in blastocyst attachment and amnion development, Luckett suggested that they were due to *Tarsius* retaining the primitively mammalian bicornuate uterine configuration and anthropoids developing a simplex uterus. If *Tarsius* were to have a simplex uterus, these substantial differences would vanish.

From Luckett's studies, and those he cites, the attainment of hemochorial placentation appears correlated with the following events: the establishment of a chorioallantoic placenta, which bypasses a transitory choriovitelline stage, in conjunction with the rudimentary development of an allantoic diverticulum and the precocious differentiation of a mesodermal body stalk. Differences between the diversity of mammals that achieve hemorchorial placentation lie in details of blastocyst implantation. Interestingly, not only do various nonprimate mammals (e.g., tenrecs, hedgehogs, elephant shrews, flying lemurs, and some bats) mirror anthropoids more precisely than does *Tarsius* in their course of hemochorial placental development, these mammals more faithfully reproduce the course of hemochorial placental development seen in anthropoids—and they do so in the environment of a bicornuate uterus.

Also in anthropoids and these nonprimate mammals, the blastocyst attaches by the embryonic trophoblast to the orthomesometrial pole of the uterine endometrium. *Tarsius* is distinguished from anthropoids and many other mammals in that its blastocyst attaches by the paraembryonic trophoblast to the mesometrial wall of the uterine endometrium. Although Luckett (1993) continues to dismiss alternative interpretations of the placental data and to maintain that *Tarsius* would develop hemochorial placentation in the same manner as anthropoids if it had a simplex uterus, the demonstration of homology between *Tarsius* and anthropoids in development of hemochorial placentation is certainly not self-evident (also see Cartmill, 1994). If, however, as Martin (e.g., 1968, 1990) has maintained, hemochorial placentation is primitive for primates, the issue is moot—but one must still be specific with regard to developmental details.

The Brain

The brain of *Tarsius* presents a series of contradictory comparisons (Stephan, 1984). It is relatively smooth and ungrooved, as is typical of small, nocturnal prosimians (e.g., *Microcebus murinus, Cheirogaleus medius,* and *Galago demidovii*), and the commissural system and simple cerebellum are (primitively?) reminiscent of insectivores. Oddly, the temporal and occipital lobes are larger than the frontal lobe. As otherwise seen in birds, *Tarsius*'s brain is excavated rostrally and its olfactory nerves, as measured between the olfactory mucosa and the secondary olfactory cortices, are long and thin. *Tarsius*'s olfactory peduncles, which course between the olfactory bulbs and the cerebral hemispheres, are short and broad and, as in lemurs, the ventricles are obliterated. In anthropoids, the olfactory nerves are short and the olfactory peduncles long. As in some mouse lemurs, *Tarsius*'s olfactory bulbs project beyond the frontal poles of the cerebrum. In *Tarsius* and all other prosimians, the inner face of the occipital lobe bears a triradiate arrangement of deep calcarine sulci that emanate from its center. Among primates, the cerebral hemispheres of only *Tarsius,* other prosimians, and marmosets develop a marked occipital extension. In general, it appears that the brain of *Tarsius* is most like that of other prosimians, but whether this reflects phylogenetic affinity or primitive retention from the common primate ancestor is unclear. Stephan (1984) commented that, for the most part, whereas *Tarsius* differs from prosimians in brain morphology, it also deviates from the configuration seen in anthropoids.

Miscellany

In a study on vitamin C biosynthesis, *Tarsius* and the anthropoids in the sample emerged as being nonsynthesizers, whereas the lemurs and lorises analyzed were synthesizers (Pollock and Mullin, 1987). Synthesizing vitamin C is apparently the primitive condition among mammals. Pollock and Mullin point out, however, not only that more data should be collected before taking these results as unequivocal, but that, among New World hystricomorph rodents—which systematists accept as constituting a monophyletic group—the guinea pig stands out autapomorphically as the only nonsynthesizer of vitamin C.

Fossil *Tarsius* and *Tarsius*-like Relatives

Tarsius eocaenus (middle Eocene, PRC) is represented by isolated teeth (two M_3 s, two $M_{1 \text{ or } 2}$ s, and a P^3) (Beard et al., 1994) and diagnosed in comparison with omomyids (broadly construed) and *Afrotarsius.* Living Tarsius and the fossil taxon are similar in having paraconids on M_{1-3} and an extended but narrow hypoconulid on the M_3 (pers. obs.). In stark contrast with *Tarsius,* however, *T. eocaenus* lacks distinct M_{1-2} hypoconulids, its M_{1-2} cristids obliquae course to the metaconid, the upper premolar is dominated by the paracone, and all teeth bear cingula/-ids (pers. obs.). Further, in *Tarsius,* the M_{1-3} are somewhat compressed and melded at their bases, forming a sheer wall to the talonid. *Tarsius*'s M_3 trigonid and talonid are almost at the same level, and not very disparate in height on M_{1-2}. In *T. eocaenus,* the metaconid and protoconid are bulbous and melded only on M_3, and the trigonids tower over the talonids on M_{1-3}. In *Tarsius,* the paraconid is bulbous, vertically oriented, and more centrally than lingually situated; it maintains the same relative distance from the metaconid on all molars and is connected to the protoconid by a complete and arcuate paracristid. In *T. eocaenus* the paraconid is more compressed, not connected to the protoconid, lingually placed, and markedly inclined forward; it is also closer to the metaconid on M_3 than on M_{1-2}. In *Tarsius,* the protoconid and metaconid are subequal in height. In the fossil M_3, at least, the protoconid is the taller of the two cusps. In *Tarsius,* the hypoconid is angular and lies slightly mesial to the entoconid; both cusps are well separated from the trigonid. In *T. eocaenus,* the hypoconid isrounded and lies quite distal to the very mesially placed entoconid, which extends essentially to the base of the metaconid. Lower molar buccal cingulids are thick in *Tarsius,* but only moderately developed in *T. eocaenus.* In *Tarsius,* the upper penultimate premolar paracone is centrally placed and compressed and it bears pre- and postparacristae. In the fossil P^3, the paracone is lingually placed and not compressed; the tooth is distended distally by a distinct metacone swelling. Since the differences between these fossil teeth far exceed the differences between extant species of *Tarsius,* it seems premature to assign the former to a species of this genus. *T. eocaenus* differs from all traditionally recognized fossil tarsiiforms, but is similar to *Afrotarsius,* in having well-separated paraconids and metaconids on all lower molars.

An isolated right lower molar from the early Miocene of Thailand referred to the species *Tarsius thailandica* (Ginsburg and Mein, 1987) appears to represent an extinct species of this genus. It differs from the extant species in that its paraconid is lingually placed and its hypoconid lies opposite the entoconid, which, in turn, lies close to the metaconid.

Xanthorhysis tabruni (middle Eocene, PRC) (Beard, 1998) is reminiscent of *Tarsius* in dental morphology. The type and only specimen consists of a partial left mandibular corpus lacking the ramus but including much of the symphysis. It retains two posterior premolars, M_{1-3}, and two anterior single alveoli, with the mesial one being large and the other moderate in size. Discrepancies between the published description and the specimen require a review of the relevant morphologies.

Xanthorhysis is similar to *Tarsius* in having a slender corpus. Both have (1) a distinct, somewhat bulbous and vertically oriented paraconid on M_{1-3} that lies more centrally than lingually, (2) relatively tall, pointed protoconids on the distal two premolars, (3) a strong, mesially directed crest running down the cusp on the ultimate premolar whose relatively short talonid basin is enclosed, (4) cingulids ringing the premolars and coursing the length of the buccal sides of the molars, (5) entoconids on all molars that lie well behind the metaconid, (6) molar protoconids and metaconids that are melded at their bases and form a steep wall upon the talonid, (7) relatively broad M_{1-2} talonids enclosed by cresting systems, and (8) cristids obliquae that course to the metaconids on all molars.

Xanthorhysis differs from *Tarsius* in that the hypoconid on all molars is not as angular and it lies just distal to the entoconid. The paracristid diminishes in prominence in the series M_{1-3}, and the penultimate premolar is relatively larger with a more prominent heel. The last premolar is much taller and somewhat compressed, and M_{1-2} possess a low and flat hypconulid. Also, the M_3 trigonid stands well above the level of the talonid, and, despite the fact that the M_3 is distended into a centrally placed heel, this tooth is much smaller, particularly in overall length and talonid width. Among the published Chinese specimens, *Xanthorhysis* is certainly the most similar to *Tarsius* with the best clues to possible relatedness seen in the molar trigonids (especially the nature of the paraconid) and the last lower premolar.

Afrotarsius chatrathi (early Oligocene, the Fayum, Egypt) has been interpreted as being perhaps closely related to *Tarsius* (Simons and Bown, 1985). The fossil resembles *Tarsius* mostly in primitive features (e.g., distinct paraconids on all molars), although its lower molar metaconids and protoconids are tall and melded at their bases (forming a steep wall facing the talonid basin) and its paraconids are low set. *Afrotarsius* differs from *Tarsius* in (1) having trigonids that are very tiny relative to talonid breadth and width, (2) talonid basins that are broad and deeply but smoothly excavated, (3) deep and relatively broad notches between protoconid and hypoconid and metaconid and entoconid, and (4) an M_3 that is smaller than M_1 and

M_2. Kay and Williams (1994) suggested that possession of a buccally oriented cristid obliqua is synapomorphic of *Afrotarsius, Tarsius,* and anthropoid primates, but the widespread distribution of this feature among fossil and living primates (cf. Schwartz, 1986; Schwartz and Tattersall, 1985) indicates that it is symplesiomorphic.

Fossils traditionally identified as tarsiiforms were grouped with *Tarsius* not only because of general similarities in molar morphology, but also because the skulls of three fossils in particular—*Pseudoloris, Necrolemur, Tetonius*—were reminiscent of *Tarsius*'s in general dental arcade and cranial shape, as was the auditory region of the skull of *Necrolemur* (Gregory, 1922; Simpson, 1940; see review by Schwartz, 1984). Through increasingly wider spheres of comparison between these fossils and others, *Tarsius* accrued numerous extinct relatives whose dental primitiveness was adapted to theories of anthropoid origins. Generally overlooked, however, is the fact that those who supported a tarsiiform assemblage often also pointed to the many details of the dentition as well as of the orbital, auditory, and mastoid regions in which the relevant fossils differed significantly from their presumed, extant relative. In addition, various paleontologists (e.g., Gregory, 1922) noted that the fossils could be compared equally well (e.g., in rostral elongation) or even more accurately (e.g., petromastoid inflation) with *Galago.*

According to Beard and MacPhee (1994) and Beard et al. (1992), cranial morphology indicates that *Shoshonius* is more closely related to *Tarsius* than other traditionally recognized tarsiiform or omomyid taxa. Although Ross (1994) argued that this conclusion is based on questionable homology and determination of character polarity, as well as a posteriori weighting of characters, there are at least some features that need to be reconciled. In light of errors in Beard et al.'s (1991) identifications and descriptions of various cranial landmarks, the discussion below relies on personal observations that both provide new information and corroborate the corrections provided by Beard and MacPhee (1994).

Beard and MacPhee (1994) united *Shoshonius* with *Tarsius* on the basis of (1) development of a basioccipital flange that overlaps the medial aspect of the auditory bulla, (2) an extremely narrow central stem (defined as the width of the basisphenoid and basioccipital bones between bullae), (3) an alisphenoid flange with bullar overlap (defined as the extension of the lateral pterygoid plate onto the bulla), (4) narrow and peaked choanae, and (5) reduction of the snout.

Beard and MacPhee (1994, p. 82) defined snout length as snout extension "beyond the alveolar border of the anteriormost teeth" and judged it to be apomorphically short in *Shoshonius, Tarsius,* and anthropoids because they thought it was plesiomorphically long in *Galago.* A broad comparative survey of primates reveals, however, that extension of the snout beyond the alveolar region of the anteriormost teeth is infrequently encountered, characterizing only *Arctocebus, Loris, Allocebus* (slight), *Phaner* and, to varying degrees, galagids, but not most prosimians or anthropoids (see illustrations in Schwartz and Tattersall, 1985). Thus, as defined by Beard and MacPhee, *Tarsius*'s reduced snout is plesiomorphic.

With regard to lateral pterygoid plate-bullar contact (the alisphenoid flange), the common condition in mammals is lack of contact. Among extant primates, only prosimians develop a contact between the lateral pterygoid plate and the anterior or anterolateral portion of the bulla (see, for example, illustrations in Gregory, 1922; Saban, 1963; Schwartz and Tattersall, 1985). In indriids, the contact is broad and complete, with the added apomorphy of appression both superiorly and inferiorly of the short medial pterygoid plate to the lateral plate such that a narrowly ovoid funnel-shaped structure is formed. A shallow and much more compressed fossa between the pterygoid plates is found in *Daubentonia, Hapalemur, Lepilemur, Varecia, Lemur,* and *Eulemur,* and contact between the lateral pterygoid plate and the bulla may be long anteroposteriorly and complete vertically, or interrupted by a foramen of sometimes large size that is functionally a continuation of the foramen ovale (through which the mandibular branch of the trigeminal nerve courses).

In galagids and more so in lorisids, the contact between the lateral plate and the bulla can be relatively extensive. However, because the foramen ovale in these taxa is situated in line with the posterior end of the lateral pterygoid plate, and thus more medially than in most primates, lateral pterygoid plate-bullar contact may be tenuous in some specimens (e.g., as Beard and MacPhee described for *Galago*). Since the articular fossa is more medially situated in *Loris* and *Arctocebus* than it generally is in primates, it may intervene between the lateral pterygoid plate and the bulla and further disrupt the bridge between these two structures.

In subfossil Malagasy prosimians, substantial contact between the lateral pterygoid plate and the bulla is preserved in *Pachylemur, Mesopropithecus,* and *Hadropithecus,* as well as in the significantly airorhynchous *Megaladapis.* In palaeopropithecines, some contact exists between the lateral pterygoid plate and the flattened bulla. Contact in *Archaeolemur* is disrupted by the linear arrangement of the foramen ovale and anterior carotid foramen between the lateral plate and the inflated bulla. Of note in archaeolemurines and *Mesopropithecus* is that the medial and lateral pterygoid plates form a distinct funnel-shaped structure, as seen in extant indriids. *Adapis, Notharctus, Necrolemur, Tetonius,* and *Rooneyia* display substantial contact between the lateral pterygoid plate and the bulla (pers. obs.; see also Gregory, 1922; Saban, 1963), although the contact may not be as extensive as in *Shoshonius* (pers. obs.; cf. Beard and MacPhee, 1994).

Since lack of lateral pterygoid plate-bullar contact characterizes most mammals, contact between these structures emerges among primates as synapomorphic of *Tarsius* and other prosimians. Beard and MacPhee (1994) suggested that the configuration of incomplete contact seen in galagids is primitive for primates, with *Tarsius* and *Shoshonius* being similarly derived in their degree of contact. However, the reason galagids (and lorisids) have incomplete contact is because they possess the derived condition of a medially situated foramen ovale lying between the lateral pterygoid plate and the bulla. Consequently, within prosimians, broad contact (as seen in indriids and others) emerges as the primitive character state, while the configuration seen in galagids and lorisids is synapomorphic for them.

A final note, though. Since the broad contact seen in *Tarsius* is actually between the lateral pterygoid plate and the vastly enlarged anterior accessory chamber (rather than the bulla itself), it might not be proper to suggest equivalence of this contact with contact in other prosimians between the lateral pterygoid plate and the bulla.

Beard and MacPhee (1994) considered the development of a basioccipital flange overlapping the medial aspect of the auditory bulla a synapomorphy of *Tarsius, Shoshonius,* and *Tetonius.* This configuration is, however, present in various galagids and cheirogaleids, and is occasionally seen in lorisids. Consequently, if development of a basioccipital flange is apomorphic (rather than a feature related to small size), it points to a clade within Prosimii. Depending on how one assesses the character "narrow and peaked choanae," one can include various lorisiforms in the comparison with *Tarsius* and *Shoshonius.* Thus, none of the features Beard and MacPhee (1994) proposed as uniting either *Tarsius* and *Shoshonius* as sister taxa or, alternatively, *Tarsius, Shoshonius,* various omomyids and anthropoid primates as a group hold up under scrutiny. There is, however, a potential synapomorphy of *Tarsius* and *Shoshonius* that has not been previously pointed out.

Tarsius is unique among extant primates in having short medial pterygoid plates that coalesce to form a funnel-shaped structure (see above). In galagids and lorisids, there is some approximation of the medial pterygoid plates toward the midline of the basisphenoid, but the prevalent condition among primates is well-separated medial pterygoid plates. Thus, there is among extant primates an apparent morphocline of narrowing of the basisphenoid/basioccipital region (creating Beard and MacPhee's "central stem"). A central stem is seen in the early Paleogene *Ignacius* as well as in *Shoshonius,* which, like *Tarsius,* also fuses the medial pterygoid plates into a funnel-shaped structure (pers. obs.; Beard, pers. com.).

With regard to tympanic morphology, *Tarsius* is unique among primates in that, after the tympanic ring becomes ontogenetically internalized and fused to the inner wall of the auditory bulla, it elongates laterally beyond the bulla as a tubular extension (see above). *Shoshonius* is generally similar to other Paleogene taxa (e.g., *Necrolemur, Rooneyia, Plesiadapis, Adapis*) as well as extant lorisiforms and tupaiids in having an internalized ring that is connected to the inner bullar wall by an annular bridge (MacPhee and Cartmill, 1986). In *Shoshonius,* the bridge is much narrower than it is in *Rooneyia* and *Plesiadapis* (Beard and MacPhee, 1994; pers. obs.). In tupaiids and extant primates with an annular bridge, a gap (recessus dehiscence) separates it from the tympanic ring, whereas in *Necrolemur, Rooneyia, Adapis,* and *Plesiadapis,* the bridge between the ring and bullar wall is complete. *Ignacius* is *Tarsius*-like in fusing the ring to the inner wall of the bulla (cf. Kay et al., 1992). It cannot be determined if *Shoshonius* had a recessus dehiscence. Beard and MacPhee (1994) concluded that the configuration seen in *Plesiadapis* and other primates is primitive for primates. The broader comparison indicates, however, that either the trait "lack of an annular ring" or the trait "an annular ring with recessus dehiscence" is the primitive condition *within* a clade that is united first and foremost by a change in the configuration of the auditory bulla from its primitive position medial to the tympanic ring to its development laterally around the ring (cf. Cartmill, 1975; Schwartz, 1986). If internalization of the tympanic ring is apomorphic for extant Prosimii, then the possession of this configuration by various Eocene forms (e.g., *Adapis, Notharctus, Necrolemur, Rooneyia, Shoshonius*) unites them with this clade.

Fossil tarsiiforms compare well with both *Tarsius* and *Galago* in details of the proximal femur (Dagosto and Schmid, 1996) as well as in calcaneal and navicular elongation and distal tibiofibular fusion (see above). *Tarsius* differs from these fossils in lacking the cuboidocalcaneal facets and a "well-developed socket for the pivot" of the cuboidocalcaneal articulation that are characteristic not only of other extant primates, but also of those extinct tarsiiforms for which these postcranial elements are known (the omomyid *Hemiacodon* and the anaptomorphids *Teilhardina* and perhaps *Tetonius*) (Szalay, 1976 401; Szalay and Decker, 1974).

In its talus, *Tarsius* bears a (primitively) short, broad facet, whereas in fossil tarsiiforms, *Galago,* and other lorisiforms, the trochlear facet is long and narrow (S. Ford, pers. com.). *Tarsius*'s talus is also compressed proximodistally, as is also seen in lorisids (Schwartz, 1992). Postcranials attributed to *Shoshonius* are not as apomorphically *Tarsius*-like as they are *Galago*-like (Dagosto et al., 1999). In general, there appears to be even less postcranial synapomorphy uniting *Tarsius* alone with anthropoids or *Tarsius* and omomyids with anthropoids (e.g., Dagosto and Schmid, 1996; Covert and Williams, 1994) than there is potential cranial synapomorphy, which is quite slim (see above, and Cartmill and Kay, 1978; MacPhee and Cartmill, 1986; Ross, 1994).

Inasmuch as studies on fossil tarsiiforms have tended not to test the hypothesis of monophyly for a group consisting of omomyids, anaptomorphids, and microchoerines, or the monophyly of each of these three groups, it is appropriate to raise these questions here.

A potential synapomorphy of some fossil tarsiiforms is the development in the lower jaw of a large, semiprocumbent anterior tooth which, in bearing a longitudinal keel and a flared lateral edge with margocristid, is virtually morphologically identical to the lateral tooth of the strepsirhine/prosimian toothcomb (Schmid, 1983; Schwartz, 1980, 1984). If the large anterior lower tooth of microchoerines and various omomyids and anaptomorphids is synapomorphic for them, then, like *Tarsius,* they, too, possessed an extremely derived toothcomb, in which only the homologue of the lateral tooth of the prosimian toothcomb remained (cf. Schmid, 1983; Schwartz, 1984). Since these fossils also share other potential dental apomorphies seen in *Tarsius* and lorisiforms (Schwartz, 1984, 1986; see above), there is reason for recognizing a prosimian clade and a *Tarsius*-lorisiform-fossil tarsiiform clade within it.

Tarsiiforms that do not have this enlarged lower anterior tooth—the omomyids *Loveina, Washakius, Chumashius,* and *Asiomomys* and the anaptomorphids *Chlororhysis* [type] and *Anaptomorphus*—are similar, for example, to *Pelycodus, Smilodectes, Notharctus, Adapis, Europolemur, Protoadapis,* and *Pronycticebus* in retaining the (primitive) configuration of two small, spatulate, incisiform teeth with a larger, trenchant, caniniform tooth behind (or specimens at least preserve the alveoli for two small anterior teeth and a larger tooth behind) (cf. Beard and Banyue, 1991; Covert and Williams, 1991, 1994; Rasmussen et al., 1995; Schwartz, 1984, 1986; Szalay, 1976). Consequently, the phylogenetic relationships of these taxa may not lie with large anterior-toothed tarsiiforms, but, rather, with various adapids, with which they share derived upper and lower molar morphologies, such as distinct protocone folds and lingually directed cristids obliquae (Schwartz, 1984, 1986).

In this light, it is noteworthy that the first-known lower jaw of *Caenopithecus* (traditionally thought of as an adapid) bears a pair of anterior alveoli that would have housed enlarged teeth (e.g., see illustrations in Gregory, 1922, and Schwartz and Tattersall, 1985), which were later found partially preserved in another specimen (Franzen, 1994). Since, as Robinson (1968) remarked, identifying a specimen as a tarsiiform, adapid, or notharctid should not be based on size or paleobiogeography, it seems productive to reconsider the relationships of *Caenopithecus* (Schwartz, 1986). For example, in having prehypocone cristae on M^{1-2}, U-shaped upper molar protocristae, distinct upper molar lingual cingula, *Caenopithecus* is broadly similar to *Omomys*-like omomyids (cf. Schwartz, 1984, 1986; see below). More specifically, *Caenopithecus* and *Macrotarsius* are similarly more derived in having (particularly on M^{1-2}) extraordinarily broad protocristae, strong mesostyles, a series of thin cristae in the prehypocone region, and pre- and postcingula that thicken at their lingual extremities and "square up" the crown. Since *Tarsius* and extant lorisiforms also develop upper molar prehypocone cristae, these features may be broadly synapomorphic of a clade that includes these extant prosimians, at least some fossil tarsiiforms, and *Caenopithecus.*

The relationships of the omomyid *Dyseolemur* are difficult to assess because, uniquely among primates, all of its antemolar teeth are premolariform, increasing in size and some morphological complexity distally (Rasmussen et al., 1995). Somewhat similar to *Tarsius, Dyseolemur*'s anterior teeth lie one behind the other, not across the front of the jaw as in toothcombed prosimians and anthropoids (callithricids included). The anteriormost lower teeth of *Shoshonius* are not known, but the single alveoli are arranged one behind the other. If the small anterior alveoli housed teeth similar to those of *Tarsius,* this would lend some support to Beard and MacPhee's (1994) claim of a special relationship between these taxa. *Dyseolemur*'s uniquely configured anteriormost lower tooth does, however, emphasize that anterior tooth morphology contradicts traditional groupings of tarsiiforms.

The removal of nontoothcombed taxa from Omomyidae and Anaptomorphidae allows for discussion of monophyly and the potential relationships of these groups on the basis of consistent dental morphology throughout the jaws (Schwartz, 1984, 1986). An omomyid clade (including *Omomys, Ourayia, Macrotarsius, Mytonius, Stockia, Dyseolemur, Lushius,* and *Caenopithecus*) can be delineated on the basis, for example, of broad and parabolic upper molar protocristae, M^{1-2} with lingual cingula swollen below the protocone as well as distolingually, anterobuccally displaced prehypocone cristae, and anteroposteriorly compressed M^3s (Schwartz, 1986). Excluded from this clade is *Macrotarsius macrorhysis* (middle Eocene, China), which Beard et al. (1994) identified on the basis of an isolated left M_1 and a right lower posterior premolar. The M_1 has an arcing paracristid, a lingually open and expansive trigonid with well-separated cusps, a relatively vertical buccal side, a hypoconid and entoconid that rise above the cristids, and a centrally placed distal flexure of the talonid, rather a distinct hypoconulid.

The M_1 of the type specimen of *Macrotarsius* (*M. montanus,* Carnegie Museum of Natural History #9592), however, has a stout and straight paracristid, a tightly compact and relatively small trigonid with closely appressed cusps, a cristid that closes off the trigonid lingually, a generally bulbous crown base with notable buccal selling, talonid cusps that are incorporated into the cristids, and a distinct hypoconulid that is situated toward the hypoconid. Similarities between the two "*Macrotarsius*" essentially lie in their being larger than most omomyids and in their M_1s having a cristid obliqua that courses to the base of the protoconid and a buccal cingulid, notably around the trigonid. The Chinese lower premolar is dominated by the protoconid, on the sides of which lie a moderately low metaconid and a very low paraconid; these three cusps subtend a steep and lingually oriented trigonid basin. In *M. montanus,* the trigonid cusps of the last lower premolar are subequal in size and height and subtend a tall and level trigonid basin. In having somewhat bulbous cusps, a not very towering trigonid, and a talonid that is longer and wider than the trigonid, the Chinese M_1 is morphologically primate (see review in Schwartz, 1986). It is premature to speculate which and how many taxa these isolated teeth represent.

An anaptomorphid clade (including *Tetonius, Absarokius, Pseudotetonius, Utahia, Anemorhysis, Arapahovius, Trogolemur, Aycrossia, Gazinius, Strigorhysis, Uintanius, Steinius,* and *Altanius*) could be distinguished by the possession of, for example, an M_1 cristid obliqua that arcs toward the metaconid and a definitive M^1 protocone fold (Schwartz, 1984), but these features also characterize the microchoerines *Nannopithex, Necrolemur,* and *Microchoerus* and the presumed omomyid, *Hemiacodon,* thereby suggesting that all of these taxa form a clade (Schwartz, 1984, 1986). The latter three taxa are further derived in having some enamel crenulation and M_2 cristid obliqua that arcs to the metaconid, and *Necrolemur* and *Microchoerus* are set apart by their marked enamel crenulation and quadrate M^{1-2}. In its lack of all lower molar paraconids, *Pseudoloris* emerges as the most derived large anterior-toothed fossil tarsiiform.

To summarize, if the large lower anterior tooth of microchoerines and various omomyids and anaptomorphids is synapomorphic for them, then we can describe these taxa as having an extremely derived toothcomb (cf. Schmid, 1983; Schwartz, 1984). As in *Tarsius,* this toothcomb would consist of only one pair of teeth, which presents itself as the morphological homologue of the pair of lateral teeth of the prosimian toothcomb. If *Shoshonius* had the derived prosimian auditory configuration of an internalized tympanic ring, it was perhaps derived within that clade in lacking anterior, toothcomb teeth altogether, as is the case in *Dyseolemur.*

Attention to tooth morphology in systematic endeavors cannot be overemphasized (e.g., Schwartz, 1980). Although there has been a long tradition in mammalian paleontology of identifying teeth by their positions and occlusal relationships, with crown shape having limitless malleability (e.g., Butler, 1974), studies on the regulation of tooth formation suggest otherwise (e.g., see Vaahtokari et al 1996; Thomas et al., 1997; Ferguson et al., 1998; Jernvall et al., 1998; Mitsiadis et al., 1998; Tucker et al., 1998; Pispa et al., 1999; Jernvall, 2000; Jernvall and Thesleff, 2000). A case in point involves the *Barx-1* gene, which is normally active posteriorly in the jaws as part of a cascade of molecular communication that produces molariform teeth. When *Barx-1* is experimentally activated in the presumptive incisor region of mice, true molar teeth develop. These teeth are not incisors that have been transmuted to look like molars. Rather, they are molars because they derive from a specific sequence of regulatory molecule communication that produces molariform teeth. Thus, wherever in the jaw a molarlike tooth is found, it is a molar, both genetically and developmentally. By extension, teeth that look like incisors, canines, and premolars have the morphologies they do because of regulatory constraints and should be identified as the teeth they look like.

In addition to identifying teeth by their morphology, we should rid ourselves of the notion that the only teeth a mammal can have are incisor, canine, and molar-class teeth (the latter including molars and their successors, premolars). Clearly, if morphology is our guide to homology, then oddly shaped teeth that do not conform to these long-standing expectations (such as the so-called lower incisors of *Eosimias* [see below]) should be regarded as representing different tooth classes. Consequently, we should acknowledge that comparability in lower anterior tooth morphology between *Tarsius* and various tarsiiforms, and the extension of this comparability to the lateral toothcomb tooth of all non-*Daubentonia* prosimians, is of definite phylogenetic potential in revealing not only homology, but also synapomorphy.

Fossils, *Tarsius,* and Anthropoid Origins

Since a consideration of *Tarsius*'s phylogenetic relationships cannot be divorced from the question, "What unites Anthropoidea?" it is necessary to discuss briefly specimens that have been offered up as potential anthropoid ancestors, such as *Eosimias* (Beard et al., 1994; MacPhee et al., 1995; Beard et al., 1996; Gebo et al., 2000), *Siamopithecus* (Chaimanee et al., 1997; Ducrocq, 1998), *Wailekia* (Ducrocq et al., 1995), and *Bahinia,* which Jaeger et al. (1999) consider an eosimiid. Embedded in the presentations of these specimens as "basal" or ancestral anthropoids is, however, the assumption that they are primates.

Beginning with Simpson's (1940) classic studies on early fossil primates, these mammals have been identified by their possession of cheek teeth with relatively low and bulbous cusps, upper molars (especially M^{1-2}) with somewhat straightened mesial and distal sides, lower molar trigonids that do not tower markedly above the talonids, lower molar paraconids that more closely approximate the metaconid from M_{1-3}, and lower molar talonids that are at least as long mesiodistally and wide buccolingually as the trigonids (see Schwartz, 1986, for review); (extant as well as fossil prosimians and anthropoids have different derived representations of these character states).

Although the type specimens *Eosimias sinensis* and *E. centennicus* do not represent the same genus morphologically, neither species is dentally primate. Both have tall and dominant trigonids on all preserved lower molars (M_{1-2} for *E. sinensis,* and M_{1-3} for *E. centennicus*). The nonprimate nature of the lower molars is even more pronounced in *E. centennicus* in which, throughout the series M_{1-3}, the trigonid remains large with fully expressed cusps (including a well-developed paraconid that stands apart from the metaconid on all three molars) while the talonid becomes buccolingually markedly narrower than the trigonid. Isolated upper teeth referred to *E.* cf. *centennicus* (Tong, 1997; pers. obs.) are not blatantly primatelike. The premolars and molar bear very tall, pointed cusps, the buccal cusps of the molar are oriented distally away from the protocone, and the distal side of the molar is deeply waisted. Thus, in light of the suggestion that there is a *Tarsius* and omomyid clade that is related to an *Eosimias* and anthropoid clade (Beard et al., 1994, 1996; also Beard and MacPhee, 1994, and MacPhee et al., 1995), the upper and lower molars of *Eosimias* are certainly more primitive than in *Tarsius* or any omomyid, much less any anthropoid primate.

The configuration of the two anteriormost teeth of *E. centennicus* are of particular note. The first tooth is noticeably smaller than the second, but the two teeth form a size-shape gradient in that their relatively small crowns bear pointed tips that recurve posteriorly and somewhat concave and vertical lingual surfaces that are completely ringed by a margocristid (cf. Beard et al., 1996). With the essentially completely preserved mandibular symphysis of *E. centennicus* properly oriented anteroposteriorly (not obliquely as in the published illustration), the lower jaw assumes a V-shaped configuration, and the linear arrangement of the two anterior teeth, one in front of the other, is immediately appreciated. No known primate has lower anterior teeth that are even vaguely morphologically similar to, or in the same relative positions as those of *E. centennicus.* Thus, outgroup comparison indicates that, even if *Eosimias* were a primate, it would be more derived than any anthropoid in lower anterior tooth design and thus excluded from ancestry of this group.

Inasmuch as *Eosimias*'s upper and lower molars do not conform to the basic criteria of being primate, to what mammalian group might this taxon be related? Given the fact that paleontology in China has only scraped the surface of potential mammalian diversity, this taxon or taxa could represent endemic clades that left no living descendants. The curious lower anterior dentition aside, the general configurations of the lower molars of *Eosimias* (as well as of the only known lower molar of *Bahinia,* an M_1) are very similar to tupaiids and talpids, both of which are found in Asia.

Bahinia differs from fossil and living primates in its preserved upper dentition in having expanded buccal and lingual moieties (with a waisted midsection in between), with tall, crest-connected, buccolingually compressed paracones and metacones that tilt in toward the well-excavated trigon basins, very mesially situated protocones that are compressed and incorporated into the arced protocristae that course to the buccal cusps, and massively ledge like lingual cingula. In addition, the apparent upper canine is disproportionately massive at its base and would probably have been quite long and trenchant. Although the upper molars of *Bahinia* are not as fully dilambdomorphic as they are in some tupaiids and talpids, the skewing of the protocone and basic configuration of the buccal cusps are consistent with the essential elements of dilambdomorphy. Importantly, the upper molars of *Bahinia* (as is the upper molar referred to *Eosimias*) are not euthemorphic, which excludes them from being considered primate (cf. Hershkovitz, 1977). As for lower teeth, even though only M_1 is known and the hypoconid region is somewhat damaged, in contrast to primate teeth, the talonid is rather narrow relative to the trigonid, and the trigonid dominates the crown.

Whatever similarities *Eosimias* and *Bahinia* share with anthropoids, they are not synapomorphies. In addition, the supposedly anthropoidlike individual features cited for *Eosimias* are themselves ambiguous. For instance, although *Eosimias* has been described as having an "anteroposteriorly abbreviated, dorsoventrally deep symphysis" (cf. Beard et al., 1996: 84), its symphysis is angled forward and not fully vertical, and, by this criterion, those New World monkeys with more primitively configured symphyseal regions would be excluded from Anthropoidea while some prosimians would be more anthropoid than *Eosimias.* Having "large and projecting [lower] canines" (Beard et al., 1996) (if this is what these teeth really are in *Eosimias*) also describes Eocene prosimians, whose lower canines are often more projecting than most anthropoids'. *Eosimias*'s vertically implanted lower incisors (Beard et al., 1996) (if this is what they are) is also not indicative of a basal anthropoid. The lower anterior teeth of most anthropoids are procumbent to some degree while the those of other mammals (carnivores, for example) are much more orthally oriented. It is rare indeed to find an anthropoid with lower anterior teeth as vertically implanted as in *Eosimias.*

Eosimias's single-rooted first lower premolar may have been the smallest of the three teeth identified as premolars (Beard et al., 1994), but single rootedness does not universally describe the lower anterior premolar of New World monkeys, in whom this tooth is typically the largest of the three premolars (Hershkovitz, 1977). *Neosaimiri*'s last and penultimate lower premolars may be similar to *Eosimias*' in being "slightly exodaenodont and obliquely oriented in the tooth row" (Beard et al., 1996: 84), but in most anthropoids (New World monkeys included) the ultimate and sometimes also penultimate premolars are oriented with one root buccally and the other lingually. Clearly, singling out and representing *Neosaimiri* as a typical anthropoid is inappropriate.

It is also incorrect to claim that *Eosimias* is a basal anthropoid because it and *Neosaimiri* have large lower molar protoconids and mesially placed entoconids (cf. Beard et al., 1994). This description does not even apply to all lower molars attributed to *Eosimias.* Nevertheless, even if this description were correct, these features do not characterize the molars of anthropoids as a group.

They do, however, describe the molars of tupaiids and various prosimians (including *Macrotarsius montanus,* but not *"M." macrorhysis*), as well as the isolated molars attributed to *"Tarsius" eocaenus.* The development of a premetacristid, as seen in *Eosimias* (Beard et al., 1994), is commonplace among fossil and extant primates as well as various insectivores and scandentians.

With regard to the remaining features that Beard et al. (1994, 1996) offer as synapomorphies of *Eosimias* and anthropoids, the observation that the "M_3 trigonid . . . [is] . . . appreciably wider than the talonid" (Beard et al., 1996: 84) cannot be taken out of context. This configuration characterizes all lower molars of *Eosimias* and thus excludes this taxon from the primate clade (see above). As for "hypoconulid lobe on M_3 being reduced both mesiodistally and buccolingually" (ibid.), this is a restatement of the preceding feature. No anthropoid or other primate has such a truncated M_3 talonid, although various tupaiids do. Finally, *Eosimias* may be similar to anthropoids in having "a rounded, nonprojecting angular region providing expanded area for insertion of pterygoid muscles" (ibid.), but so are fossil and extant indriids, *Adapis* and related species, lorisids, *Hapalemur, Daubentonia,* the plesiadapiforms *Platychoerops* and *Chiromyoides,* and numerous perissodactyls and artiodactyls.

Given the dubious association of eosimiids with primates in general (much less with a specific primate subclade), it is appropriate to reconsider claims that a petrosal fragment (MacPhee et al., 1995) and isolated tarsal bones (Gebo et al., 2000) discovered in the same fissure fill as *Eosimias* belong to that taxon and, therefore, that these specimens reflect the primitive anthropoid configurations of the bullar and ankle regions. With regard to the petrosal, MacPhee et al. (1995) argued that it must have come from an eosimiid because it could not be anything else. It is much smaller than expected of the omomyid from that locality (the supposed *Macrotarsius*), and it is not very *Tarsius*-like. This petrosal is primatelike in having a "long, plate-like continuation of the otic capsule in the plane of the tympanic cavity" (ibid.: 508). It differs from fossil tarsiiforms (or lorisiforms) in having a relatively large stapedial artery (as is found, for example, in lemuriforms, including *Adapis* and kin), but the course of the promontory artery is most reminiscent of *Necrolemur* and *Rooneyia* (ibid.).

Although the authors state in their article's abstract that "the element does present arterial features consistent with its being haplorhine," in their text, the most favorable comparisons are with omomyids. It is only because it was assumed that this petrosal fragment came from an eosimiid, which, in turn, was assumed to be a basal anthropoid, that the otherwise ambiguous morphologies of this bony element were then interpreted as being primitively anthropoid. That is, because these general features are found in a presumed anthropoid ancestor, they must represent the configuration from which the apomorphically anthropoid condition evolved. Clearly, this is tautological.

A similar assumption underlies the interpretation of the talus and calcaneus assigned to *Eosimias* (Gebo et al., 2000). First, these postcranial elements were assumed to be eosimiid (and thus a basal anthropoid) because of their minuscule size, and then their morphologies were explained. Given that Gebo et al. (2000) offered only one feature of the talus as being potentially diagnostic of anthropoids—a reduced medial facet on its body for the tibial malleolus—it might be that the tiny talus is actually from an anthropoid primate, but one that would be more derived than *Saimiri,* at least, because, as illustrated, the facet in the eosimiid is relatively much smaller than in this New World monkey.

Since, however, Gebo et al. (2000) basically compared their specimen only to one New World monkey, *Saimiri,* and to a tarsally very derived fossil tarsiiform, *Hemiacodon,* the single shared talar feature is overshadowed by the greater number of similarities seen in the tali of their eosimiid and *Hemiacodon:* e.g., a moderate talar neck angle, moderately high talar body, shallow trochlea, small posterior trochlear shelf, and relatively narrow talar body (p. 277). Gebo et al. (2000) interpreted these features as apomorphies of their group adapiforms, but, if they are derived compared to other primates, the comparison also subsumes the tali of their eosimiid and *Hemiacodon.* Consequently, there is again cause to recognize a prosimian clade. It is unfortunate that Gebo et al. (2000) did not expand their relatively small comparative sample to include extant lemurs and lorises because this would have clarified the extent to which these apomorphies are shared more broadly among prosimians.

With regard to the eosimiid calcaneus, the limited published comparisons make the delineation of synapomorphy difficult. In relative length of the distal segment, the eosimiid calcaneus is relatively longer than in *Adapis,* shorter than omomyids, and more like *Saimiri*, while, in transverse width, it is narrower than in New World monkeys and wider than in omomyids. The calcaneocuboid joint of eosimiids is flat, as in *Notharctus* and omomyids, but it bears a nonarticular region in its medioplantar section, as in anthropoids. Although Gebo et al. (2000) state that the articular surface in their eosimiid calcaneus is similar to that of anthropoids (being represented only by *Saimiri*), their illustration suggests the better comparison is between *Saimiri* and *Hemiacodon*.

Review of the features that Gebo et al. (2000) list as synapomorphic of the haplorhine clade they reconstructed using PAUP reveals contradictions with their earlier published interpretation of character polarity. There, Beard (1988) argued that all nonstrepsirhine primates retain the primitive eutherian talar configuration of having both a vertical talofibular facet from which a small plantar process protrudes and a groove for the m. flexor hallucis longus tendon that lies plantad and central to the tibiotalar joint. In Gebo et al. (2000), these primitive retentions are used to support the grouping Haplorhini. Regardless of the interpretation of character polarity, only the talus attributed to *Hemiacodon* can be described by this list of features. The tali of *Tarsius* and those assigned to the anaptomorphids *Tetonius* and *Teilhardina* cannot (Schwartz, 1992).

In addition, the platyrrhine *Aotus* displays the presumed strepsirhine condition of a slightly laterally oriented and broad m. flexor hallucis tendon groove, but various prosimians (e.g., *Eulemur, Propithecus*) do not (cf. Beard, 1988; Schwartz, 1992). With regard to other aspects of the PAUP analysis (in which scandentian, dermopteran, and plesiadapiform tarsal morphology is taken collectively as reflecting the primitive outgroup state), adapiforms and haplorhines are presented as sister groups. If this relationship is indeed supported by synapomorphy, then the eosimiid and the omomyid (*Hemiacodon*) are subsumed in it.

What, then, of *Eosimias* and a potential eosimiid clade? Although the teeth attributed to *Eosimias* and *Bahinia* are not apomorphically primate (and thus cannot be basal anthropoids), the eosimiid petrosal fragment and postcranials appear to be. Could these elements be from the same, tiny taxon? Since MacPhee et al. (1995) and Gebo et al. (2000) point specifically to various morphological similarities between these specimens and omomyids (i.e. tarsiiforms as used here), these specimens may represent a taxon or taxa whose relationships lie close to or within this larger group. In this regard, although the few known teeth attributed to *Tarsius eocaenus* may not represent a species of the extant taxon, they are of the right size (cf. MacPhee et al., 1995; Gebo et al., 2000) to be associated with the petrosal and postcranials. More complete specimens are needed to assess these phylogenetic possibilities. With regard to the family Eosimiidae (Beard et al., 1994), since *"Eosimias" centennicus* and *Bahinia* are generally similar in dental morphology to the type specimen of the genus and species *E. sinensis,* these taxa provide a small window onto a long-lost group of extinct, nonprimate Asian mammals.

Wailekia and *Siamopithecus* (both middle-late Eocene, Thailand) are clearly dentally primate. Although Ducrocq et al. (1995) suggested that *Wailekia* (known from a partial lower jaw with the last two molars and an isolated lower molar) was an early anthropoid, there are clear dental similarities between it and the Asian sivaladapid-like *Hoanghonius* (Ducrocq, 1998; C. Beard, pers. com.; pers. obs.), including the development on the lower molars of a stout, anteriorly arcing paracristid and a distolingual entoconid-hypoconulid notch—both compelling synapomorphies. In terms of preserved mandibular morphology (e.g., relatively shallow and long corpus, thin and high-rising coronoid process, relatively lower condyle, and forwardly inclined symphysis), *Wailekia* retains the primitive mammalian configuration.

Siamopithecus is regarded as a basal anthropoid with possible links to another supposed early anthropoid, the Burmese *Pondaungia* (Chaimanee et al., 1997; Ducrocq, 1998). Presumed anthropoid features of *Siamopithecus* include "large body size; upper cheek teeth that are not medially waisted and lack conules, but have an external expansion of the paracone; very bunodont lower molars that lack a paraconid with a mesially directed cristid obliqua; and a very deep mandible" (Ducrocq, 1998: 99). Nevertheless, "some of these features are found in some prosimians, but this suite of features is more likely that of an anthropoid" (ibid.). With an estimated body mass of 6500–7000 g, *Siamopithecus* was large, but, then, so were some species of *Pelycodus, Notharctus,* and *Leptadapis* and even more so (often tenfold more) all subfossil Malagasy prosimians. Even the extant *Indri* falls into this size range. Since morphological comparisons between *Siamopithecus* and prosimians were limited to Eocene adapiforms, rather than to a greater taxonomic representation of primates, the anthropoid features of the former deserve comment.

For instance, "deep mandible" is not in and of itself diagnostic, as many fossil prosimians (including *Adapis* and *Leptadapis*) and extant prosimians also have deep mandibles. The lack of a paraconid and the possession of a mesially directed cristid obliqua may typify anthropoids, but many extant and fossil prosimians can be similarly described (Schwartz, 1984, 1986; Schwartz and Tattersall, 1985). Since only the last two molars of *Siamopithecus* are intact, and the M_1 lacks all but the distal portion of the talonid, one cannot know if the cristid obliqua on the latter tooth did not course lingually and even contact the metaconid, as is the case in *Pelycodus* and most anaptomorphids, which also have mesially directed cristids obliquae on M_{2-3}. In their general bunodonty and distinct, paraconid-less paracristids that enclose mesiodistally short but relatively deep trigonid basins, the preserved M_{2-3} of *Siamopithecus* are comparable to these teeth in *Necrolemur* and *Microchoerus*. A buccally expanded upper molar paracone is not a characteristic of extant anthropoids, but it is a feature of the upper molars of the Eocene *Moeripithecus* and *Algeripithecus*, which are presumed early anthropoids. Anaptomorphids had expanded upper molar buccal surfaces, and many of these taxa also had other characteristics noted in the upper dentition of *Siamopithecus*, such as upper molars with long lingual slopes (particularly on M^2, in which the protocone is quite centrally placed) and constricted trigon basins (also on the last upper premolar), distinct protocone folds that became confluent with the postcingulum, buccolingually exaggerated M^2s, reduced M^3s, and enlarged last premolars. In short, the preserved dental features of *Siamopithecus* display more potential synapomorphy with members of the anaptomorphid and microchoerine clade hypothesized here than wit anthropoids. Among *Siamopithecus*'s autapomorphies are large body mass and a deep mandible (which might be a consequence of large size). Since it appears that some kind or kinds of omomyids or omomyidlike primates were present in Asia during the middle-late Eocene (such as "*Macrotarsius*" *macrorhysis* and "*Tarsius*" *eocaenus,* as well as *Asiomomys* [Beard and Banyue, 1991]), it is not surprising that an anaptomorphid or two would also be sympatrically present, as is clearly the case among the North American Eocene faunas.

Conclusions

Without a doubt, *Tarsius* is an extraordinarily unique mammal. Yet, while its uniquenesses make it an intriguing primate, scientists have obscured its potential phylogenetic relationships, which are dictated by a presumed scala naturae envisioning transformation series from lower to higher primates that, somehow, include a tarsierlike phase. Taken on their own, however, *Tarsius*'s morphologies data do not easily lend themselves to any version of this scenario.

Tarsius shares with extant prosimians a grooming claw on the second pedal digit and a toothcomb (autapomorphically reduced in the former), as well as ontogenetic internalization of the ectotympanic. Among extant prosimians, *Tarsius* resembles lorisiforms in having (1) a prehypocone crista at least on M^1, (2) on M_1, a tall protoconid and metaconid that are melded at their bases, (3) an angular and buccally distended hypoconid on the lower molars, (4) some rostral elongation, (5) a downward distension of the premaxillary alveolar region, and (6) marked orbital enlargement with medial constriction (cf. Schwartz, 1984; Schwartz and Tattersall, 1985). *Tarsius* also shares with galagids and cheirogaleids some degree of tarsal elongation and at least tibiofibular syndesmosis if not total fusion.

If lorisids and galagids are sister taxa (e.g., Schwartz, 1986), then a consequence of the latter presumed synapomorphy is secondary tarsal shortening in lorisids. If *Tarsius* is related specifically to a lorisid and galagid clade to the exclusion of cheirogalids, then its lack of an ascending pharyngeal artery (cf. Cartmill, 1975) demands explanation. *Tarsius* and galagids alone share a number of femoral uniquenesses (Dagosto and Schmid, 1996), but this is contradicted by *Tarsius*'s lack of the lorisiforms' long, narrow trochlear talar facet. *Tarsius* shares with all lorisiforms reduction/loss of the stapedial artery in the adult and with lorisids and galagids development of a small tympanic cavity and lack of an annular bridge. However, these features also occur in anthropoids (MacPhee and Cartmill, 1986).

The most clear-cut similarities between *Tarsius* and anthropoids include (1) primary supply of the middle meningeal artery via the maxillary artery, (2) lack of a tapetum, (3) lack of a moist, hairless rhinarium, and (4) the inability to synthesize vitamin C. Accepting features of the auditory region, the eye, placentation, the oro-nasal region, and the skull in general as synapomorphic of *Tarsius* and anthropoids requires a posteriori explanations.

As the preceding review has hopefully illuminated, there is still much to be sorted out about the phylogenetic relationships of *Tarsius* to both extinct and extant taxa.

Acknowledgments

I thank Sharon Gursky, Elwyn Simons, and Pat Wright for inviting me to contribute to their timely effort; Colin Groves and Susan Ford for sharing unpublished data; and Chris Beard for discussing *Shoshonius* and the Chinese specimens with me and giving me full access to originals and casts. I also thank the curators and their assistants at the American Museum of Natural History (Departments of Anthropology and Mammals), New York City, National Museum of Natural History (Smithsonian Institution, Department of Mammals), Washington, D. C., and the Rijksmuseum van Natuurlijke Historie, Leiden (Department of Mammals) for allowing me to study their collections.

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