

The Face of *Strigorhysis*: Implications of Another Tarsier-Like, Large-Eyed Eocene North American Tarsiiform Primate

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ABSTRACT

The hypothesis that hypertrophic eyeballs were widespread among Eocene tarsiiform primates can be tested by qualitatively examining an integrated set of anatomical features involving the middle face, palate, and orbital floor that are also manifest in *Tarsius*. The North American anaptomorphine *Strigorhysis*, restudied via micro-CT, is presented as an example, one of about nine fossil tarsiiforms (FTs) with moderately to enormously enlarged eyes—some possibly tarsier-sized. The eyeballs of *Strigorhysis* likely were ectopic and comparable in relative size to the smallest-bodied living tarsier, *T. pumulis*. These fossils, constituting approximately one-third of the Eocene tarsiiform adaptive radiation and possibly others still known essentially from dental remains, appear to form a monophyletic group that includes *Tarsius*. Small-eyed genera usually classified as omomyids, such as *Teilhardina* and *Rooneyia*, are not part of this clade. Although the precise affinities of *Tarsius* cannot yet be established, the widespread presence of meticulously similar orbital and facial morphology among the fossils suggest it is an ancestral condition—derived for haplorhines—shared by them and not multiply evolved via parallelism or convergence. Consequently, the rarer, tarsier-like postcranial characters found only among European microchoerines, which all exhibit degrees of orbital hypertrophy, should be revisited as potential *Tarsius* synapomorphies. The overwhelming evidence from the skull and from phylogenetics makes it a vanishingly small possibility that *Tarsius* is more closely related to anthropoids than to a subset of FTs. *Anat Rec*, 294:797–812, 2011. © 2011 Wiley-Liss, Inc.

Key words: *Strigorhysis*; omomyids; tarsiers; *Tarsius*; fossils; orbits; micro-CT; anthropoid origins

Fossil primates belonging to the Eocene radiation of Tarsiiformes have long been considered important to the origins of *Tarsius* (e.g., Cope, 1882; Osborn, 1902; Wortman, 1903–1904; Gregory, 1922; Le Gros Clark, 1959; Simons, 1972; Szalay and Delson, 1979; Fleagle, 1999). As such, they are also informative about anthropoid origins. If the tarsier is not phylogenetically linked with fossil tarsiiforms (FTs), its nearest relative must be Anthropoidea. Either model has profound consequences for understanding anthropoids and their origins.

Grant sponsor: PSC-CUNY.

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Received 22 January 2010; Accepted 3 November 2010

DOI 10.1002/ar.21367

Published online 23 March 2011 in Wiley Online Library (wileyonlinelibrary.com).

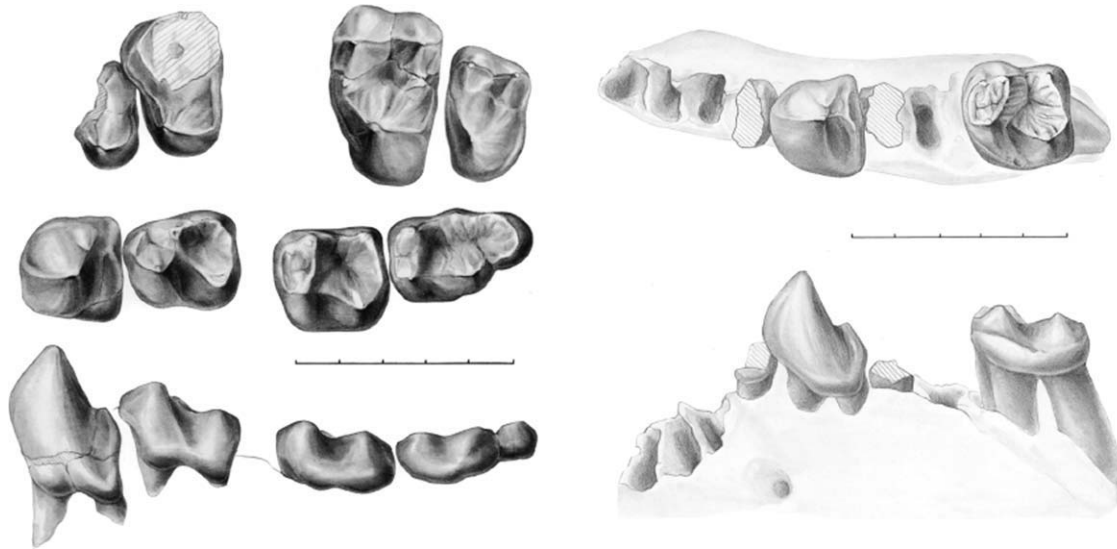


Fig. 1. Samples of the dentition of *S. huerfanensis* (left) and *S. bridgerensis* (right), after Bown and Rose (1987). Scales equals 5 mm. Left panel, top to bottom: right P3,4-M2,3 (reversed), occlusal view; left p4-m3, occlusal, and buccal views. Right panel, top to bottom: left p4, m2 in occlusal, and buccal views.

Taxonomically, the bulk of FTs come from North America, where more than 30 genera are recognized in Gunnell and Rose's recent synopsis (2002), nearly 40 if one includes the various questionable forms. All but two appear to be endemic; *Teilhardina* also occurs in Europe and Asia, and *Macrotarsius* occurs in Asia as well. Current practice refers all these to Family Omomyidae even though the higher level systematics of Tarsiiformes is quite unsettled. There is a consolidating consensus among active workers, explicit or implicit, that Omomyidae *sensu* Szalay, 1976, in the most recent monographic revision of the group, is a nonmonophyletic assemblage (e.g., Rosenberger, 1985; Beard et al., 1991; Beard and MacPhee, 1994; Dagosto et al., 1999; Kay et al., 2004; Bajapai et al., 2008). The same could be said for the Anaptomorphinae and Omomyinae, the two North American subfamily taxa in widespread usage, as well as the European Microchoerinae (Microchoeridae to some). For these reasons, in a provisional classification relating to this project, resurrecting earlier views (e.g., Simons, 1972) I suggested an alternative scheme that builds on the concept of Family Tarsiidae as a first step toward adjusting the classification of the fossils (Rosenberger et al., 2008). This tarsiid group would accommodate FTs thought to share synapomorphically with *Tarsius* very large eyes, for example. A second family, Anaptomorphidae (the prior nomen if *Omomys* is reallocated to Tarsiidae), would include the more primitive, small-eyed forms. For the present purpose, however, it is convenient to use the more familiar arrangements following Gunnell and Rose.

These tarsiiforms are also considered to be the oldest haplorhines, one of the two major clades of euprimates; the other constitutes the strepsirhines (e.g., Szalay and Delson, 1979; Fleagle, 1999; Hartwig, 2002). Thus, they are important to understanding what is behind the evolution of core taxonomic divisions of the order, the Strepsirhini (lemurs, lorises, and their fossil relatives) and Haplorhini (tarsiers, monkeys, apes, hominins, and their

fossil relatives). These groups are well-established clades. Modern haplorhines, for example, share derived features such as the hemochorial placenta and a dry-nosed snout. Modern strepsirhines uniquely share the toothcomb, a derived functional set integrating proclivous lower incisors with the canines, and reduced upper incisors.

The first FT skull came during the early history of tarsiiform paleontology (Cope, 1882) with the discovery of *Tetonius*. Among other similarities, its orbits were considered to resemble tarsiers in particular, housing greatly enlarged eyeballs (e.g., Cope, 1882; Wortman, 1903–1904; Matthew, 1915; Gregory, 1922), thus, setting up the expectation that FTs would be generally characterized this way. However, the scarcity of cranial remains, especially specimens that preserve intact orbital apertures, has made this hypothesis difficult to test. Consequently, researchers have come to rely heavily on dental morphology (e.g., Gazin, 1958; Simons, 1972; Szalay, 1976) to organize the systematics of North American FTs (NAFTa), although progress in integrating postcranial information has been substantial in more recent years (e.g., Dagosto, 1993; Dagosto et al., 1999; Anemone and Covert, 2000). In the process, two views became well entrenched: (1) few, if any, NAFTa share sufficiently detailed dental resemblances with tarsiers to warrant hypothesizing an especially close cladistic relationship; and, (2) the tarsiiforms are sufficiently diversified dentally to enable their division into several major groups (subfamilies). A less evident effect of stressing teeth may have contributed to an under appreciation of the cladistic and adaptive implications of enlarged orbits when they do occur among FTs, whereas material and methodological limitations may have inhibited us from recognizing how common hypertrophy may actually be.

In addition to *Tetonius homunculus*, the only other NAFTa represented by a skull suitable for measuring directly the orbital aperture is *Shoshonius cooperi* (Beard et al., 1991; Beard and MacPhee, 1994). A Chinese

congener of *Teilhardina*, *T. asisatica*, is represented by a skull as well, with sufficiently preserved orbits, that is, visualizable via CT scanning (Ni et al., 2004). These specimens were only discovered during the last 20 years. Although the excellent cranium of *Rooneyia viejaensis*, known since the 1960s (Wilson, 1966), had been considered another North American example, there is a growing awareness that this genus is not phylogenetically tarsiiform, though opinions differ widely on its affinities. For example, to Szalay and Delson (1979), Fleagle (1999), and Gunnell and Rose (2002), it is an omomyid, though a problematic one for Gunnell and Rose; to Kay et al. (2004), it is Semiotherium *incertae sedis* not allocatable to either strepsirrhines or haplorhines; to Rosenberger (2006; Rosenberger et al. 2008) it is a simiiform, the sister-taxon to Anthropoidea. But there is no debating the importance of *Rooneyia* in puzzling out the implications of orbit size in tarsiiforms, for it is one of the rare Eocene primate skulls where orbit and eyeball size can be well estimated metrically.

In this report, I present *Strigorhysis* as another large-eyed anaptomorphine omomyid from North America. *Strigorhysis* is an early middle Eocene genus from Wyoming and Colorado that includes three species, *S. bridgerensis*, *S. huerfanensis*, and *S. rugosus* (Gunnell and Rose, 2002). Bown and Rose (1987) provide the most detailed systematic account of the animal. As the specimen on which this study is based is the holotype of *S. bridgerensis*, it seems convenient to retain this terminology although Szalay (1982) questioned the separation of *Strigorhysis* from *Absarokius*, another anaptomorphine.

Not well known, *Strigorhysis* has been described from collections featuring teeth (Fig. 1), also fully treated by Bown and Rose (1987). Following them, the molars have been described by Gunnell and Rose (2002) as having crowns with “rugose, complex enamel,” which is usually associated with nonshearing, nonpiercing functions. This is opposite the evident shearing and puncturing functions which dominate *Tarsius* cheek teeth, the masticatory foundations for its extreme form of predation. Additionally, however, the *S. bridgerensis* holotype preserves important information about the orbital floor and facial shape bearing on orbit size and both indicate substantial eyeball enlargement. Much of this was obscured in the past by a block of preservative that concealed the specimen’s morphology, which has now become accessible virtually by CT scanning.

MATERIALS AND METHODS

United States National Museum (USNM) 250556, holotype specimen of *Strigorhysis bridgerensis* with the following measurements, all in mm: P3 (length, breadth) 1.3, 1.8; P4 2.0, 2.8; M1 2.3, 3.4; M2 2.0, 3.9; M3 1.3, 2.5. Maximum width of palate across M1/M2 (Bimolar Breadth): 11.5. Maximum width of the specimen as preserved: 17.8. For reference, average length and breadth measurements for a series of tarsier molars are as follows (sample sizes in parentheses): *T. syrichta* (4): M1 2.6, 3.3. *T. spectrum* (10) M1 2.4, 3.4. *T. pumulis* (1) M1 1.9, 2.8. All measurements were taken with calipers unless indicated otherwise. Two nontraditional dimensions are also used in this study.

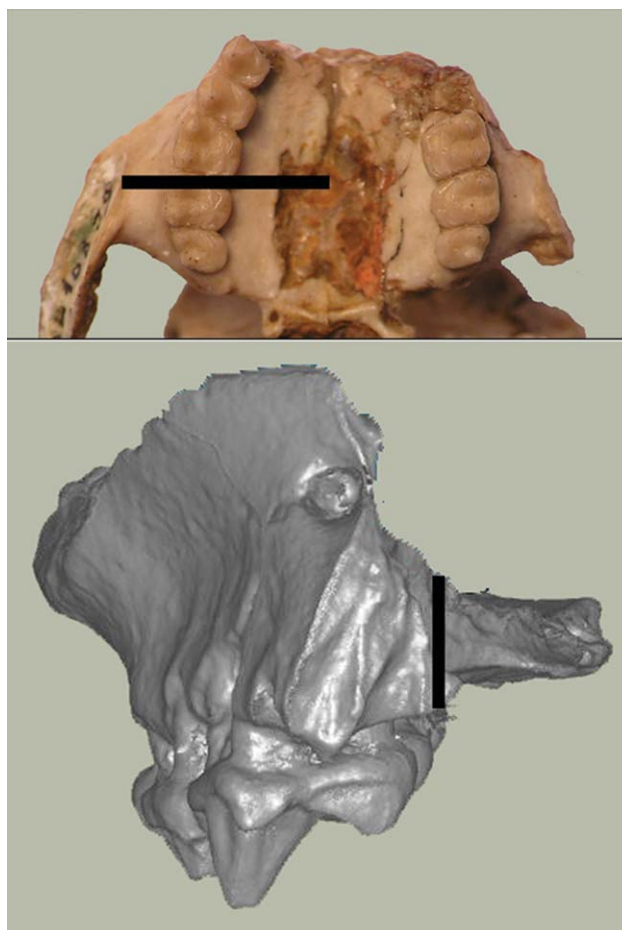


Fig. 2. The palatal view (top, *Microchoeroid*) illustrates half of the span used to measure paralveolar extension width, whereas the anterior view (bottom, *Hemiacodon*) illustrates medial maxillary depth (not to same scale). The latter measures the distance between the orbital and palatal surfaces perpendicular to the plane of the palate at the medial root of M1 and/or M2. This was done in software using micro-CT scans or laser surface scans. On actual specimens, the measure was taken on broken material that exposed the medial aspect of a specimen so calipers could be used.

Paralveolar Extension Width (Fig. 2)

This is a measure relating to the eversion of the maxilla in tarsiers, that is, the extent that the maxilla is displaced laterally beyond the dental arcade as a horizontal shelf (see below). It corresponds to the maximum width across the orbital fossae taken near the level of the orbital floor, which is proportional to the actual maximum biorbital breadth of a complete aperture located higher up on the orbital margins. The measurement is taken as the minimum width of the midface between the bilateral muscle scars for the origin of the superficial masseter muscle. The position of the masseter entheses also approximates the anterior root of the zygomatic process. On *Strigorhysis*, paralveolar extension width was estimated by doubling the span between the insertion and the midline.

Medial Maxillary Depth (Fig. 2)

The measurement was taken on CT-scan images of *Strigorhysis*, on a laser scan model of *Rooneyia* (digitized

TABLE 1. Measurements used to assess relative depth of the suborbital midface (see text), arranged alphabetically and rounded to the nearest tenth of a mm

Taxon	N	Molar length (mm)	Medial maxillary depth (mm)
<i>Anemorhysis (Anemo)</i>	1	1.6	1.1
<i>Absarokius abbotti (Absaab)</i>	4	2.2	2
<i>Absarokius</i> sp. (<i>Absa</i>)	1	2	1.5
<i>Aotus</i> sp.	1	3	3.4
<i>Arapahovius gazini</i>	4	2.4	1.3
<i>Dyseolemur pacificus</i>	3	1.9	1
<i>Hemiacodon gracilis</i>	8	3.6	1.8
<i>Loris</i> sp.	1	2.8	3.6
<i>Macrotarsius siegerti</i>	2	3.8	3.3
<i>Microchoerus erinaceus</i>	1	2.9	1.8
<i>Omomys carteri</i>	2	2.3	1.4
<i>Ourayia</i> sp. (<i>Ourayiasp</i>)	3	4.4	3.1
<i>Ourayia uintensis</i>	1	4	3.3
<i>Rooneyia viejaensis</i>	1	3.2	2.8
<i>Shoshonius cooperi</i>	2	2.1	1.3
<i>Strigorhysis bridgerensis</i>	1	2	1.6
<i>Tarsius1</i> (sp. unidentified)	1	2.5	1.2
<i>Tarsius2</i> (sp. unidentified)	1	2.5	0.9
<i>Teilhardina americana (Teilhaa)</i>	1	1.7	1.7
<i>Teilhardina crassidens (Teilhac)</i>	1	1.7	1.3
? <i>Tetonius (Teto)</i>	1	2	1.3
<i>Tetonius homunculus (Tetonius)</i>	2	2.2	1.6
<i>Tetonius matthewi (Tetonma)</i>	1	2.1	1.3
<i>Tetonius</i> sp. (<i>Tetonsp</i>)	3	2	1.6
<i>Washakius insignis</i>	3	2.4	1.8

Medial maxillary depth in *Strigorhysis* was measured on a rendered 3D model based on micro-CT data, using Image J. Upper molar mesiodistal length is based on M1, M2, or the average of both teeth when available. Abbreviations used in Fig. 8 are in parentheses. Among living samples, the species of *Tarsius*, *Loris*, and *Aotus* were not identifiable.

from a sharp epoxy cast) and on actual specimens (accessible because they were broken) for the remainder of the sample using digital calipers (Table 1). It is similar to a metric collected by Seiffert et al. (2005). In this case, it was taken as a perpendicular diameter oriented on the plane of the maxilla (palate) medial to the lingual root of M1 or M2. It is essentially a measurement of the thickness of bone beneath the orbital floor medially, or the elevation of the orbital floor above the plane of the tooth-row, that is, mid-facial depth.

The specimen was scanned with a Skyscan 1172 high-resolution micro-CT outfitted with an 11 megapixel X-ray camera. Data were collected at a pixel size of 11.54 μm over 410 cross-sectional slices, each comprised of a 1048 \times 1440 pixel matrix.

Regarding taxonomic terms, I tend to refrain, for the most part, from using “omomyids,” because the concept is problematic. But with no simple solution to this issue, I often use the expression FTs, and its derivative NAFTa to specify North American anaptomorphines, as alternatives.

RESULTS

Morphology

The specimen (Figs. 3–5) is a palate and midface that preserves most of the postcanine crowns on either right

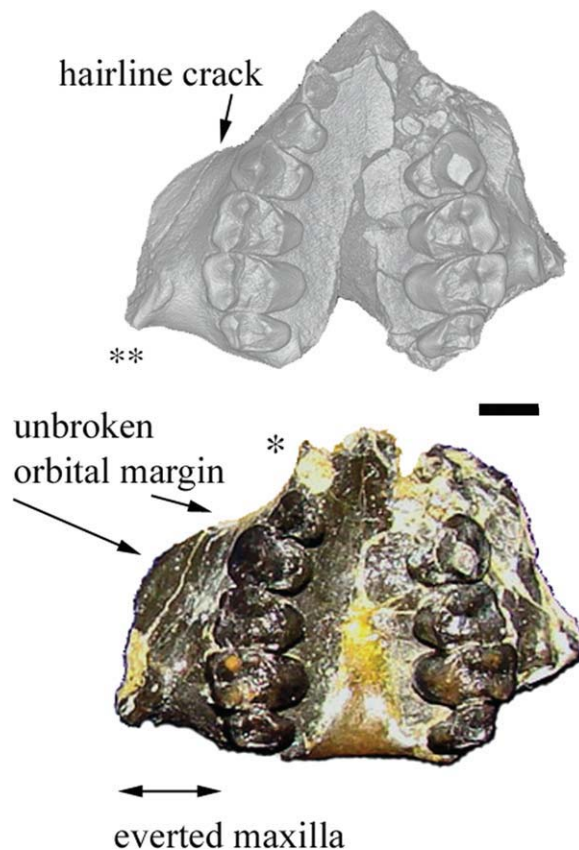


Fig. 3. Palatal views of *Strigorhysis bridgerensis* (USNM 250556), including a rendering (above) based on micro-CT scanning (also in Figs. 3 and 4). The single asterisk marks the preserved C/P2 interalveolar septum. The double asterisks indicate the position of the superficial masseter scar, near the anterior root of the zygomatic process. Scale bar represents 2 mm.

or left side, including RP3-M3 and LP4-M3. The main disruptive damage to the fossil in the current state is on dorsal and lateral aspects. The anatomical region of interest here is the orbital floor. Based on a tarsier model, the floor can be identified as a roughly triangular surface bounded by the medial orbital wall, the posterior margin of the maxilla and the oblique, arcuate line representing the free inferior margin of the orbital fossa anterolaterally. As with tarsiers, the general geometry of the orbital floor can be inferred reasonably well from its obverse palatal surface, to compliment direct inspection of the floor in the computer graphics reconstruction, and through the semitranslucent consolidant still affixed to it.

On the palatal surface (Fig. 3), it is evident that the right-side is intact as one piece and undistorted. It is complete as far forward as the partial alveolus for the right canine, and posteriorly to the maxillary tuberosity behind the M3s. The tuber is laterally continuous with the pristine posterior maxillary margin of the orbital floor, clearly framing its limit. The left side is nearly a match, but part if it has been shifted slightly, and the maxilla has suffered some crushing. On the whole, the hard palate is little distorted although it is not complete posteromedially; the palatines are missing. Anteriorly, at

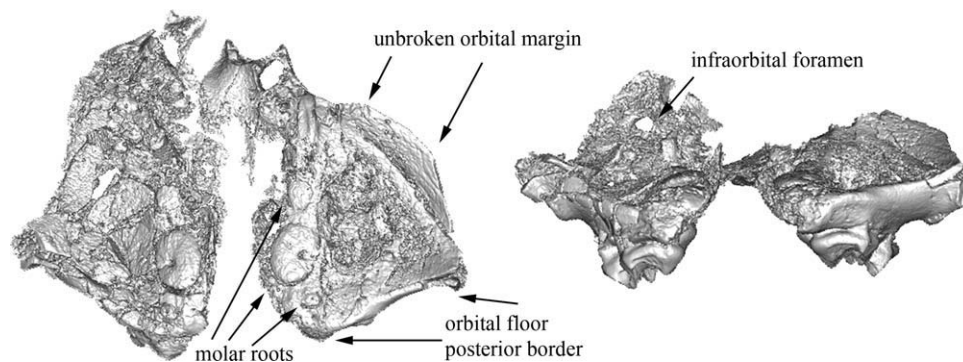


Fig. 4. Dorsal (left) and posterior (right) views of the orbital floor of *Strigorhysis bridgerensis*. Some of the preserved bone between the premolars (see Fig. 2) was not rendered. The unbroken segment of the right inferior orbital margin is clearly visible on the left.

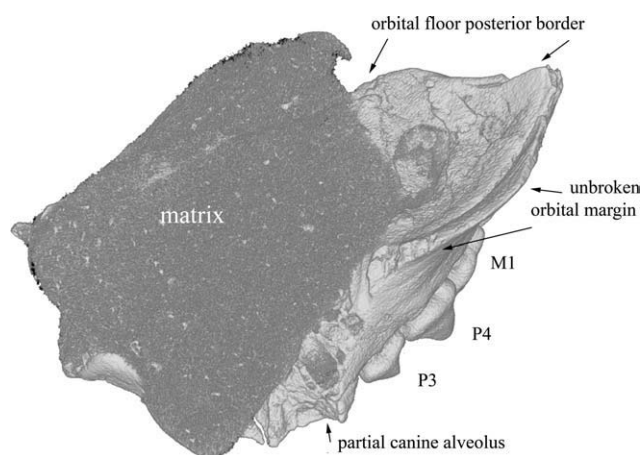


Fig. 5. Three-quarters view of the right side of *Strigorhysis bridgerensis*, here reversed and oriented on the unbroken segment of the inferior orbital margin. Note the areal extent and deeply concave contour of the orbital fossa. Matrix could not be removed in this view, because it is not easily differentiable from bone.

the level of C-P3 it is complete across the midline. The original arcuate shape of the arcade is exhibited without need for reconstruction on the right side, from the canine alveolus to M3.

In general terms, the shape of the maxillae and arcade closely resembles the half hourglass shaped arcade of *Tarsius*, characterized by a very narrow snout and a dramatically flaring row of posterior teeth (see Fig. 11). The exaggerated posterior width of the tarsier tooththrow is reflected in bimolar breadth which, when plotted against skull length, is a considerably larger span than comparably small-bodied living primates (Fig. 6). On the fossil, an inflection point near P3 can be defined where side-to-side tooth spacing shifts to radically broaden the palate. Behind this point, in inferior view the maxillae extends laterally well beyond the dental arcade until reaching the broken edges of the specimen, which is near the scar for the origin of the superficial masseter muscle. In tarsiers, the maxilla then turns upward (dorsally) to become part of the expanded postorbital bar that supports the huge eyeballs. The fullness of this

region cannot be seen on the broken fossil, but the overall pattern forming the base of it is well preserved on the right side, as exhibited in the dorsal and three-quarter views of the specimen (Figs. 4 and 5).

Although the left side sustained more damage, it preserves the infraorbital foramen, the open circle situated well above the tooththrow in Fig. 4. In palatal and dorsal views, on the right side, anterior to the root of the zygomatic arch is a hairline fracture that extends obliquely across a segment of the orbital floor. It roughly parallels the free-margin edge of the specimen, which is one of two small remnants demarcating the actual orbital aperture in the specimen. One, on the right, is a perfectly undamaged segment 3.2-mm long, situated 4 mm above the alveolar plane. On the left side, a small, ~1.4 mm long, slightly weathered edge appears to be another remnant. It is situated above and anterior to the infraorbital foramen, further forward than the remaining margin on the right side. Its posterior break lies immediately above the foramen. This indicates the minimal anterior limit of the orbital aperture.

Posteriorly, the pristine free margin of the floor is clear on the right side (Fig. 4), marred only by a medial break near the pyramidal process. This point, and its symmetry with the left side, indicates the processes would have been situated close to the midline, that is, the choanae would have been relatively narrow, as in tarsiers. The visible strip of bone near the broken medial edge of the floor exhibits a series of three circular mounds, which are the lingual roots of the three molars naturally piercing (on both sides) through the maxillary bone and into the orbital floor itself. There is only a small hint of the original medial orbital wall on the left side, which represents the inner boundary of the orbital floor near the roots.

In the three-quarters view (Fig. 5), here oriented on the unbroken fragment of the aperture, many of these details are easily observed in context, and the size and deeply concave contour of the floor can be appreciated. Note that the full anterior extent of the floor cannot be visualized here because it proved difficult to accurately differentiate bone from the exogenous material affixed to it in the rendered CT scan.

Relative Orbit Size

To attempt a metrical assessment of relative orbit size in *Strigorhysis* several comparisons were made relating

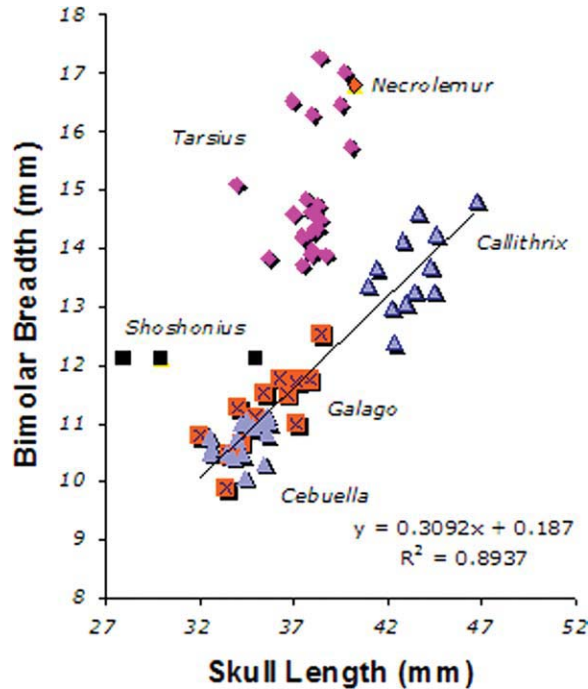


Fig. 6. The relationship between skull length and bimolar breadth in selected primates. The regression line and equation is based on the living nontarsiiform species (samples in parentheses): *Callithrix jacchus* (12), *Cebuella pygmaea* (17), and *Galago demidovii* (15). Tarsiers include, *T. bancanus* (1), *borneanus* (1), *spectrum* (14), and *syrichta* (5). Average estimated skulls length for *Necrolemur antiquus* is from Kirk (2006). The minimum skull length for *Shoshonius cooperi* is the actual length (28 mm) of the broken best preserved skull in the Carnegie Museum of Natural History collection (CM 60494). Other values (30, 35 mm) are arbitrary and for illustrative purposes only. Tarsiers and the fossils have relatively wide posterior dental arcades in connection with their hypertrophied orbits and eyeballs.

linear features of the maxilla to molar or palatal measurements.

Paralveolar extension width. As noted, the differentially expanded width dimension of the posterior face is reflected in the structure of the everted maxilla, especially in the far lateral position of the insertion area for the superficial masseter muscle. Based on a sample of 13 adult individuals across four species, *spectrum*, *borneanus*, *syrichta*, and *pumulis*, in tarsiers paralveolar extension width is closely correlated with bimolar breadth ($R^2 = 0.9297$). With *Strigorhysis* included in the sample (Fig. 7), R^2 increases to 0.9371, as the dimensions of the fossil are closely comparable with *T. pumulis*. This indicates that orbital expansion at the level of the orbital floor in *Strigorhysis* is comparable with the pattern of the smallest living tarsier.

Medial maxillary depth. Seiffert et al. (2005) suggested the relative shallowness of the suborbital floor, and particularly, the thinness of the plate formed by fusion of the laminae of the orbital floor and the palate in tarsiers (as opposed to a deeper suborbital space where these layers are separated by compact bone and/or a sinus) is proportional to the extent of the eyeball

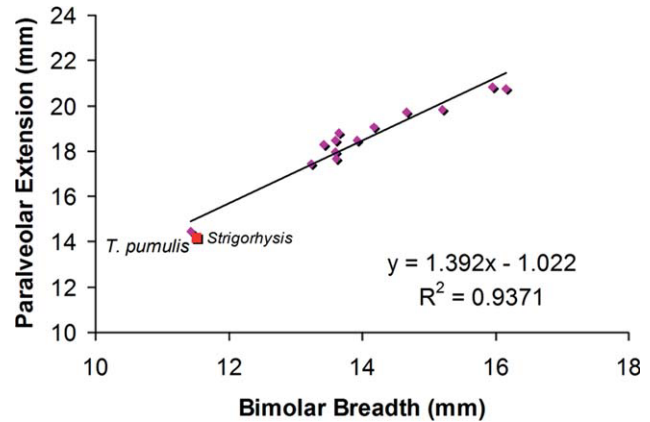


Fig. 7. Bivariate plot of bimolar breadth and paralveolar extension width, the span across the right and left masseter muscle scars (in mm), in a selection of modern tarsiers and *Strigorhysis*. The measurement for *Strigorhysis* was estimated by doubling the measurable perpendicular distance of the right entheses to the midline. The regression equation represents the full sample of individuals. The size and proportions of *Strigorhysis* and *Tarsius pumulis* are similar, indicating a comparably enlarged (wide) orbital floor in *Strigorhysis*.

hypertrophy: tarsiers plot far below diurnal anthropoids when this feature is regressed against a body size proxy. For reference, they compared tarsiers against a regression line based on an array of diurnal platyrrhines. They also noted that the laminar orbital floor of *Tarsius* had molar roots penetrating through the floor, exposing them in the orbit. To extend their work and test the conditions of *Strigorhysis*, a similar set of measurements and observations were made on the fossil, in *Tarsius*, a range of FTs and several other pertinent primates (Table 1).

Figure 8 plots medial maxillary depth against upper molar length (length of M1, M2, or the average of both when each was present on a specimen). The Seiffert et al. (2005) diurnal anthropoid regression line is shown (dashed), as is an “omomyid” line based on all subsamples consisting of two or more individuals (Table 1). The distribution appears to be more complex than the conditions assessed by Seiffert et al. in a taxonomically narrower study. Several points are noteworthy. As expected, the nocturnal *Aotus* and, more dramatically, *Tarsius*, both exhibit shallower suborbital depths relative to the diurnal anthropoid line. FTs estimated to have enlarged orbits based on aperture measurements, *Tetonius*, *Necrolemur*, *Microchoerus*, *Shoshonius*, and *Omomys*, do not show the extreme shallowness of tarsiers, although the latter two genera have been inferred to have greatly enlarged eyes (see below). The position of *Strigorhysis* falls amidst the cluster of points representing samples of *Tetonius*. In conjunction with the morphology already discussed, this is consistent with the notion that the fossil’s orbital floor is built to maximize orbital volume. However, the evidence also suggests caution when interpreting shallow suborbital depths as an indicator of orbit size, for specimens of *Teilhardina* can have comparably a shallow midface, and this genus is thought to have relatively small orbits (see below).

Although none of the FTs that are similar to tarsiers in molar length appear to have the paper thin floor or

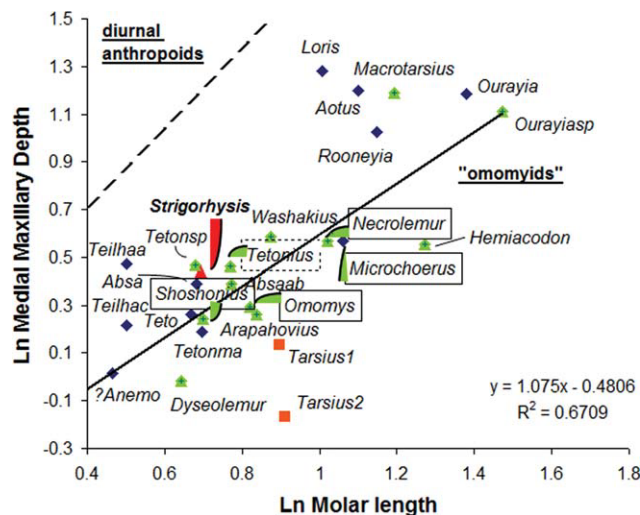


Fig. 8. Bivariate plot of upper molar length (M1 or M2, or the average of both when available) and medial maxillary depth to illustrate relative depth of the maxilla below the orbital floor. The dashed diurnal anthropoid regression line, from the equation given by Seiffert et al. (2005), is shown for perspective. It has bearing on the distribution of the current sample, but the measurement of orbital floor depth used by Seiffert et al. differs slightly from the method used here. The omomyid regression line and equation, inset, is based on FT samples (green) with an N of two or more (abbreviations in Table 1). Neither of the tarsier specimens, nor Loris or Aotus, was identifiable to species. Fossil genera shown elsewhere to have enlarged orbits (see Fig. 10) are framed; Tetonius (only one sample highlighted) with a broken line to indicate its orbital aperture may be relatively the smallest of this group. Although none of the FTs, which are comparable in molar length appear to have the paper thin sub-orbital floor of *Tarsius*, the actual differences in bony dimensions among fossils with the most shallow suborbital depths are less than 1 mm (most substantially less), hence sample variability and measurement error cannot be ruled out as an explanation for their specific distributions, as opposed to effects relating specifically to eye size. *Strigorhysis* (red) plots near Tetonius and Absarokius, a dentally similar genus. The haplorhine Rooneyia, considered to be relatively small-eyed (Fig. 10), has a shallower suborbital depth than diurnal platyrrhines and the nocturnal Aotus and Loris.

midface of *Tarsius*, the actual differences in bony dimensions (Table 1) among *Tetonius*, *Microchoerus*, *Shoshonius*, *Omomys*, and the two examples of tarsiers, are less than 1 mm, in most cases substantially less. Hence, sampling and measurement error cannot be ruled out as an important distinguishing factor, as opposed to effects relating specifically to eye size. Nor would it be counter-intuitive for *Tarsius* to have the most accentuated state of a common pattern. Among the genera sampled, it is also common for the shallow orbital floor to expose molar roots. This has been confirmed in *Absarokius*, *Tetonius*, *Omomys*, *Macrotarsius*, *Arapahovius*, *Dyseolemur*, *Pseudoloris*, and *Nannopithecus*. But roots also penetrate into the floor in the relatively small-eyed fossils as well, including *Rooneyia* and *Teilhardina*.

DISCUSSION

Taking Measure: *Strigorhysis* and *Tarsius*

The facial and cranial skeleton of *Tarsius* exhibits a large series of anatomical features that are adaptive and developmental adjustments to spatially packaging, balancing, and moving hypertrophic eyeballs (see Rose-

berger, 2010). The facial elements allow for an enlarged surface area of the orbital floor and a capacious orbital fossa volume. In the horizontal axis, these specialized features include: widely spaced posterior cheek teeth and an everted maxilla with wide paralveolar extensions; sagittally shifted medial orbital walls, compromising the space of the nasal fossa and narrowing the width of the posterior nares. In the vertical axis these include: a low, plate-like orbital floor that fuses with the hard palate (see Hershkovitz, 1977; Seiffert et al., 2005) to deepen the orbital fossa from below, and everted superior orbital margins to raise the overall height of its brim. The exaggerated bimolar span of tarsiers is documented quantitatively in Fig. 6.

Although this build maximizes the capacity of the fossa, it hardly accommodates the huge eyeball (Fig. 9), which is nearly equal in volume to the mass of the tarsier's brain (e.g., Stephan, 1984). The superior orbital flange, in fact, reflects the ectopic location of the tarsier eyeball outside the eye cup: Schultz showed (1940) that more than half the globe lies beyond the bony perimeter. The flange helps anchor the tough periorbital ligament that girdles the eye (Fig. 10). It is strongly influenced by eyeball growth during fetal development and presumably thereafter (Jeffery et al. 2007). For the one individual that Jeffery et al. document in their ontogenetic study as being a fully mature neonate, the eyeball had reached only 68% of brain volume. The morphology of the circumorbital margin also changes a lot after birth and its flanging becomes more prominent (see Fig. 10), indicating continued growth and further externalization of the eyeball.

The ectopic position of the eyeball is a function of eyeball hypertrophy and primitive haplorhine features retained in *Tarsius*, especially the relatively small size of the frontal bone and the laterally facing and upwardly tilted orbits (Fig. 9; Ross, 1995). Eye position is also constrained in *Tarsius* by retraction of the orbital fossa to a position partly below the forebrain, which may be related to head balance (Rosenberger, 2010). On the more complete, right side of *Strigorhysis*, the orientation of the unbroken fragment of the anterior inferior aspect of the aperture closely resembles the angle seen in tarsiers (Figs. 4 and 9), indicating a forward, anterolateral expansion of the fossil's orbital floor. This can only mean the eyeballs were greatly enlarged and extended far anteriorly onto the rostrum. As the root of the zygomatic, thus the base of the postorbital bar, was positioned near the back of the tooththrow, unless *Strigorhysis* had a massively enlarged frontal bone to roof over the eyeballs, the frontation plane of the orbital fossa must have been tilted significantly. This makes it likely that the eyeballs of *Strigorhysis* were ectopic, like a tarsier's. One would thus also predict that a frontal of *Strigorhysis* will be found to have everted superior orbital margins.

One cannot accurately establish and compare absolute or relative eyeball size in *Strigorhysis* and relate it to *Tarsius*, but even orbital aperture measures fall short in this regard when applied to tarsiers for the eyeball is ectopic. However, the overall morphology of the fossil manifests precisely the same pattern of structural details. This involves the same set of derived features, seen rarely among extant euprimates—one noteworthy exception being the several exhibited by *Aotus* albeit

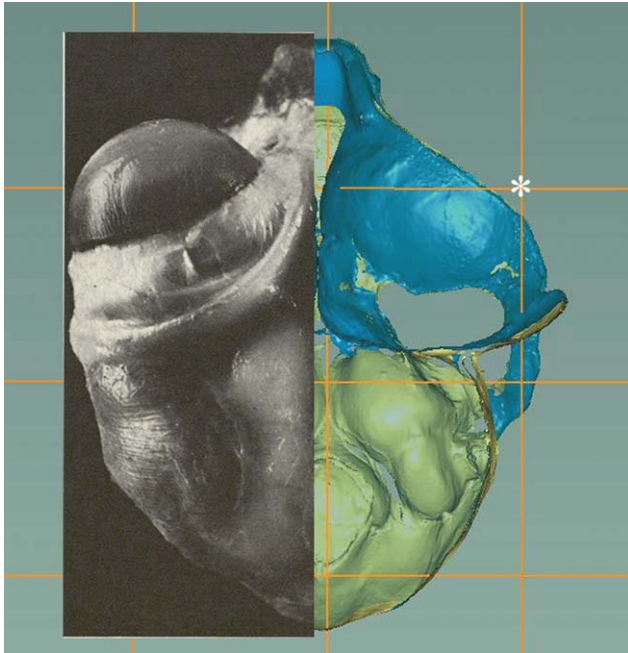


Fig. 9. The ectopic eyeball and orbital fossa of *Tarsius* sp. (modified from Sprankel, 1965, left, and Rosenberger et al., 2008, right). The skin on the snout (darkened area), temporalis musculature, and periorbital ligament are visible on the left. The cutaway on the right is based on a laser surface scan 3D model, with the basicranium flipped into dorsal view to illustrate spatial relationships. The everted superior orbital flange is evident on the left. On the right, the asterisk marks the approximate position of medial edge of the superficial masseter muscle scar (see text). The ectopic position of more than half the eyeball is a function of eyeball size, the relatively small frontal bone (thus limited orbital frontation) and laterally facing superior orbital margins.

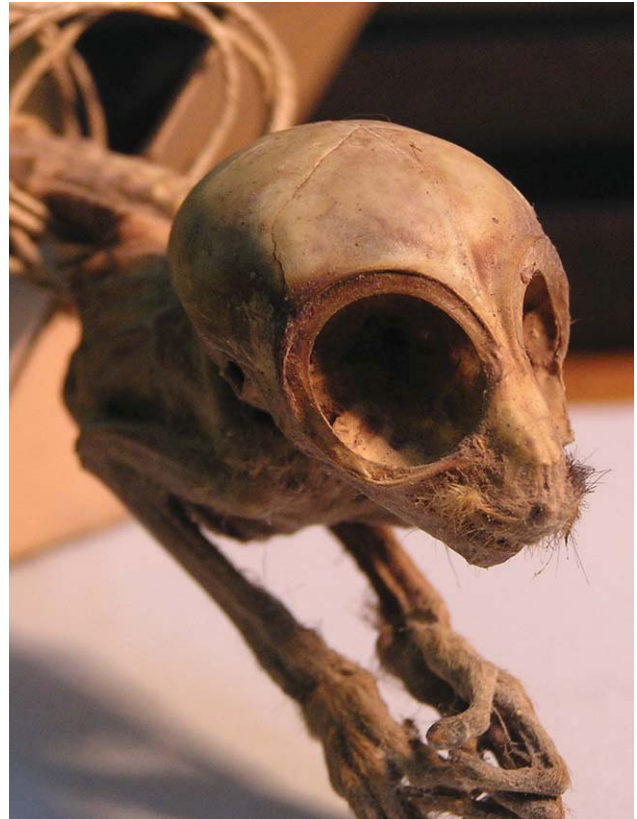


Fig. 10. An immature specimen of *Tarsius* sp. illustrating the tough periorbital ligament attached to the orbital margin and the still-developing everted flange of the superior orbital margin. They combine to help fix the ectopic eye in position. Dark brown blotches in the right orbital floor are molar roots piercing through.

much more modestly (see below)—and are all explicable as modifications pertaining to a large-eyeball morphology. The indirect measures reported here pertaining to the orbital floor, which relate to expanded orbital volumes and bimolar span, paralveolar extension width, and medial maxillary depth, and all are consistent with a hypertrophic-eye model. The transverse dimensions (Fig. 7) suggest *Strigorhysis* posterior facial width, in a relative sense, resembled the smallest living tarsier, *Tarsius pumulis*.

To make the same point about orbit size by way of contrast, the morphological basics of *Strigorhysis* and *Tarsius* differ from the small-eyed Eocene haplorhine *Rooneyia* (Fig. 11), for which we do have metrics that rate aperture size in a broad taxonomic context (Fig. 12). Although its face is wide, *Rooneyia* lacks the half hour-glass shape of the arcade and the everted maxillae, and it exhibits wide choanae, all reflections of a small-eyed anatomy. A similar contrast between a small-eyed diurnal New World anthropoid, *Callicebus*, and a moderately large-eyed, nocturnal and crepuscular platyrrhine, *Aotus*, both of about the same body mass (1 kg; Rosenberger, 1992), demonstrates the same principles (Fig. 13). To house the large eyeball, the orbital floor is transversely expanded in the owl monkey, which results in a widening and prolongation of the maxilla laterally beyond the dental arcade and root of the zygomatic arch.

Also, as in tarsiers the mediolateral width of the posterior nares is reduced in *Aotus*, reflecting approximation of the medial orbital walls against the nasal fossa.

As an indicator of orbit size in FTs, the shallowness of the suborbital floor is a feature that must be treated with caution. A generalized, shallow-face anatomy may be related primarily to the flat build of the early euprimate midface, that is, a substantial maxillary sinus had not emerged as a major structural feature below the orbits. The shallow floor seen in *Teilhardina*, for example, and even the relatively deeper—but shallow by anthropoid standards—suborbital floor of the small-eyed *Rooneyia* (Fig. 8), may be primitive retentions of the ancestral euprimate condition. The paper thin *Tarsius* pattern may thus involve the exaggeration of a retained primitive state, a shallow midface that was constrained to remain as such until becoming accentuated as the eyeball hypertrophied bizarrely. If correct, this means that falling well below the diurnal anthropoid regression line of Seiffert et al. (2005) may be a coincidence of history rather than a highly robust indicator of hypertrophic eyes or nocturnality in FTs or early anthropoids.

To summarize, much like *Tarsius*, *Strigorhysis* presents an ensemble of interrelated traits pointing to orbital floor expansion and eyeball hypertrophy: a half hour-glass shaped dental arcade that radically diverges in the molar region, thus widening and prolonging the

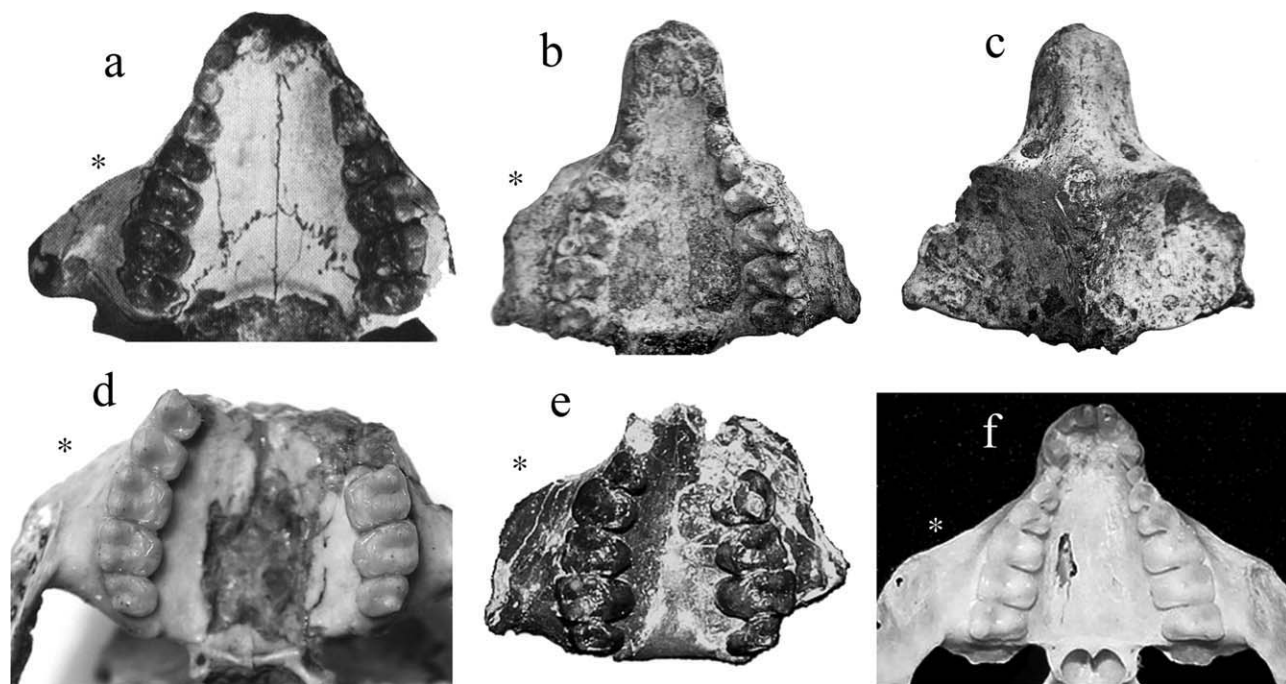


Fig. 11. Palatal views of: a, *Rooneyia*; b, *Pseudoloris*; c, *Pseudoloris* in dorsal view (same specimen as b); d, *Microchoerus*; e, *Strigorhysis*; f, *Tarsius*. Not to the same scale. Asterisks mark the approximate position of the superficial masseter enthesis. Roots of M2 and M3 are visible in the right orbital floor of *Pseudoloris*. Note the unique,

upturned, flange-like posterior maxillary process in *Tarsius*. The extensive shelf-like paralveolar morphology, enlarged in anteroposterior and transverse dimensions, is evident in all but *Rooneyia*. Among FTs, the shelving is more exaggerated in smaller smaller than in the larger species, due the negative allometry of eyeball size.

supporting platform for the large eyeball; large paralveolar maxillary extensions to further expand the surface area of the orbital floor laterally and anterolaterally; a shallow orbital floor, which enables maximization of fossa volume; and a narrowed choanae reflecting approximation of the medial orbital walls, thus, medially expanding the orbital floor. In all respects, the morphology of *Strigorhysis* is symmetrical with *Tarsius*, meaning there is no *a priori* reason to suspect their similarity of pattern is a matter of parallelism or convergence. There is little doubt the configuration is derived among euprimates, and there is evidence that it is fairly widespread among FTs, occurring among North American and European forms (Rosenberger et al., 2008), as further discussed below.

Paleobiologically, the finding that *Strigorhysis* was a very large-eyed early tarsiiform implies it was also both nocturnal and predatory to a considerable degree, considering the adaptive explanations for hypertrophy in *Tarsius* (see Rosenberger, 2010), even though its molar teeth tend to be rugose (Bown and Rose, 1987; Gunnell and Rose, 2002). In this regard, assessing body mass in *Strigorhysis* is important, because the *Tarsius* feeding niche is clearly predicated on very small body size. Fleagle (1999) suggests a weight of 500 g, which is much larger than any modern tarsier. Gursky (2007) summarizes the data for five living species, presented here as known ranges: *T. bancanus*, 117–128 g; *T. dianae*, 100–130 g; *T. spectrum*, 104–126 g; *T. syricta*, 120–141 g; *T. pumulis*, 58 g. In terms of dental dimensions (see above), the M1 area of the *S. bridgerensis* holotype is about 92%–97% the size of an average M1 of *T. syricta* or *T.*

spectrum, respectively, and 47% larger than the smallest tarsier, *T. pumulis*. For all intents and purposes, then, *S. bridgerensis* must have been tarsiersized, thus falling within the faunivorous profile boundary as delimited by *Tarsius*. However, one must be cautious in inferring body mass from the molar teeth among tarsiiforms. The upper molars of many FTs are consistently (and primitively) relatively wider buccolingually than those of *Tarsius*, and they may be unusually large relative to body size (Dagosto and Terranova, 1992). Taking this into account and using molar mesiodistal lengths alone, *Strigorhysis* is only 21% larger than *T. pumulis*. So, it is reasonable to conclude that *Strigorhysis* was the size of a small modern tarsier and not outside the range of the living tarsier species.

***Strigorhysis* as a Large-Eyed Tarsiiform: Phyletic and Adaptive Implications**

***Strigorhysis*, *Tarsiers*, and *Omomyids*.** Were enlarged eyeballs widespread among FTs? If so, how enlarged were they, and what does this mean functionally, ecologically, and phylogenetically? Both qualitative and quantitative information are instrumental but these questions can only be addressed in the most general ways. I use several criteria in attempting to characterize eye size among FTs. Two involve departures from regression lines describing the relationship between orbital and bimolar diameters relative to length in primates, especially the diurnal forms (i.e., anthropoids, which comprise 23 of 28 species) that make up much of the sample in Fig. 12. The other is based less on quantitative criteria

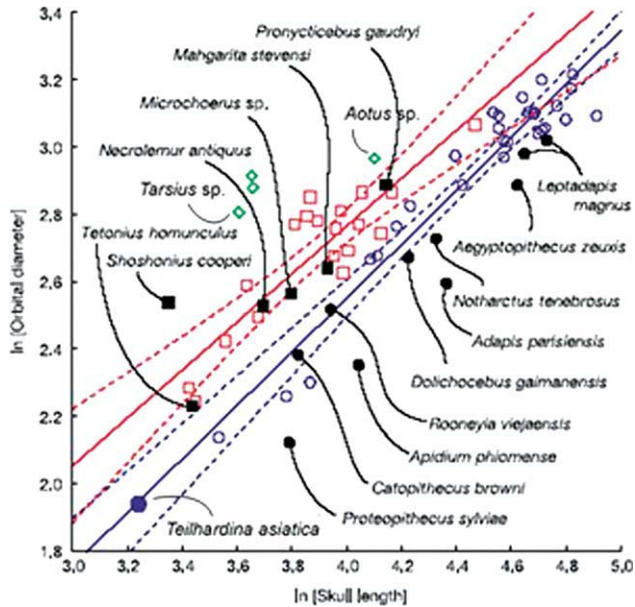


Fig. 12. Plot of orbital aperture diameter against skull length is a large sample of primates (modified from Ni et al., 2004). Blue and red solid and dotted lines are best lines of fit and 95% confidence limits for diurnal primate (23 of 28 species belonging to Anthropeidea) and nocturnal strepsirhine regressions, respectively. Note that *Teilhardina* and *Rooneyia* fall on the small-eyed, diurnal regression line, meaning they have eyes that are essentially anthropoid-like in proportion. The FTs plot at (*Tetonius*) or outside (all others) the diurnal species' confidence limits. *Omomys* is not shown, but it plots between *Shoshonius* and *Tarsius* in another study (Heesy and Ross, 2001) that relates orbital aperture against an alternative proxy (molar length) for body mass. If *Teilhardina*, *Rooneyia*, and small-eyed Fayum anthropoids (*Proteopithecus*, *Catopithecus*, *Apidium*, *Aegyptopithecus*) reflect the ancestral haplorhine condition, the enlarged FT eyes are all likely to be derived, indicating these genera are monophyletically related to *Tarsius*.

than the qualitatively assessed features described above. Obviously, in both situations the hypertrophic *Tarsius* is also a standard; and although its ultra large eyes are unique among all living primates, there is evidence that the orbits of some FTs approach the *Tarsius* condition in varying degrees. Therefore, I use a set of descriptive terms for the fossils which lumps most as being very large but also attempts to sort the scale of their magnitude according to the limited evidence available.

It should also be recalled that measures of eyeball size based on orbital diameter, while an accurate reflection of globe size in some primates (Kirk, 2004), does not accurately capture eyeball size where it is ectopic, as in *Tarsius*. So, additional morphological information must be taken into account when assessing the fossils as well. For example, marked superior orbital flanges will signal that the eyeballs are ectopically positioned, hence hypertrophic. Such is the case (Rosenberger et al., 2008) with an isolated frontal bone exhibiting everted superior orbital margins that has been attributed to the anaptomorphine *Hemiacodon* (Gazin, 1958; Szalay, 1976).

For those fossil FTs preserving measurable orbital margins (*Teilhardina*, *Tetonius*, *Necrolemur*, *Microchoerus*, *Shoshonius*), or fractions thereof that permit orbital diameter estimates (*Omomys*), at least three categories or character states of relative eye size can be discerned (Table 2; Figs. 7 and 12). For convenience, these can be called: (1) Small eyes—in *Teilhardina*. It falls on the regression line describing the proportions of diurnal extant primates, mostly the anthropoids, which have unusually small eyes (Kirk, 2004). (2) Moderately enlarged eyes—in *Tetonius*, *Necrolemur*, and *Microchoerus*. These genera are aligned at roughly similar levels outside the confidence limits of the diurnal regression line. (3) Hypertrophic eyes—in *Shoshonius* (and *Tarsius*). It plots well above the diurnal best fit line. *Omomys*, which is not depicted here, also has hypertrophic eyes, apparently falling between *Shoshonius* and *Tarsius*, as shown by Heesy and Ross (2001) using a different body mass proxy.



Fig. 13. A comparison of the nocturnal *Aotus* (left, Owl Monkey) and diurnal *Callicebus* (right, Titi Monkey) showing convergence to large-eyed tarsiiiforms in paralevolar extension of the maxilla beyond the toothrow, and narrowing of the choanae (modified from MacPhee and Horovitz, 2004).

TABLE 2. A synopsis of all FTs known from cranial and/or facial remains indicating orbital enlargement, including notations regarding the most decisive postcranial characters bearing on their phylogeny and adaptations

Geuns	Subfamily	Distribution	Material	Orb size	Features	Major references	Foot and leg	Major references
<i>Strigorhysis</i>	Anaptomorphinae	North America	Patial face	Hypertrophic	Qualitative	this report	NA	
<i>Teilharaina</i>	Anaptomorphinae	Laurasia	Skull	Small	Aperture measures	Ni et al., 2004	Tarsus mod. long	Gebo, 1988
<i>Tetonius</i>	Anaptomorphinae	North America	Skull	Moderately enlarged	Aperture measures	Martin, 1990, Kirk and Kay, 2000; Heesy and Ross, 2001; Martin, 1990	??	Dagosto, 1993
<i>Hemiacodon</i>	Omomyinae	North America	Frontal bone	Hypertrophic ?	Qualitative	Simons, 1963; Szalay, 1976	Fib. unfused	Anemone and Covert, 2000
<i>Omomys</i>	Omomyinae	North America	Partial face	Hypertrophic	Aperture measures	Heesy and Ross, 2001	Tarsus mod. long; fib. unfused	Anemone and Covert, 2000
<i>Shoshonius</i>	Omomyinae	North America	Skull	Hypertrophic	Aperture measures	Beard et al., 1991	Tarsus mod. long; fib. unfused	Dagosto, et al. 1999
<i>Nannopithecus</i>	Microchoerinae	Europe	Crushed skull	Moderately enlarged?	Qualitative	Thalman, 1994; ALR, 2008	Tarsus mod. long	Thalman, 1994
<i>Pseudoloris</i>	Microchoerinae	Europe	Partial face	Hypertrophic	Qualitative	Simons, 1972	Tarsus mod. long	Thalman, 1994
<i>Microchoerus</i>	Microchoerinae	Europe	Skull	Moderately enlarged/hypertrophic	Aperture measures	Kirk and Kay, 2000; Heesy and Ross, 2001	Tarsus hypertrophic	Schmid, 1979
<i>Necrolemur</i>	Microchoerinae	Europe	Skull	Moderately enlarged/hypertrophic	Aperture measures	Kirk and Kay, 2000; Heesy and Ross, 2001; Marti,n 1990	Tarsus hypertrophic, fib. fused	Schmid, 1979; Godinot and Dagosto, 1983

The Features column relates to how orbit size was inferred from morphology. Regarding postcranials, the references pertain to the extreme *Tarsius* character states, fusion of the tibia and fibula and marked anterior elongation of the tarsus (Fib. = fibula; mod = moderately). It should be noted that in all the FTs where the tibia is known, there are morphological indications that can be interpreted as preadaptations for tibio-fibula fusion.

Conservatively speaking, the relative wide bimolar widths of *Necrolemur* and *Shoshonius* are consistent with this assessment (Fig. 6). For *Necrolemur antiquus*, sufficient cranial remains enable accurate average measurements of skull length (Kirk, 2006) and a plot of skull length and bimolar breadth. *Necrolemur* falls clearly among modern tarsiers and well above the regression line representing three other primate species of roughly similar body mass. The incomplete material of *Shoshonius* means only gross estimates of skull length can be obtained. Its position is less dramatically elevated above the regression line, but the range of skull length estimates given, rather arbitrarily, suggests an impressively wide bimolar span as well.

Although it is likely that a functional shift in eyeball organization characterizes the bizarrely huge eyes of tarsiers and comparable FTs, these rankings need to be treated with caution. Because of the negative allometry of eyeball size relative to body mass (Schultz, 1940; Kay and Kirk, 2000), within-lineage body size differences can be distorting. As *Necrolemur* and *Microchoerus* are the largest FTs in the sample (Fig. 12), they would be expected to have proportionately smaller eyes for their body mass than the smallest tarsiform species. This means we have to consider the possibility that eye function may not differ greatly from some of the smaller tarsiforms even though the latter may have relatively larger eyes per skull size. Additionally, having moderate as opposed to massively enlarged eyes does not necessarily mean *Microchoerus* and *Necrolemur* are more primitive within the FT morphocline for this feature (contra Rosenberger et al., 2008). There may have been selection for reducing eye size for ecological and metabolic reasons (see Ankel-Simons and Rasmussen, 2008; Rosenberger, 2010).

Morphologically, the correlative bony specializations pertaining to ectopic, hypertrophic eyes are also less evident in *Necrolemur* and *Microchoerus* (Fig. 11), as would be expected in larger-bodied forms: paralveolar shelving is exhibited but not marked; the half hour-glass shaped arcade is not as exaggerated as in tarsiers; and, the superior orbital flanges are not very impressive. However, the width differential between the molar series and the choanae is retained, suggesting its primary role in forming an expansive orbital floor. In contrast, tiny forms, such as *Strigorhysis* and *Shoshonius*, are destined to have allometrically large eyes in accordance with their small body mass even before factoring in any potential quantum increases in globe size. So, cranially, these small forms present the full series of exaggerated character states of the osseous features supporting tarsier-like hypertrophy.

There are two additional microchoerines where the set of qualitative criteria indicate enlarged orbital fossae, *Pseudoloris* and *Nannopithec* (Fig. 11; see Rosenberger et al., 2008). Both present everted maxillae, extensively fused medial orbital walls, narrow posterior nares, a half hour-glass shaped dental arcade, and a shallow sub-orbital floor with penetrating molar roots. *Pseudoloris* also exhibits extensively fused medial orbital walls anterior to the broken sphenoid, indicating the posterior nares would also have been narrow. Thus, while the eye-size ranks of *Pseudoloris* and *Nannopithec* cannot be established and related to metrics of the floor are still unavailable, the orbits of these fossils were almost certainly relatively larger than the condition of *Teilhardina*,

at a minimum; one can assume safely their eyeballs were at least moderately enlarged. The *Nannopithec* skull is crushed. But the available morphology of *Pseudoloris* actually suggests a hypertrophy on par with *Tarsius* according to Simons (1972, 2003; see also Rosenberger et al. 2008; Fig. 11).

Thus, impressive degrees of relative eyeball enlargement, at or well beyond the confidence limits of living diurnal primates, are not exclusive to the North American omomyids but may have been widespread among FTs (Table 2), even appearing in genera with disparate dental and postcranial morphologies. About nine of the 30–40 FT genera appear to have enlarged eyes, representing each of the major subfamilies and spanning the Old and New World. Although we may still consider the *Tarsius* condition unique on account of the breadth of our empirical knowledge of the tarsier eye, the supposition that its mass is autapomorphic as a genus specific trait needs to be further tested. Qualitatively, the only clear craniological difference *Tarsius* exhibits in the orbital floor region specifically appears to be the presence of a superiorly directed posterior maxillary process. Like the superior orbital flange, this process may play a similar role at the posterior aspect of the globe, but its functional significance is unclear.

This view raises a question about the allocation and significance of *Teilhardina*: Is *Teilhardina* cladistically “omomyid,” or is it a more primitive tarsiform (or haplorhine) outside that group? The small size of *Teilhardina* eyes, which are approximately the size of a diurnal primate’s (Ni et al., 2004), which essentially means an anthropoid’s, may relate specifically to the development of a fovea centralis, that is, selection for a diurnal eye modified from the relatively large eye that typified the earliest euprimates (e.g., Martin and Ross, 2005). However, as tarsiers illustrate large eyeballs and foveae are not mutually exclusive characteristics, so the evolution of small eyes *per se* in ancestral haplorhines may need a separate explanation. Optics may be part of the reason (Kirk, 2004). Geometry and metabolism may also be factors. When built around a foveal spot, the retina, almost by definition, is designed around the qualities of a point (metaphorically) as opposed to a surface area, for example, the tapetal reflecting layer. Therefore, in the presence of a fovea natural selection can effectively shrink down the sheet-like retina, thus, reducing the volume of the eyeball. The imperative to do may arise from the high metabolic costs of developing and maintaining large eyes, including their expensive neurally derived tissues (Niven and Laughlin, 2008; see also Rosenberger, 2010).

Thus, ancestral haplorhines may have experienced physiological benefits by evolving smaller eyes, in addition to the ecological advantages gained by mastering the diurnal adaptive zone via the foveal system. By extension, maintaining a small eyeball may have been a crucial preadaptation to the origins of the fully enclosed eye socket unique to anthropoids, as the orbital fossa became retracted beneath the forebrain and the sizes of the frontal bone and zygomatic expanded to encircle it (see Rosenberger, 2006; Rosenberger et al. 2008).

The finding of very large eyes in *Strigorhysis* and a broad taxonomic sweep of other FTs (Table 2) also has implications for how we assess the adaptive role of eye size in the origins and differentiation of tarsiforms, including tarsiers. *Strigorhysis* is not, metaphorically, a

large-eyed tarsier: its teeth do not particularly resemble *Tarsius* overall. “Rugose, complex enamel” (Gunnell and Rose, 2002) on the crown surface is usually associated with nonshearing, nonpiercing functions, that is, a non-insectivorous diet, although a preference for soft-bodied insects cannot be ruled out. So, we have in *Strigorhysis* an adaptive combination that challenges the implicit generalization that very large eyeballs among nocturnal tarsii-forms ought to be associated with a hyper-predatory lifestyle that is the tarsier métier. In fact, tarsiers have assembled a large list of anatomical specializations of the head that make its unique style of extreme vertical clinging and leaping predation possible (Rosenberger, 2010). Their outlier status indicates we should expect other related genera, perhaps a robust radiation of them, occupying intervening adaptive zones—or other adaptive modalities within the same adaptive zone—predicated on mosaics involving features less derived than the tarsier condition, as well as local novelties. The extreme eye size of *Tarsius*—or proportions that are less exaggerated but somewhat comparable—may be a large-eyed FT retention that evolved in the context of a more generalized feeding regime. The cranial and postcranial evidence of some North American omomyids, such as *Shoshonius* and *Omomyys*, suggests that tarsier-level eyeball hypertrophy may have been under selection even as ancestral tarsiers were more like galagos than modern *Tarsius* in their positional behaviors (see Dagosto, 1993; Anemone and Covert, 2000; Rosenberger, 2010).

The Omomyid Higher Taxa. Although this study focuses on only one of many genera, it demonstrates an unanticipated—or rarely acknowledged—situation in which a dentition perceived to be unlike tarsiers is combined mosaically with hypertrophied eyes that would appear to approach (or match?) the tarsier condition. This same lesson can be drawn from the morphology of *Omomyys* and *Shoshonius*, though the dental differences are less trenchant. If the large eyes of these fossils are a synapomorphy shared exclusively with *Tarsius* among the living, and FTs underwent a morphological radiation as manifest in other body parts, it is reasonable to expect that tarsiers may not be an outlying sister-lineage to the rest of the Tarsiiformes. Rather, tarsiers may be nested phyletically among them (see Simons, 1972; Rosenberger, 1985; Beard et al., 1991; Beard and MacPhee, 1994; Dagosto et al., 1999), related to a subset that potentially encompasses a different dental gestalt.

This possibility has been obscured by an outmoded classification. The underlying taxonomy of anaptomorphines and omomyines was fashioned in the late 1800s as purely classificatory units rather than phylogenetic concepts, then as today overwhelmingly based on dental remains. Several criteria seem to have been used, in the main, for organizing the genera. One is the gap they exhibit with respect to modern tarsiers, which the craniofacial information now begins to narrow. Another relies on the coherence afforded by a common continental geography, which is also undermined by discovering faunal continuity on the generic level with Asia and Eurasia during the early Eocene (Beard, 1998; Ni et al., 2004). Each of these working principles assumes or is driven by the expectation of a within-group uniformity balanced against discontinuity, the latter specifically with respect

to tarsiers. That this model is an oversimplification is illuminated by two examples stressing cranial morphology. One entails the small-eyed *Teilhardina* and the other involves the large-eyed *Strigorhysis*. Both are currently attributed to Family Anaptomorhinae, Tribe Anaptomorhini, as Gunnell and Rose (2002) follow their predecessors (e.g., Gazin, 1958; Szalay, 1976) in defining these two higher taxa almost entirely by dental characters. But how well does the dental morphology, or its assessment, track phylogenetics? The present study suggests the heavy reliance on teeth, which has been inevitable, has also been problematic.

In a comparable way, dental morphology seems to have driven views of microchoerine systematics (see more below), especially concerning *Necrolemur* and *Microchoerus*, even though the cheek teeth of five genera allocated the this subfamily are not morphologically uniform, and it has not been demonstrated that the group is monophyletic. Both *Necrolemur* and *Microchoerus* are known to exhibit one (tarsal) or more (tarsal and tibiofibula) of the major derived postcranial complexes that are otherwise considered unique to *Tarsius* (e.g., Gebo, 1988; Dagosto, 1993; Dagosto and Gebo, 1994; Dagosto et al., 1999; Anemone and Covert, 2000), in addition to having at least moderately enlarged eyes. However, most workers prefer to see the hindlimb elements as parallelisms (e.g., Dagosto and Gebo, 1994; Anemone and Covert, 2000), distinguishing microchoerines from the postcranially primitive NAFTas but not as homologous synapomorphies linking them to *Tarsius*.

The pertinent lesson drawn from the cranial morphology as outlined here would see things differently, that one phenetically contrasting anatomical complex—head, teeth, legs, or feet—should not be exclusionary when assessing the affinities of microchoerines and *Tarsius*. *Necrolemur* and *Microchoerus*, which are probably sister-genera noteworthy for having blocky quadrate upper molars and orbits less enlarged than a tarsier’s, may simply represent a lineage that benefited by secondarily moving into a feeding niche that separated them ecologically from the potentially coexisting, larger-eyed, and probably more predaceous *Pseudoloris* and *Nannopithec*. Although we commonly assume (e.g., Rosenberger et al., 2008) a less-than-tarsier optic hypertrophy is either a more primitive state or a parallelism, other hypotheses are also expedient.

Very large eyes involve proportionately large metabolic costs (see Niven and Laughlin, 2008; Rosenberger, 2010). One can imagine the *Necrolemur-Microchoerus* lineage advantageously reducing this overhead by shifting from an exclusively nocturnal cycle (one assumes) to one that is more cathemeral. Indeed, the co-occurrence of highly advanced vertical clinging and leaping behaviors with frugivore-like teeth seems an anomalous combination. If *Necrolemur-Microchoerus* were predominantly frugivorous initially, why evolve highly advanced VCL features as an adaptive complement? The combination of advanced VCL locomotion and blunt, quadrate molars in a medium-sized FT suggests this small clade shifted its morphology and niche from something that would have been more predaceous and tarsier-like. The possibility that their dentitions imply predation on softer-bodied prey is also possible, but it would still seem paradoxical that the last common ancestor of *Necrolemur-Microchoerus* shifted under selection to evolve a highly unusual tarsier-like hindlimb for vastly different target foods and foraging methods.

In other words, we cannot discount the possibility that *Tarsius*, with all its evident genus-level apomorphies, is but one member of an adaptive radiation that differentiated along several dimensions from within a fairly broad insectivorous-frugivorous, nocturnal-cathemeral adaptive zone. If the tarsier is not a singular outlying lineage but nested within Tarsiiformes, its closest relatives, with less modified features, need not have been hyperpredaceous. It follows from this that it may be more valuable heuristically to organize the systematics of the tarsiiform higher taxa along ecophylogenetic lines, beginning with the grouping of all forms having hypertrophic orbits and synapomorphic postcranial features into the same family (Tarsiidae), and separating them from other FTs under a different family rubric.

The Tarsier-Anthropoid Hypothesis. This analysis also has important implications for the notion that *Tarsius* is more closely related to anthropoids than to any FT, a view that has been pressed for about 30 years and still has advocates (e.g., Cartmill and Kay, 1978; Cartmill, 1980; Kay and Williams, 1994; Ross et al., 1998; Bajapai et al., 2008). It speaks to two foundational aspects of this proposition, the features suggested as derived homologies shared with anthropoids and the strength of a counter proposal as to the tarsier's phylogenetic affinities. The latter point has already been elaborated throughout this treatment, but it is worth framing the basic thesis in probabilistic, parsimonious terms. As the number of cases rise among FTs, especially among dentally and postcranially divergent FT groups, of inferred or confirmed examples of hypertrophic eyeballs, the likelihood increases that *Tarsius* is cladistically related to one of the assemblages of fossils we now classify within Omomyidae *sensu* Szalay, 1976. *Tarsius* may thus represent nothing but a highly derived and adaptively specialized genus of that same adaptive radiation. By corollary, the likelihood that *Tarsius* is more closely related to anthropoids diminishes proportionately.

Regarding homologies, the crucial point of (nonbasiscranial) resemblance held by advocates of the tarsier-anthropoid school of thought to be the principle synapomorphy shared by anthropoids and *Tarsius* is the so-called postorbital septum. Tarsiers are the only tarsiiforms that have a structure in the posterior compartment of the orbital fossa that is called a partial postorbital septum, whereas a fully closed off orbit, relative to the temporal fossae, is a universal trait among anthropoids. There are a variety of objections to this assessment (e.g., Simons and Rasmussen, 1989; Rosenberger et al., 2008), and I maintain these features are convergent. One flaw that has perhaps not been put forth adequately is that the argument of homology treats the tarsier septum (including its alisphenoid part) in morphological isolation rather than a component integrated with other very specialized parts of the orbital fossa *per se*. The present analysis (see also Rosenberger, 2010) shows there are many correlated elements comprising the tarsier's unusual orbital fossa. As many as eight FT genera (nine, if one counts the *Hemiacodon* frontal) preserve all or most of them as a complex but none of these features, other than the questionable "septum," are character states found in anthropoids. New ontogenetic information (Jeffery et al., 2007) amply confirms the unusual nature of the tarsier postorbitum as an ontogenetic slave to hyper-

trophic eyeball growth. Undoubtedly, the rest of the fossa will be found to behave in much the same way. The most parsimonious explanation of this distribution is that *Tarsius* inherited almost all of these features from a FT and only added two additional traits to the complex, both localized in the form of an osseous backing behind the eyeball, that is, the "postorbital septum" and the posterior maxillary process. It is far less economical to maintain that the septum of anthropoids and tarsiers are homologous, and that *Tarsius* and a host of FTs evolved precisely the same set of complex anatomical solutions to enlarging the orbital fossa.

CONCLUSIONS

Perhaps because tarsiers—one of the primates' farthest anatomical outliers—occupy such an extreme and narrow ecological niche as the only fully predaceous primate, we appear to have underestimated the possibility that there was a broad radiation of fossils quite closely related to tarsiers but without a precisely comparable commitment to this lifestyle—fossils that might have less monstrous eyeballs, or less spindly legs and shorter hindfeet, or less pointy teeth, or various combinations of the likely extremes. Some of the difficulties in seeing this are a consequence of the Tarsiiformes being organized in a heuristically antiquated taxonomic scheme, a status that continues to be hampered as well by a limited variety of morphological evidence, which has led to a heavy reliance on interpreting the abundant cheek teeth. Like cercopithecoids, perhaps the molars of these small-bodied, largely predaceous tarsiiforms are canalized, actually varying little—and are thus less informative about phylogeny at our current power of resolution—less than one might expect in a radiation estimated to comprise an enormous 30–40 genera. By contrast, with their varied sizes, diets, and life histories, the molars exhibited by the 16 or so genera each of modern strepsirhines and platyrrhines are spectacularly more prolific structurally, and evidently more easily amenable to phylogeny reconstruction.

Strigorhysis is the fourth North American FT genus demonstrating an enlarged orbital fossa, thus an enlarged eyeball. Seven to nine of the Eocene FT genera, occupying both Europe and North America and involving each of the three recognized subfamilies appear to have enlarged orbits, and there are likely to be others. All exhibit elements of the same derived anatomical modifications of the facial skeleton that support ocular hypertrophy in *Tarsius*, indicating this is a common homologous pattern that may be universal in a greater tarsier clade. One early fossil attributed to the omomyid group, *Teilhardina*, has relatively small orbits, which raises questions about its taxonomic allocation within Tarsiiformes if eyeball hypertrophy is as widely distributed among these Eocene omomyids as expected. A similar query involves *Rooneyia*, another small-eyed form whose standing as an omomyid and tarsiiform has already been called into question. A reclassification may be in order for any other small-eyed forms that might be found among the fossils now allocated to Omomyidae. At first glance this appears to be a narrow taxonomic question only, but it may be fruitful to ask if *Teilhardina* might belong to a nontarsiiform haplorhine lineage.

The array of dental and postcranial morphologies found among the large-eyed FTs indicates that tarsier-like eyeball hypertrophy may not be an exclusive, narrow-niche, hyperpredatory adaptation. Although their eyeballs are all large by comparison with anthropoids, the range of eye sizes among FTs exhibit also suggests variations in activity rhythms along the nocturnal-diurnal continuum. For example, the forms having the most derived, tarsier-like lower limbs, one known to have a fused tibio-fibula and both with radically lengthened tarsals, are *Necrolemur* and *Microchoerus*. Typically considered as FTs only distantly related to *Tarsius*, they may just as easily be seen as diverging from a common ancestor shared with *Tarsius* after differentiation of the larger-eyed NAFTas *Shoshonius* and *Omomys*, which lack these hindlimb specializations. European *Necrolemur* and *Microchoerus* may have departed a hyperpredaceous morphotype condition to occupy a different feeding niche, possibly more cathemeral and predicated on a larger body-size niche dimension. *Pseudoloris*, historically classified with *Necrolemur* and *Microchoerus*, appears to be even more tarsier-like in facial and dental morphology; its postcranium is unknown, however. This means *Shoshonius* and *Omomys* may have simply retained an ancestral, less extreme form of VCL locomotion while also maintaining the ancestral oversized eyes of the tarsier clade.

It would be a mistake to perpetuate the neontological perception that *Tarsius*, the modern morphological outlier, is also the phylogenetic outcast of a radiation that flourished during the Eocene and clearly generated adaptive variety. The demonstrable, profoundly derived craniological continuity between *Tarsius* and a burgeoning intercontinental group of FTs indicates tarsier relatives are found among them. If correct, this would appear to be an insurmountable objection to the tarsier-anthropoid hypothesis, which holds that tarsiers are most closely related to anthropoids (e.g., Williams et al., 2010).

From a morphological standpoint, the most illuminating working hypotheses concerning the course of primate evolution have always been predicated on remarkable adaptations or structural innovations, cardinal characters, even when the latter's functions and biological roles are difficult to discern or the anatomy is difficult to demonstrate satisfactorily in fossils—upright bipedalism, bilophodonty, toothcombs, prehensile tails, the postorbital bar, hemochorial placenta, strepsirhine and haplorhine noses, and so forth. Arguably, most or all of these morphological complexes are coincident with the opening of a new adaptive zone or the differentiation of a single clade into a radiation. The hypertrophic eyeballs of tarsiforms are another such feature. Whatever lifestyle shift it signals—acutely sensitive spatial mapping and prey detection under nocturnal conditions is as good an explanation as any—this seems to have preceded radicalization of the vertical clinging and leaping behaviors shared in common by a subset of the tarsiform radiation. Contrary to most expectations, orbital hypertrophy may have kicked off the successful parade of FTs, and that is the reason for the evidently widespread occurrence of this remarkable trait among them.

To summarize:

1. Current taxonomic models, including family-level classifications, do not adequately reflect the well corroborated hypothesis that tarsiers are phylogenetically closely related to a subset of FTs. *Strigorhysis* is among roughly seven to nine genera of large-eyed Laurasian tarsiforms monophyletically related to *Tarsius*.
2. Fossil currently seen as extinct tarsiforms differentiated into an array of ecological niches defined by variations in diet, locomotion, and activity rhythms within the obligate predatory adaptive zone exemplified today only in the most radically modified genus of this adaptive radiation, *Tarsius*.
3. Some relatively small-eyed “tarsiforms,” such as *Teilhardina*, may fall outside this monophyletic group, which raises questions about their phylogenetic position within Haplorhini. Eyeball hypertrophy preceded the evolution of advanced postcranial traits such as tibio-fibular fusion and tarsal elongation among the tarsier's closest relatives. This demonstrates a shift from galago-like pursuit foraging to the ambush prey capture techniques of tarsiers, predicated on extreme vertical clinging and leaping adaptations of the limbs and skull.
4. The tarsier-anthropoid cladistic model, which relegates FTs to a more basal haplorhine branch, has been independently falsified on multiple anatomical grounds and is untenable. By corollary, the credibility of data and methods that continue to generate this result in studies of primate interrelationships is equally subject to doubt and demands greater scrutiny.

ACKNOWLEDGMENTS

Among the individuals the author thanks are colleagues Ken Rose, Xijun Ni, Chris Beard, and Siobhán Cooke for access to specimens and/or helpful conversation. Sai Man Wong and Xijun Ni helped greatly with the graphic visualizations. The CT work was kindly done by Luis Cardosa and his students at CCNY. The author is also indebted to several institutions for assisting with this research, especially: American Museum of Natural History; United States National Museum; Carnegie Museum of Natural History; San Diego Natural History Museum; Museum of Paleontology, University of California, Berkeley; Naturhistorisches Museum, Basel; Natural History Museum, London; Muséum national d'Histoire naturelle, Paris.

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