The Evolution of the Tarsiid Niche

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Long before indisputable fossil evidence of tarsiers was discovered, tarsiers were considered "living fossils." This assignment was based as much on their primitive gestalt as on the morphological affinities of tarsiers to members of various Paleogene primate and plesiadapiform taxa, and on predictions based on cladistic reconstructions of the tarsier's phylogenetic position. Thus, through many years of learned discourse on tarsiers, "the 'living fossil' [had] no fossil record!" (Schwartz 1984, 47). In recent years, this situation has improved, although the fossil record of tarsiers is still more gap than record. The fragmentary remains of fossil tarsiids recovered from deposits of middle Eocene age onward from Egypt, China, and Thailand indicate that the tarsier's "living fossil" moniker is well deserved. The morphology of these fragments is remarkably modern, or perhaps better said, the body plan of modern tarsiers is remarkably ancient and conservative. This leads to the inevitable question: What made tarsiers successful in the first place, and why have they persisted, little changed, through most of the Tertiary through to the present day? These questions are at the heart of this paper.

Reconstructing the niche of an extinct species or the successive niches of the members of an ancient lineage is difficult because missing or fragmentary data are many and unassailable facts are few. The exact nature of the forest environments inhabited by the fossil tarsiids of the Eocene and Miocene, for instance, is not known, yet a great deal is known about the character of Paleogene and early Neogene forest environments in general (e.g., Upchurch and Wolfe, 1987) and the forests in which tarsiers currently dwell (e.g., Davis, 1962; Crompton and Andau, 1986; Musser and Dagosto, 1987; Whitten et al., 1987; MacKinnon et al., 1996). Similarly, relatively little is known of anatomy, ecomorphology, and life-history parameters of ancient tarsiids, but much is known in all of these areas in connection with the living species of tarsiers (e.g., Niemitz, 1977; Crompton and Andau, 1986; Jablonski and Crompton, 1994; Roberts, 1994; Gursky, 1997). The similarities in habitat preference between extinct and extant tarsiids, and the strong morphological (especially dental) resemblances between these forms, thus mean that the tarsiers of today likely appear and behave similarly to those
of the distant past. In this chapter, the ecological role of tarsiers is examined, and the reasons for their success and persistence through 45 million dynamic years of mammalian evolution are explored.

Tarsiids Past and Present

The fossil record of the Tarsiidae comprises mostly isolated teeth and lower jaws. These elements have proven useful for determining the phyletic relationships and the putative diets of the animals they represent, but they leave us begging for more. Tarsiers today are distinguished by their enormous eyes and greatly elongated hindlimbs—the seeming anatomical underpinnings of their success. Thus, we must recognize that the absence of crania preserving any portions of the orbits and the near absence of postcranial remains in the tarsiid fossil record are impediments to understanding the evolution of the tarsiid niche.

The earliest recognized Tarsiidae species have been recognized from Middle Eocene deposits of China. *Tarsius eocaenus* has been recovered from fissure-filling deposits at Shanghuang in Jiangsu Province, China (Beard and Qi, 1994; Qi, Beard, et al., 1996; Beard, 1998). The species is represented by isolated teeth and was almost certainly sympatric with the basal anthropoid, *Eosimias sinensis*, the omomyid, *Macrotarsius macrocephalus*, and at least two members of the adapiform clade Adapina recovered from the same locality (Beard and Qi, 1994; Dagosto and Gebo, 1996; Gebo and Dagosto, 1996; Qi et al., 1996; Beard, 1998). The Shanghuang fossil mammal assemblage is rich in micromammals, including a primitive lagomorph, two species of microchiropterans, several species of primitive cricetid rodents, and numerous insectivores (Qi, Beard, et al., 1996). Larger mammals from Shanghuang include other species known to favor closed, tropical or paratropical forest environments such as miacid carnivores, representatives of several families of browsing perissodactyls, and a small, primitive anthracothere (Qi, Zong, et al., 1991; Beard and Qi, 1994; Qi et al., 1996). Biostratigraphic correlation indicates that the mammalian fauna of the Shanghuang fissures is likely to be about 45 myr old (Qi, Beard, et al., 1996).

*Xanthorhysis tabrani* is another Paleogene ancient tarsiid that has been recovered from China. This species was recovered from a small drainage in Yuanqu County of southern Shanxi Province and is estimated to be of Late Middle Eocene age. Based on the morphology of the dentary and its contained teeth, *X. tabrani* has been described and interpreted by Beard as being a sister group of all living and fossil tarsiers, including *Tarsius eocaenus* (Beard, 1998).

*Xanthorhysis tabrani* and *Tarsius eocaenus* are the oldest known tarsiers (*sensu lato*), but how close they are to the phyletic and biogeographic origin
of the Tarsiidae is still a matter of speculation. Beard has presented a convincing case that these fossil species are ancient, but are probably not the oldest tarsiers (Beard, 1998), and that the origin of the Tarsiidae can be traced to the early Paleogene of the Asian mainland. The Eocene tarsiids of China are smaller than any of the living species of *Tarsius*, but the close similarity in molar morphology between *X. tabrurin*, *T. eocaenus*, and living tarsiers is so clear as to leave no doubt that the fossil species truly are ancient tarsiers, and that the molar morphology of modern tarsiers is primitive (Martin, 1994). The important dietary implications of this molar morphology are discussed below.

The next oldest fossil tarsiid is also the only one, living or fossil, of African origin. *Afrotarsius chatrathi* was first described on the basis of a fragmentary mandible, with molar teeth very similar to those of living *Tarsius*, derived from early Oligocene sediments of Quarry M of the Jebel Qatrani Formation of the Fayum Province of Egypt (Simons and Bown, 1985). Since the recovery of the type mandible, a nearly complete tibiofibula was found in the same quarry and was assigned to the same species on the basis of its near identity to the comparable element in living tarsiers (Rasmussen et al., 1998). As is discussed below, the morphology of the fused tibiofibula in *Afrotarsius* is a strong indication that it exhibited a mode of leaping locomotion very similar to that of modern *Tarsius* (Rasmussen et al., 1998) and implies a similarity of ecological role between fossil and living forms that previously was only suspected.

The early Miocene form, *Tarsius thailandicus*, is represented by only a single isolated lower molar found at the site of Li in northwestern Thailand, as part of a forest-associated fauna dominated by rodents and insectivores (Ginsburg and Mein, 1987).

The five recognized species of living tarsiers inhabit rain-forest environments in island southeast Asia. (See fig. 8 in Musser and Dagosto [1987] for a summary distribution map.) The three most widely distributed species, *Tarsius bancanus, T. syrichta*, and *T. spectrum*, live in a zoogeographic regions distinct and different from one another. *T. bancanus* is native to islands on the Sunda Shelf, namely mainland Borneo, Pulau Serasan in the South Natuna islands, Pulau Belitung, Pulau Bangka, and southern Sumatra (Musser and Dagosto, 1987). *T. syrichta* occurs in several islands of the southern Philippines once united as a land mass called Greater Mindanao during the Late Pleistocene (Musser and Dagosto, 1987). *T. spectrum* is known only from the Sulawesi region, including mainland Sulawesi, the Sangihe Islands, Pulau Peleng, and Pulau Selayar (Musser and Dagosto, 1987). The two remaining tarsier species, *T. pumilis* and *T. diadema*, enjoy highly geographically restricted distributions within Sulawesi. The former inhabits the montane mossy forest of central Sulawesi while the latter inhabits the lowland forest
of the same area (Musser and Dagosto, 1987; Niemitz, 1991). The degree to
which these species are actually sympatric with one another or with \textit{T. spec-
trum} is unclear (Musser and Dagosto, 1987; Niemitz, 1991).

Tarsiid Environments Past and Present

The establishment of \textit{T. eocaenus} as the oldest tarsiid establishes a minimum
age for the lineage of about 45 myr (Beard and Qi, 1994; Qi, Beard, et al.,
1996). The period spanning the Late Cretaceous through the Eocene,
which no doubt witnessed the origin of the group, was a time of climatic qui-
escence and dramatically increasing mammalian diversity. It was one of the
warmest intervals in the history of the Earth, and climatic patterns followed
closely the zonal component of atmospheric circulation (Parrish, 1987). It
was in this environment of stability that angiosperms underwent their greatest
diversification (Parrish, 1987). A conspicuous restructuring of vegetation
al communities appears to have occurred after the mass kill of vegetation
at the Cretaceous-Tertiary boundary (Wolfe and Upchurch, 1986; Up-
church and Wolfe, 1987). The vegetational recovery that occurred at this
time resembled a modern secondary succession in many respects, although
over a longer time course (Wolfe and Upchurch, 1986; Upchurch and
Wolfe, 1987). At low and middle latitudes, precipitation increased greatly,
initiating the expansion of humid multistratal rain forests with closed can-
opies (Wolfe, 1985; Upchurch and Wolfe, 1987; Wing and Tiffney, 1987).
It is interesting to note, in the broader context of mammalian evolution, that
the earliest extensive closed-canopy multistoryed rain forests appeared only
after the disappearance of the dinosaurs at the end of the Cretaceous (Mor-
ley, 2000). Their proliferation may, in fact, be directly linked to the removal
of large generalist herbivores and their replacement by seed-dispersing
small mammals (Morley, 2000).

By the early Eocene, angiosperms had come to dominate late success-
ional communities, for the first time forming a closed forest vegetation
of modern aspect (Wing and Tiffney, 1987). Such forests, characterized by
tall trees with buttressed trunks, lianas, epiphytes, and a distinct understory,
would have provided many new or greatly expanded niches for plant and
animal adaptation (Upchurch and Wolfe, 1987). Of particular relevance to
the discussion in this chapter is the fact that the early Tertiary saw great
increases in the abundance and diversity of lianas and understory plants
(Upchurch and Wolfe, 1987). The acme of global temperatures, tropical-
ity, and angiosperm-dominated closed forests was achieved at this time
(Behrensmeyer and Damuth, 1992; Janis, 1993), with subtropical vegetation
probably having extended to 60 degrees north latitude and full tropical
multistratal rain forests occurring as far north as 30 degrees north latitude (Wolf, 1985).

The closed angiosperm forests of the early Tertiary were dominated by large trees with large diasporas, and were populated mostly by small vertebrate herbivores such as multituberculates, primates, and rodents who concentrated on fruit and seeds (Rose, 1981; Wing and Tiffney, 1987; Collinson and Hooker, 1991; Janis, 1993). These "little herbivore/big angiosperm" systems (Wing and Tiffney, 1987) were also the homes of many insect pollinators and phytophagous insects (Crepet and Friis, 1987) and the vertebrates that preyed on them. It is significant that most of the nonflying vertebrates that evolved to occupy rain-forest environments were consumers of the fruits, seeds, and leaves that were its primary products (Collinson and Hooker, 1991; Emmons, 1995). Only a small fraction of these animals concentrated on invertebrates, and of these the only groups to achieve significant diversity were bats and birds (Emmons, 1995). The mammals inhabiting Early and Middle Eocene forests were broadly analogous to modern ones, but their community structures emphasized terrestrial frugivores and arboreal insectivores to a much greater extent than do the tropical and subtropical forests of the present day.

The emergence of the understory as a significant component of the humid multistratal rain forests of the Eocene provided important ecological opportunities for several evolving lineages of Paleogene mammals (Morley, 2000). At the forest floor, rain forests have low relative illuminance of visible light, often less than 1% (Grubb and Whitmore, 1967). The high moisture and low light conditions that characterized the understory selected for plants with large leaf size and the ability to photosynthesize under suboptimal light conditions (Upchurch and Wolfe, 1987). The leaves of understory plants are also characterized by softer textures and lower toxicities (Lowman, 1995), features that would have facilitated their exploitation by arthropods.

The arthropod fauna of the understory, like those elsewhere in the rainforest canopy, shows greater numbers of small-bodied rather than large-bodied species because there is more usable space for smaller animals living on vegetation than for larger animals (Morse et al., 1985). The rain-forest understory with its larger average leaf size, however, supports a greater proportion of larger-bodied arthropods than do other forest environments (Morse et al., 1985). There is also some evidence that rain-forest arthropods are less host-plant specific than are the arthropods of other forest ecosystems, possibly because of the greater heterogeneity of plant species in rain forests and the reduced number of seasonal changes in tree condition that is found there (Stork, 1987).

Since the Middle Eocene, the distribution and composition of humid,
multistratal rain forests have undergone significant changes as the result of a major cooling at the end of the Eocene (the terminal Eocene event) and the origin and spread of low-biomass vegetation types (e.g., savanna, steppe, and tundra) during the Neogene (Wolfe, 1985; Collinson and Hooker, 1991; Leopold et al., 1992). Of all the areas of the Old World once covered by tropical or paratropical rain forest in the Eocene, it is only small, low-latitude areas of southeast Asia that have retained such forests through the Neogene (Collinson and Hooker, 1991). Although the rain forests of southeast Asia have undergone some floristic changes since the late Eocene, the physical characteristics of the forest today appear to be essentially the same as they were 55 million years ago, as judged by similarities in foliar physiognomy and wood morphology (Wolfe, 1985; Upchurch and Wolfe, 1987; Collinson and Hooker, 1991; Morley, 2000).

The nature of the arthropod communities associated with the tropical and paratropical rain forests of the Eocene is not well known. The rise of the insect pollinators associated with early angiosperms is reasonably well understood, largely through inferences based on pollen and leaf remains (Crepet and Friis, 1987), but little is known of the details of what was no doubt an explosive diversification of phytophagous arthropods in the humid multistratal forests of the early Tertiary. The great antiquity of the Coleoptera (beetles) and the orthopteroids (including crickets and cockroaches) (Carpenter, 1976) and their prominence in the communities of leaf-eating arthropods in modern Asian rain forests suggest that their evolution and diversification were closely linked to that of the plants they exploited. In modern rain forests, many larger-bodied beetles and orthopteroid insects are nocturnal, presumably to avoid predation by birds and reptiles, and it is likely that the activity patterns of their early Tertiary relatives were the same. The lower level of host-plant specificity observed in tropical forest arthropods suggests, further, that the arthropods that preyed on the plants of the early Tertiary rain-forest plants may not have changed appreciably over time. This is also supported by the recognized functional comparability of rain-forest vegetation through time and space, in terms of leaf structure and toxicity (Morley, 2000).

This evidence leads us to conclude that the humid forests of eastern Asia occupied by Tarsius tarsier and its putative ancestors were closely comparable to the tropical rain forests of southeast Asia today. This comparability extends from canopy structure through foliar physiognomy and physiology to the composition of the arthropod guilds that inhabited the forests.

The five recognized species of living tarsiers inhabit parts of southeast Asia that have been covered with tropical rainforests continuously since the Middle Eocene (Morley, 2000). These forests have a dynamic history of their own, having undergone considerable floristic changes as a result of cli-
matic oscillations and migrations resulting in fluctuating land connections. Continuous land connections between southeast Asia and mid-latitude Asia since the earliest Tertiary allowed elements of Paleogene Northern Hemisphere rain forests to find refuge in the lower montane forests of southeast Asia following the mid-Tertiary global climatic deterioration (Morley, 2000). This event has no parallel in other regions (Morley, 2000) and accounts for the fact the rain forests of southeast Asia, despite fluctuations in composition and diversity, have a primitive character and more closely resemble the rain forests of the Paleogene than do rain forests elsewhere.

When the fossil evidence of Eocene tarsiers is considered together with this botanical information, the inescapable conclusion is that tarsiers as a group originated in the tropical forests of the early Paleogene in the Asian mainland, as argued by Beard (Beard, 1998), and that their range shift into Sundaland probably coincided with the southward migration of some elements of Asian mainland forests at the end of the Eocene. Tarsiers thus can be said to have inhabited more or less the same forests for the last 45 million years.

The Bornean tarsier, Tarsius bancanus, and its Philippine congener, T. syrichta, are restricted in their distributions to lowland evergreen rain forests (both primary and secondary). The distribution of the spectral tarsier of Sulawesi, T. spectrum, spans a greater altitudinal range from lowland evergreen rain forest near sea level through lower montane rain forest at 1500 m (Musser and Dagosto, 1987). T. diana occurs in primary rain forest within the altitudinal range of T. spectrum. The pygmy tarsier, T. pumilis, of central Sulawesi, although still poorly known, appears to occupy the mossy upper montane rain forest at altitudes of approximately 1700 to 2200 m.

The subcanopies of lowland rain forests that are the homes to most tarsiers support an amazing density and diversity of arthropods, especially termites (Isoptera) and beetles (Coleoptera), that form the core of the decomposer community (Whitten et al., 1987). These animals are, in turn, the prey of frogs, toads, and skinks, which comprise the most numerous and diverse elements of the subcanopy vertebrate fauna (Whitten et al., 1987). Larger leaf-eating arthropods such as cockroaches (Blattopteroidea) and grasshoppers (Orthopteroidea) occur at lower densities in subcanopy environments and represent some of the most ancient elements of the rain-forest invertebrate fauna (Rohdendorf, 1991). Much has been said about Paleogene mammalian evolution being dominated by “little herbivore/big angiosperm” systems (Wing and Tiffney, 1987), but this was not where the tarsiids succeeded. From the Paleogene onward, tarsiers have occupied a stable niche little affected by shifts in the composition or diversity of rainforest plant communities, in which their primary focus has been the exploitation of relatively large, nutrient-dense arthropods and invertebrates.
The Tarsiid Niche

Modern tarsiers inhabit what has been termed the sapling trunk and ground zone of Asian rain forests, consisting of the lower understory and adjacent forest floor (Davis, 1962; Crompton and Andau, 1986; Crompton, 1989). Tarsiers spend most of their time foraging, specifically in the active scanning for food from perches near ground level (Crompton and Andau, 1986; Crompton, 1989). Clinging to vertical substrates is the dominant postural mode for living *Tarsius*, while leaping between such substrates, or between vertical supports and the ground, is the primary mode of locomotion (Crompton and Andau, 1986; Crompton, 1989). Tarsiers do not require undisturbed, primary rain-forest habitats, and in fact appear to favor secondary forests, at least in Borneo (Davis, 1962; Crompton and Andau, 1986; Crompton, 1989), perhaps because of greater densities of favored prey items found there. Although primary and secondary forests differ in floristics, their physical structures are similar. For tarsiers, the essential requirement of a rain forest is that it contain an understory with large arthropod and small invertebrate prey.

The nonflying mammals that evolved in early modern rain-forest environments were faced with many locomotor challenges, including how to move up and down large vertical tree trunks, how to balance on thin, flexible branches and lianas, and how to cross gaps (Emmons, 1995). Leaping has been a common solution evolved by several lineages of small, forest-dwelling mammals to the problem of crossing gaps and moving between widely dispersed resources (Emmons, 1995).

The prodigious leaping abilities of modern tarsiers can be attributed to the great elongation and increase in mass of its hindlimb elements (Covert, 1995; Rasmussen et al., 1998; Niemitz, 1984; Crompton and Andau, 1986; Anemone and Nachman, chapter 4). The calcaneus and navicular bones of the ankle are greatly elongated, and the fibula is reduced and fused to the tibia. Until recently, the postcranial morphology of extinct tarsiers was a matter of speculation. Thanks, however, to the recent recovery of a diagnostic tibiofibula from the early Oligocene *Afrotarsius chatrathi* (Rasmussen et al., 1998), we now have some direct and tantalizing evidence about the nature of posture and locomotion in ancient tarsiids. The fused tibiofibula of *A. chatrathi* closely resembles that of modern tarsiers in size and morphology and provides strong evidence that the species was engaged in a style of leaping very similar to that of modern tarsiers. The shaft of the fossil is gracile, and its proximal end is compressed mediolaterally as an adaptation to resist bending moments in the sagittal plane during leaping (Rasmussen et al., 1998). The anatomy of this important element thus demonstrates not only that *A. chatrathi* was a "classic tarsier" in its locomotor adaptation, but
also suggests that leaping locomotion was part of the original tarsier adaptation that defined the tarsiid niche.

The strong similarities in molar structure between ancient and modern tarsiers denote strong similarities in molar function and, therefore, diet, between extant and extinct tarsiids. Modern tarsiers have been observed to eat a variety of arthropods and occasionally vertebrates, but large-bodied coleopterans and orthopteroids are the most common components of their diets (Davis, 1962; Crompton, 1989). These items are seized with the hands and then ingested whole in a process made possible by an extraordinary gape (Jablonski and Crompton, 1994). The masticatory apparatus of modern tarsiers is capable of extremely wide jaw opening and powerful jaw closure. The temporomandibular joint permits extensive anterior translation of the mandible, powered by strong mandibular depressor muscles (the M. digastricus), when the mouth needs to be opened (Jablonski and Crompton, 1994). Large, fleshy, and long-fibered jaw adductors (M. temporalis and M. massetericus) permit extremely wide jaw opening and the ability to initiate forceful jaw closure to initiate ingestion and chewing (Jablonski and Crompton, 1994). The molars of modern tarsiers make possible the rapid, forceful cracking of brittle insect exoskeletons as well as the skeletons of small vertebrates (Crompton, 1989; Jablonski and Crompton, 1994). This process quickly liberates the protein-, fat- and readily digestible carbohydrate-rich tissues of insect and small vertebrate bodies for digestion in the tarsier's simple gut (Crompton, 1989; Jablonski and Crompton, 1994). Although the smaller size of Eocene tarsiids compared to modern tarsiers suggests that they focused on arthropod prey items of smaller average size, the inference from their molar morphology was that their diet was comparable in structure and content to that of modern tarsiers. The molars of *Afrotarsius chatrathi* and *Tarsius thailandicus* are comparable in size and cusp morphology to modern tarsiers (Simons and Bown, 1985; Ginsburg and Mein, 1987), supporting the hypothesis of comparability of diet and dental function in all known tarsiids.

If ancient tarsiids concentrated on the same kinds of arthropod prey that modern tarsiers do, some cautious inferences about foraging behavior in the fossil species are possible. The large-bodied coleopterans and orthopteroids favored by modern tarsiers are relatively rare elements of the arthropod faunas of Asian rain forests and are widely scattered (Davis, 1962; Crompton and Andau, 1986; Crompton, 1989). Also, many are only active and visible at night. Concentration on such prey requires, among other things, the ability to travel quickly at night within the forest so as to locate and seize prey. This is one of many reasons why the niche of the tarsier has been likened to that of the owl (Niemitz, 1983). Ancient tarsiids, exploiting large, nocturnal arthropods and small vertebrates as prey items, almost
certainly employed comparable, if not identical, foraging strategies as modern tarsiers to obtain those items. The preserved anatomy of Paleogene and early Neogene tarsiers provides few details here, and our reconstruction of ancient tarsiid foraging strategies and the nature of the tarsiid niche relies both on careful speculation and interpretation of stable form-function relationships through time.

The prey items favored by tarsiids today (and probably in the past) are more active at night than during the day, adding credence to the proposition that tarsiids throughout most or all of their history have been nocturnal. A nocturnal habitus makes possible the exploitation of uniquely nocturnal food resources and avoidance of diurnal predators, but is limiting in many other respects (Wright, 1989; Wright, 1994). Major adaptations in the realms of vision, energy expenditure, communication, ranging behavior, and social structure distinguish nocturnal primates (Charles-Dominique, 1975; Wright, 1989). For highly visually oriented mammals like primates, adaptation to reduced light levels has been the most important aspect of their success in nocturnal niches. The tarsier, like all nocturnal primates, has evolved a highly enlarged eyeball and a large retina capable of capturing and focusing available light (Castenholz, 1984). Importantly, modern tarsiers lack a tapetum lucidum, the highly reflective layer behind the retina that assists vision at reduced light levels in many nocturnal mammals but reduces visual acuity (Wright, 1989). Tarsiers instead have a well-developed fovea in the center of an all-rod retina, where visual acuity is concentrated and where the visual image is intensified because of the dense arrangement of visual receptor cells (Castenholz, 1984). This provides the tarsier with the most acute scotopic vision of all primates (Castenholz, 1984).

Among the most profound adaptations to nocturnality that have evolved in tarsiers and other nocturnal primates are those relating to metabolism, energy expenditure, and reproduction. Small animals facing cool nighttime temperatures could, potentially, exhaust their energy reserves if they attempted to maintain high metabolic rates around the clock and throughout the year. It is, therefore, not surprising that prosimians and tarsiers have low basal metabolic rates and low body temperatures (McNab and Wright, 1987). Tarsiers do not exhibit torpor, however, and in this way are distinct from several nocturnal prosimians who enter a lengthy period of physiological quiescence as an adaptation to seasonal food shortages (Wright and Martin, 1995). In tarsiers, a host of reproductive parameters appear to be related to their slower metabolism and reduced body temperatures (McNab and Wright, 1987). Tarsiers have single offspring and long gestation periods (Izard et al., 1985), and their rates of fetal and postnatal growth are among the slowest recorded for any mammal (Roberts, 1994). Tarsier infants exhibit the largest neonatal sizes of all nonanthropoid primates, and a large
proportion of their neonatal mass is invested in brain mass, eyes and cranium (Roberts, 1994). Because of the precocious development of the brain, maturation of foraging and locomotor behaviors in tarsiers is extremely rapid (Roberts, 1994). This "slow" life-history pattern is characteristic of anthropoid primates that have evolved in the stable ecosystems of equable forests (Jablonski et al., 2000).

Tarsiers teeter on an energetic knife-edge. They must not only leap to eat and cat to leap (Jablonski and Crompton, 1994), they must stay warm and reproduce. Growing evidence from studies of maternal time budgets in tarsiers suggests that the burden of reproduction in female tarsiers is enormous. Observations by Gursky (1997) indicate that pregnant female tarsiers exhibit lower mobility, impaired foraging abilities, and maintain smaller home ranges than do nonpregnant females. Postpartum females, further, appear to be unable to sustain the energetic costs of lactation and continual infant transport (Gursky, 1997).

The niche or ecological role of tarsiids through time has been that of the small-bodied nocturnal insectivore and carnivore of the tropical rain-forest understory. Clearly, the survival of tarsiers in the short and very long term is related to their focus on arthropod and small vertebrate prey that are less subject to dramatic seasonal fluctuations than are plant resources. Once filled, the tarsid niche was not subject to high levels of competition because flying (by bats or birds) is not easily accomplished in the dense understory at night. Poikilothermic vertebrates would also have posed little competitive threat to tarsiers because of their inability to chase large, highly mobile arthropods at night.

Conclusions

Dwight Davis (1962, 55) wrote that tarsiers "are astonishingly deliberate and stupid-appearing in behavior, so much so that it seems a miracle that they can survive." But survive they have. Many facets contribute to the original success and persistence of tarsiids. Certainly their ability to detect, hunt, and quickly ingest high-quality food items has been one of the most important keys to their success and survival. Leaping is an energy-intensive mode of locomotion, but it appears that the costs of leaping in tarsiids have never exceeded the benefits because of the high-quality nature of the food rewards that occasion the leaps. Are tarsiids in the jaws of a perilous evolutionary trap, or are they simply occupying a stable, if unusual, niche made possible by long-term environmental stability? Well, probably both, but the ecological and morphological evidence available suggests "so far, so good."

The tarsiid niche is unique among primates in many respects, but is perhaps most remarkable because of its great antiquity. Tarsiid primates, as well
as sivaladapine adapiforms, maintained relictual distributions in southern and southeastern Asia long after their close relatives on other Holarctic continents became extinct (Qi and Beard, 1998). This was made possible by the persistence in parts of southern and southeast Asia of humid multi-stratal rain-forest ecosystems from the earliest Tertiary to the present day (Morley, 2000). Although the composition of these forests has changed subtly through time, the physical structure of the forests and the nature of the insect guilds inhabiting the forests has not. The tarsiid niche has persisted for at least 45 million years because of the environmental stability of the tropical forest refuges of southeastern Asia and because of the trophic level (of the insectivore/carnivore) at which tarsiers exist.

References


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