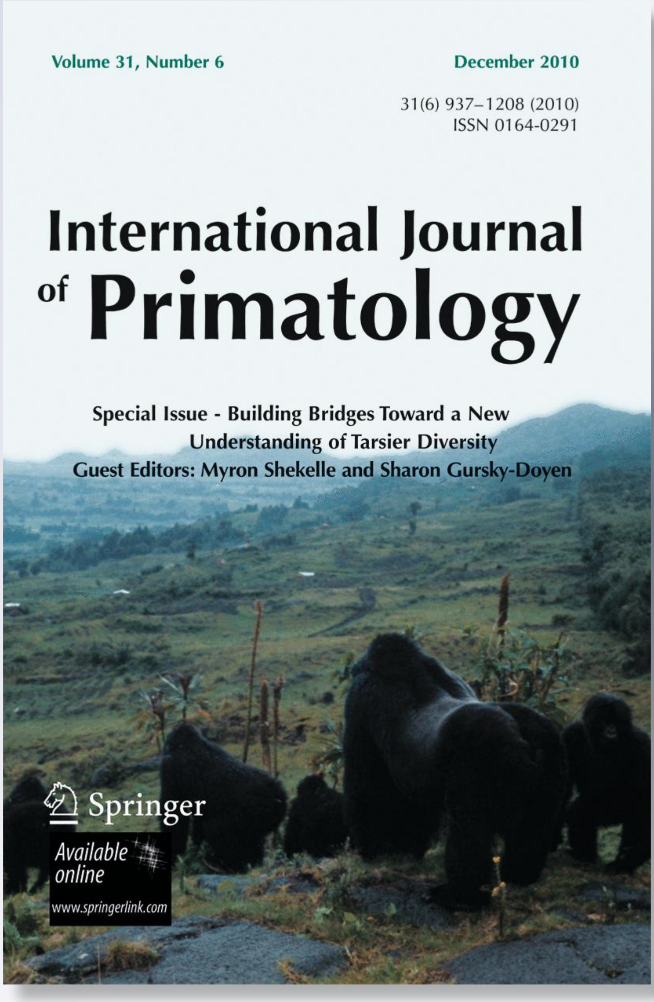
The Skull of Tarsius: Functional Morphology, Eyeballs, and the Nonpursuit Predatory Lifestyle

International Journal of Primatology
The Official Journal of the International Primatological Society

ISSN 0164-0291
Volume 31
Number 6

Int J Primatol (2010)
31:1032-1054
DOI 10.1007/s10764-010-9447-x



Springer

Int J Primatol (2010) 31:1032–1054
DOI 10.1007/s10764-010-9447-x

The Skull of *Tarsius*: Functional Morphology, Eyeballs, and the Nonpursuit Predatory Lifestyle

Alfred L. Rosenberger

Received: 6 May 2009 / Accepted: 28 January 2010 /

Abstract Little is known about the impact of enormous eyeballs on the tarsier's head, apart from facial morphology. I used a biomechanical analysis to compare the cranium of *Tarsius* with the Eocene fossil *Necrolemur*, a moderately large-eyed surrogate for ancestral tarsiid cranial morphology. Eyeball hypertrophy has radically influenced the neurocranium and basicranium, driving the evolution of such derived features as recession of orbital fossae, ectopically located eyeballs, uptilted brain and rounded braincase, anteroventrally shifted foramen magnum, enlarged and horizontally leveled nuchal plane, laterally displaced and narrowed tympanic cavities, and shortened external auditory tubes. The gestalt is an adaptation to efficient orthograde head carriage, balanced head-turning movements, and spatial packaging of cranial components, responses to an extreme loading regimen in which the eyes, with a mass approximating twice the bulk of the brain, profoundly eccentrically load the skull. Specializations of the retina and cortex suggest tarsiers have an acutely developed spatial sense, especially adept at detecting and mapping motion. Spanning several anatomical systems, this configuration represents an extreme form of vertical clinging and leaping (XVCL) geared for noiseless, nonpursuit predation, an energy-minimizing procurement strategy that may be a trade-off for relying on metabolically expensive, outsized eyeballs, maintained by a highly nutritious, super-specialized, animalivorous food source. A more varied galago-like locomotor profile and

---

A. L. Rosenberger (✉)
Department of Anthropology and Archaeology , Brooklyn College,
The City University of New York CUNY,
Brooklyn, NY 11210, USA
e-mail: alfredr@brooklyn.cuny.edu

A. L. Rosenberger
The Graduate Center, The City University of New York, New York, NY, USA

A. L. Rosenberger
New York Consortium in Primatology (NYCEP), New York, NY, USA

A. L. Rosenberger
Department of Mammalogy, The American Museum of Natural History, New York, NY 10024, USA

foraging habit was common among fossil tarsiiforms and preadaptive to this lifestyle, partly by canalizing the forward orientation of the tarsier's predatory gaze in VCL mode. Tarsier ecomorphology evolved to minimize the costs of being extraordinarily "top heavy," carrying a heavy load that is roughly equivalent to 3 brains.

Keywords Adaptation · Biomechanics · Eyes · Locomotion · Predation · Primates · Skull · Tarsiers

Introduction

The skull of *Tarsius* is ultramodified. Various researchers have discussed aspects of its morphology as local responses, primarily in the face, to accommodate hypertrophic eyeballs. Examples include compression of the nasal fossa and appression of the medial orbital walls (Cartmill 1972; Cave 1967; Starck 1984); development of an olfactory tube carrying nerves to the nose over the extensive, sheet-like interorbital septum (Cartmill 1972; Starck 1975); downward tilt of the muzzle relative to the cranial base (Biegert 1963; Spatz 1969); formation of a partial postorbital plate or septum (Cartmill 1980; Hershkovitz 1977; Rosenberger *et al.* 2008); postnatal development of circumorbital flanges (Cartmill 1980; Collins *et al.* 2005; Rosenberger *et al*. 2008; Simons and Russell, 1960); and alterations of the craniofacial junction and the morphology of the choanae (Rosenberger 1985; Rosenberger *et al*. 2008). Less attention has been given to the biomechanical consequences of eyeball hypertrophy per se (Fig. 1) as a factor in skull design overall, its possible influence on head posture and positional behavior, and how these relationships may correspond with the evolution of the tarsier's unique predatory lifestyle. Here I address these issues by first presenting a simple biomechanical model that illustrates ways in which the tarsier skull, especially the braincase, has been redesigned from a more primitive morphology as a functional-adaptive solution to the evolution of huge eyes. Lest it be forgotten, while we tend to think of the famed tarsier eye —relatively the largest of all vertebrates— as a unitary

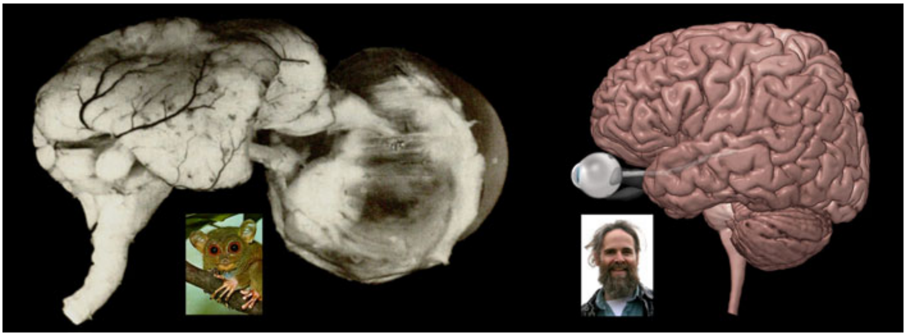


Fig. 1 A true-to-scale comparison of tarsier and human eye:brain proportions, with brains brought to the same length. The tarsier preparation is after Sprankel (1965). The human model was done by Mark Dow (University of Oregon), based on a CT scan of a human cadaver.

structure, there are in fact 2 of them loading the skull; thus the consequences are considerable. I also attempt a synthesis of recent information bearing on tarsier eyes in an effort to advance our thinking on a more fundamental question: Why are tarsier eyes so large in the first place?

The approach used in the first part of the article builds on modeling biomechanics and anatomical transformations based on accurate lateral view illustrations of skulls as well as direct study of the morphology. Theoretically modeling cranial functional morphology is a time-tested research strategy that has yielded numerous insights into the evolution of the mammalian skull. Weishampel (1993) gives many examples, commenting (p. 338) that "….modeling approaches yield both accurate and heuristic information about the operation of vertebrate skulls." Plotnick and Baumiller (2000) refer to the application of these approaches to fossils as "paleobiomechanics," wherein an analysis strives to identify what a structural design is capable of doing efficiently, according to mechanical principles. One of the most influential studies of primates utilizing a comparable method was Cartmill's (1974) comparative functional analysis of aye-aye facial morphology.

I used *Necrolemur* as an exemplar of a more primitive tarsiiform skull from which a tarsier-like pattern can be derived. Its orbits are clearly not as enlarged as in *Tarsius* (Martin 1990), and the only evident cranial feature that appears to be autapomophic relative to tarsiers is not material to the analysis, the hypertrophic petromastoid region (Szalay 1976). There is phylogenetic justification that makes *Necrolemur* appropriate for this purpose as well for, while its precise affinities are still unresolved, the fossil shares a host of homologous derived features with *Tarsius* in the skull and postcranium (Beard and MacPhee 1994; Beard *et al.* 1991; Dagosto *et al.* 1999; Rosenberger 1985, and references cited therein) which, I would argue (Rosenberger *et al.* 2008), justifies placing it within a monophyletic tarsiid clade that includes tarsiers and a number of Eocene genera frequently allocated to Omomyidae (including Microchoerinae).

Materials and Methods

I used free body diagrams to examine and illustrate the pertinent forces acting on the skull (excluding gravity, musculature, other soft tissue mass, etc.). One set of variables employed to model the conditions of static equilibrium in *Tarsius* and *Necrolemur* was based on mass estimates of the eyes and brain drawn from the literature (Table I). Other measurements were based on accurate, scaled lateral view drawings of the skulls made by Radinsky (1967, 1970), from which measurements of moment arms were derived graphically (Fig. 2). Radinsky's studies focused on brain shape and skull form, and his illustrations provided outlines of the brains based on his extensive research on endocasts. This approach was deemed appropriate for the purpose at hand because the moment arms of the eyeball and brain rely on determining the center of mass of each structure. Regarding the eye, this information will always be impossible to obtain directly for *Necrolemur*. For the eye of *Tarsius* and the brains of both genera, better estimates may prove feasible in the future using computed tomography (CT) scans. I tested the accuracy of Radinsky's illustrations as lateral profiles of the skulls by comparing their proportions to measurements

Table I Measurements of the moment arms, dimensionless variables, used in each of the free body diagram models and of mass estimates, in cubic millimeters, of the brain and eyeball

	Model	M_e	M_b	M_n	F_e	F_b	Fn	Major features and source variables used in the models
Tarsius	1	33	15	15	2.7	2.8	14.7	Actual tarsiers, wet specimens
	2	33	15	15	2.6	3	14.3	Actual tarsiers, osteology specimens
	3	33	15	15	1.8	2.9	10.7	Actual tarsiers, wet, with minimal eye size
	4	33	15	15	3.1	2.9	16.3	Actual tarsiers, wet, with maximal eye size
	Average				2.6	2.9	14	
Necrolemur	1	35	30	10	1.8	4.1	25	*Necrolemur* at 2/3 tarsier eye size
	2	35	30	10	1.8	2.7	20.7	*Necrolemur* with minimal brain size
	3	35	30	10	0.5	4.1	16.1	*Necrolemur* with minimal eye size
	4	35	30	10	0.5	2.7	11.8	*Necrolemur* with minimal eye and brain size
	5	35	30	10	2.7	2.8	27.3	*Necrolemur* with tarsier eye and brain size
	6	35	30	10	2.7	4.1	31.3	*Necrolemur* with tarsier eye and average *Necrolemur* brain size
	Average				1.7	3.4	22	

See text and Fig. 2 for definitions and additional explanation

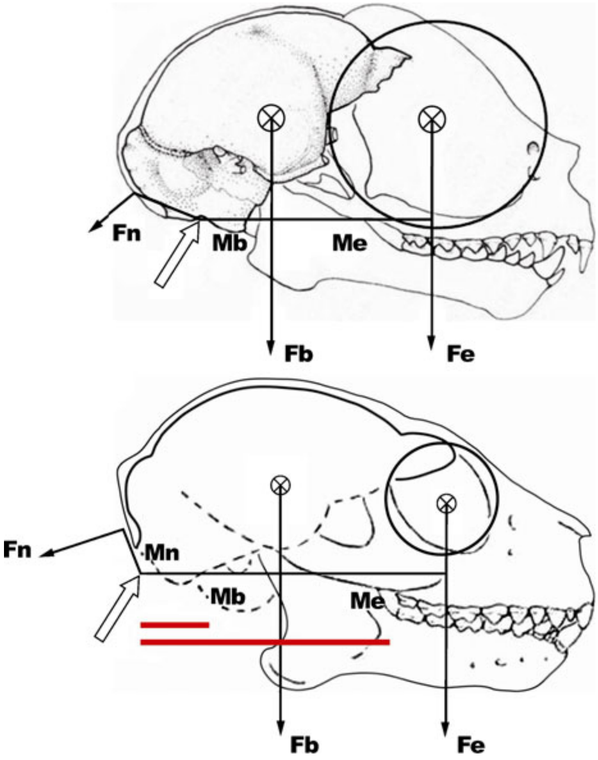


Fig. 2 Free body diagrams of static equilibrium conditions for *Tarsius* **(above)** and *Necrolemur* **(below)**. Abbreviations and other explanations are given in the text. Tilting the brain upward and drawing the eyeballs posteriorly shifts the centers of mass closer to the foramen magnum and occipital condyles in tarsiers, improving balance of the skull. The two red lines are the scaled, dimensionless moment arms of the brain (above) and eyeballs (below) in *Tarsius*, showing their reduction relative to the conditions in *Necrolemur*. Large arrows at the center of the foramen magnum are taken as the approximate center of rotation of the skull on the vertebral column (see text).

taken on casts of a tarsier (from the Wenner-Gren series, species unknown) and *Necrolemur antiquus* (Montaubaun 5), neither one used by Radinsky. The ratio of toothrow length to maximum skull length for the 4 are as follows: Fig. 2 (from Radinsky): *Tarsius*, 0.40; *Necrolemur*, 0.41; casts in hand: *Tarsius*, 0.39; *Necrolemur*, 0.41.

For each, the moment arms represent dimensionless units, calculated by taking the length of line segments, measured in Photoshop, and converting each to a ratio against maximum skull length × 100. The center of mass of the brain was calculated via Image J, by finding the geometric center of its outline. The center of mass of the eye was taken as the center of a sphere whose fit into the orbital fossae was approximated by eye. The center of rotation of the skull was assumed to be the midpoint of the plane of the foramen magnum, for convenience and because it was deemed a reliably fixable point on Radinsky's *Necrolemur* illustration. The placement of the vector representing the nuchal muscles is simply at the midpoint of the nuchal plane, with a perpendicular drawn from the plane to approximate their line of action.

To compensate for the fact that our knowledge of *Necrolemur* remains incomplete and must be conjectural, and because the parameters describing eye size and brain size in *Tarsius* varies in the literature owing to differences in the measurement techniques used, to individual and ontogenetic variability, and to taxonomic differences among the samples, I provide several permutations of the models describing both genera. Several come directly from weights of fluid preserved specimens, others from osteological measurements. For comparability, mass values are presented in cubic centimeters, converted from diameter measurements in cases where eye size was determined by the span of the external orbital aperture. In addition, I assume the eyeballs of tarsiers and *Necrolemur* are spherical, even though in tarsiers they are anteroposteriorly elongate and quasi-tubular (Castenholtz 1984).

The equation for static equilibrium of the basic model is:

$$F_\mathrm{n} = [(2F_\mathrm{e}{*}M_\mathrm{e}) + (F_\mathrm{b}{*}M_\mathrm{b})]/M_\mathrm{n},$$

which in solving was rounded to 1 decimal place. The conventions are: F_e, F_b, F_n: forces (mass) acting on the paired eyeballs (F_e), brain (F_b), and nuchal muscles (F_n); M_e, M_b, M_n: moment arms of the eyeballs (M_e), brain (M_b), and nuchal muscles (M_n). Source measurements and summaries of the models are given in Table I and further explained below.

Tarsius

Model 1 F_e and F_b, using the average volumes of 3 individuals representing 2 species (Spatz 1968), directly measured from wet specimens.

Model 2 F_e, with eye volume calculated from external orbital aperture diameter measurements of 3 skulls (Kay and Kirk 2000); F_b, with brain volume averaged from the mixed species sample of Martin (1990).

Models 3 and 4 Fe, with volumes calculated from minimum and maximum diameters of the eyeball (Collins *et al.* 2005).

Necrolemur

Model 1 F_e, with eye volume assumed to be 0.66 tarsier volume; F_b, using as brain volume the average of 3 estimates (Jerison 1979; Martin 1990; Radinsky 1977).
Model 2 F_b, with brain volume given the lowest published value (Gurche 1982, cited by Martin 1990).
Model 3 Fe, with eye volume calculated from the orbital diameters of 4 skulls (Kay and Kirk 2000).
Model 5 F_e and F_b assume an eye and brain volume equivalent to a tarsier, using *Tarsius* Model 1 values.
Model 6 F_e and F_b assume a tarsier eye volume and a *Necrolemur* brain volume using *Tarsius* Model 1 and *Necrolemur* Model 1 values.

Results

Morphology and Cranial Biomechanics: Head Carriage

Anatomically, apart from sheer differences in orbit/eye size, the scaled lateral views of *Tarsius* and *Necrolemur* (Fig. 2) show important disparities in the position of the orbit relative to the braincase and the foramen magnum, the inclination of the craniocaudal axis of the brain relative to the long axis of the skull or toothrow, and the size and inclination of the nuchal plane. Anatomically, the common denominator here is the disposition of the brain. The uptilted set of the brain reduces the distance between its center of mass and the craniovertebral joint and enables the orbits to retreat posteriorly, and thus occupy a position partly below the forebrain. Resetting the position of the braincase also corresponds with a shift of the nuchal plane into a more horizontal orientation. The consequences of this redesign are a relatively shortened moment arm for the eyeballs and the brain and a relatively lengthened moment arm for the nuchal muscles. The theoretical advantage of this pattern is that in the neutral position less muscular force would be needed to maintain head balance in *Tarsius* by comparison with *Necrolemur*, all else being equal. The evolutionary explanation for the changes toward the derived tarsier condition is that the head of *Tarsius* has evolved accommodative adjustments for efficient balance as a response to selection for hypertrophic eyeballs.

The free body analysis provides estimates of the mechanical advantage of the morphological design under various loading conditions (Table I). I have used the summed weight of both eyeballs in the calculations, as this is more reflective of the true loading conditions. The moment arms of the eyeballs and brain are smaller in *Tarsius* than in *Necrolemur*, although the magnitude of the reduction in tarsiers appears less impressive because this is masked by the sheer enormity of the eyes, which displaces the center of mass rostrally. Without retracting the orbits posteriorly into a subcerebral position, M_e would increase in proportion to the increase in the diameter of the globe. Anterior shift of the foramen magnum is chiefly responsible for the tarsier's increase in the moment arm of the nuchal muscles. The models show that the amount of nuchal force (F_n) required to maintain equilibrium is basically the same in *Tarsius* if either wet measurements or osteological proxies of eyeball size are used, which helps justify applying these principles to the fossils. However, there is a notable range of differences in this measure if eye size is set to the minimum or maximum values presented in the literature. For illustrative purposes, I take the rounded average of all four measures, 14, to represent the genus.

Necrolemur presents a contrasting picture. In 3 of the 4 models that substitute different estimates of eye or orbit volume, F_n is substantially higher. Only in Model 4, which sets *Necrolemur* eyes and brains at their minimal values, does the fossil approximate the tarsier pattern. The highest estimates, in Models 5 and 6, where F_n is *ca.* 1.9–2.2 times the magnitude of tarsier's average, occurs when *Necrolemu*r eyeballs are set to be either 2/3 or the equivalent mass of a tarsier eye. These are anatomical impossibilities, but they highlight the dramatic biomechanical differences in skull design between these taxa. In other words, they illustrate how relatively inefficient the tarsier skull would be in controlling pitch of the head if the primitive cranial morphology had not been repackaged to accommodate the added weight of hypertrophic eyes.

Basicranial Morphology: Lateral Balance and Head Turning

Many of the differences in the basicranial and ear region morphology of *Tarsius* and *Necrolemur* may be attributed to biomechanical and packaging adjustments correlating with eyeball hypertrophy, which are linked with body posture well. A basicranial view (Fig. 3) clearly shows that the foramen magnum is considerably more rostrad in tarsiers than in *Necrolemur*. When brought to the same cranial length, the middle ear compartments of the bullae and the external auditory meati of both forms are on the same horizon. However, in *Tarsius* about half of the space of

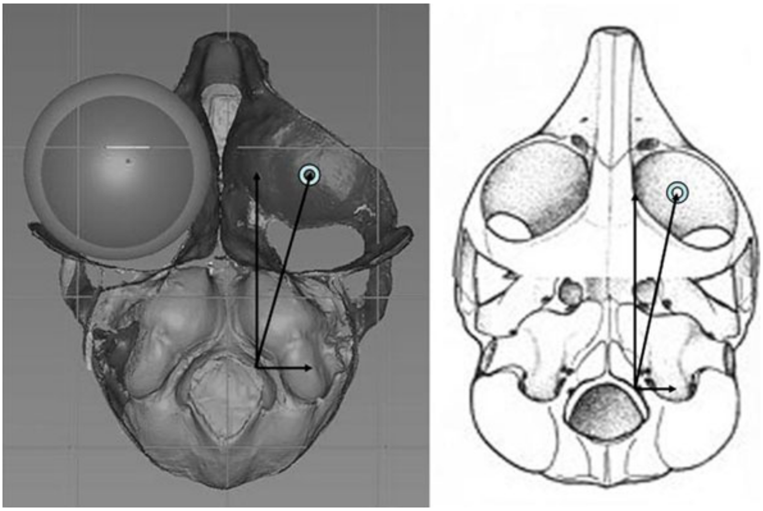


Fig. 3 A composite dorsal-ventral view of *Tarsius* **(left)** and *Necrolemur* **(right)** showing the spatial relationships and organization of the basicranium and face. Perpendicular vectors are the resultant forces in the horizontal plane at the occipital condyle, generated by the load of an eyeball. The larger horizontal vector in *Tarsius* counteracts the tendency to tilt the skull by rolling it to the side, owing to the lateral displacement of the center of mass of the enlarged eyeball relative to the midline. (Modified from Rosenberger *et al*. 2008 and Szalay 1976).

the foramen magnum falls anterior to a tangent across the posterior poles of the bullae, whereas most of the foramen magnum is posterior to this line in *Necrolemur*. The literature provides limited quantification of the anteroposterior location of the foramen magnum of *Tarsius*. Without offering tabulations, Schultz (1955) cited values that showed tarsiers have a markedly anterior foramen magnum, distinctly different from modern strepsirhines. Shultz noted *Tarsius* is most comparable to the short-faced, larger-brained anthropoid *Cebus capucinus* in the index he devised to measure position. The relative size of the foramen also differs, with the tarsier's being conspicuously larger than that of *Necrolemur*. Martin (1990), who plotted foramen magnum area against cranial capacity, showed that *Necrolemur* had a relatively small foramen magnum when examined this way. He also showed that relative to body weight, *Tarsius* appears to have at least a slightly enlarged foramen magnum, plotting just above the regression line for living strepsirhines.

As indicated, this shift of the foramen magnum corresponds with an increase in the moment arm of the nuchal muscles while also decreasing the moment arms of the eyeballs and brain. With the foramen magnum of *Tarsius* located anteroventrally, the nuchal plane is both enlarged and reoriented, having moved, more or less, from the coronal plane and into the transverse plane of the skull (Fig. 2). Thus the occipital condyles face ventrally rather than caudally, as in *Necrolemur*. The tarsier condition corresponds with the orthograde body posture of a habitual clinger, whereas the morphology of *Necrolemur* reflects a skull that is designed to be cantilevered at the end of a more pronograde vertebral column, although this does not obviate facultative vertical clinging and leaping (VCL) body and head postures. A fully horizontal disposition of the nuchal plane would tend to reorient the line of action of the nuchal and suboccipital muscles which, by analogy with the human, may increase their efficiency in a nonquadrupedal manner of head carriage. With the nuchal region oriented more nearly coplanar with the horizontal plane and optical axis, the tarsier condition may also advantage the suboccipital muscles in maintaining stability at the craniovertebral joint and efficient control of head turning movements.

By comparison with *Necrolemur*, the larger foramen magnum of tarsiers corresponds with a wider transverse spread of the occipital condyles. This "wide wheelbase" arrangement increases the head's lateral stability via the atlanto-occipital joints. Because the center of mass of an eyeball moves further from the midline as its volume increases, each imparts a moment that tends to roll the head laterally out of the horizontal plane, in proportion to eyeball diameter (Fig. 3). This lateral moment is minimized anteriorly by adjusting the location of the eyeballs: appression of the medial orbital walls places the centroid of the eyeballs as close to the midline as is possible. Posteriorly, the eccentricity of this load is minimized by the lateral shift of the condyles, which reduces the moment to roll the head. A "narrow wheelbase" would increase the magnitude of the moment to roll the head.

The lateral roll of the head to one side is also resisted by the tension of the contralateral suboccipital muscles acting on the opposite side. The mechanical advantage of this system can be enhanced by lengthening the transverse processes of the atlas, thus augmenting the muscles' moment arms. Ankel-Simons (1999) pointed out that the atlas of *Tarsius* is relatively the largest of all primates. This corresponds with the enlarged f. magnum, laterally situated condyles, and an enhanced leverage of the suboccipitals inserting on the transverse processes.

The forward location of the f. magnum in *Tarsius* is also important for head stability during yawing motions, i.e., rotating right and left. As the head turning model illustrates (Fig. 4), for the same angular displacement of the face, the anteroposterior and transverse resultant components of the moment acting on the pivot are small when the latter is located closer to the geometric center of the skull. In the generalized tarsier model, the differential between these components is minimized throughout the range of excursion, making head turning a relatively simple act of balance. A large portion of the tarsier's ability to swivel the head through a great angle is probably associated with the biomechanical efficiencies of this pattern, working in concert with a twisting cervical vertebral column.

When the craniovertebral pivot is posterior, as in *Necrolemur*, the component forces are relatively larger, tending to pitch and roll the skull downward, and especially to the side at larger excursion angles. A posterior f. magnum, therefore, places constraints on the evolution of eyeball hypertrophy. In the case of the cantilevered skull of *Necrolemur*, which has a vertical and frequently rugose nuchal plane, and a high and typically crested superior nuchal line, the nuchal muscles evidently play an important role in head balance during quadrupedal positional behaviors. Though this is generally the case in mammals, as a haplorhine *Necrolemur* has a rather foreshortened face, so less of an inherently forward, snouty mass to balance. But *Necrolemur* is also unusual among early haplorhines in having an enlarged petromastoid (Szalay 1976), which may have biomechanical significance. The latter presumably serves, in part, as an attachment site for the cleidomastoid muscles. Perhaps this development signals an enlargement of these prevertebral muscles as a complementary adaptation to help balance the head during VCL postures when the nuchal muscles have less leverage against the craniovertebral pivot, especially if the head is somewhat overbalanced anteriorly and laterally by the mass of moderately enlarged eyes and the primitively long moment arms of the brain and eyeballs.

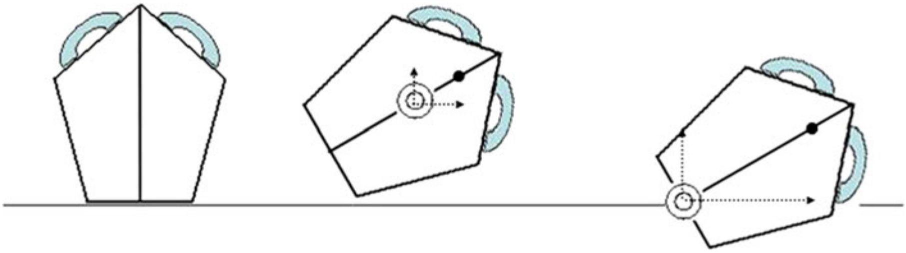


Fig. 4 A model illustrating the influence of position of the skull's pivot in the horizontal plane given equivalent amounts of head rotation to the sides. On the **left**, the eyes face forward. The **middle** image represents a central position of the foramen magnum, as in *Tarsius*, here located at the geometric center of the pentagon. The **right** image represents a posterior position, as in *Necrolemur*. The black dot is the approximate center of mass of both eyeballs combined. The dotted orthogonal lines represent the resultant vectors at the pivot point of the dens. Irrespective of the turning angle, with a more posterior foramen magnum there is a greater tendency to displace head mass and pitch and roll the skull. The tarsier's more central pivot provides a more efficient platform for balance and movement control.

Basicranial Morphology: The Auditory Region

The bullae of *Tarsius* and *Necrolemur* share several important resemblances, but tarsiers are widely acknowledged as being highly unusual morphologically (Fig. 3). Several features, all apparently interconnected, are of interest here: the transversely narrowed, toroidal shape of the tympanic cavity; medial orientation of the anteroposterior diameter of the tympanic cavity; transverse wasting at the junction between tympanic and hypotympanic sinus (the location of the intrabullar transverse septum); central, or anterolateral, as opposed to posteromedial, position of the posterior carotid foramen; inflation of the hypotympanic sinus; and narrowness of the ectotympanic tube. Much of this can be summarized in the form of a comparison. As in *Necrolemur*, the root of the tarsier ectotympanic emerges from a relatively flattened, vertical, lateral tympanic cavity sidewall, which represents the external, obverse bony surface that carries the crista tympani. But in *Necrolemur* and other tarsiiforms, the middle ear chamber is more evenly inflated anteromedially and ventrally opposite the tympanic cavity proper. In tarsiers, the inflation occurs anterior to the tympanum, which results in the latter appearing like a circular, mound-like rise. This constellation of unique features may be related to the spatial packaging of adjacent nonbullar structures.

Tarsiers have an unusually enlarged first cervical vertebra (Ankel-Simons 1999). Because of the forward position and wide span of the occipital condyles, which are now situated between the auditory bullae, the enlarged C1, including its anterior arch and transverse processes, encroaches the posteromedial face of the middle ear, including the medial aspect of the tympanic cavity posteriorly and the hypotympanic sinus anteriorly. This limits the mediolateral diameter of the middle ear compartment. Because *Tarsius* is evidently under selection to maintain a large inflated auditory bulla, it is possible that the unusually large size and irregular shape of the hypotympanic compensates for the limited space available for a medial or anteromedial dilation of the tympanic cavity proper, which is the condition of *Necrolemur*, where the tympanic and hypotympanic sinuses are continuous. Surely, the deep ventral inflation of the tarsier anterior accessory cavity is a function of the lack of expansion space medially, given the narrowness of the basioccipital, in turn related to mediolateral compression of the facial skeleton and choanae due to eyeball hypertrophy and reduction of the posterior nasal fossa.

An additional aspect of this pattern is that tarsiers have experienced a wholesale lateral displacement of the tympanic cavity as the foramen magnum shifted anteriorly, such that its lateral wall is much closer to the sidewall limit of the braincase. As a consequence, the transverse diameter of the external auditory tube is abbreviated, the orientation of the lateral wall of the tympanic cavity bearing the eardrum may have become more vertical from its primitively inclined setting, and the long axis of the tympanum is oblique to the sagittal plane.

For tarsiers, the coupling of a forwardly migrated foramen magnum and an enlarged C1 needs to be considered as a possible driving factor behind the novel location of the posterior carotid foramen. Rather than entering the bulla medially and almost horizontally, as in *Necrolemur* and other early haplorhines like *Rooneyia*, in *Tarsius* the foramen in shifted laterally and anteriorly away from the condyles. It enters into the bulla from a ventral and more anterior spot, well forward on the promontorium of the tympanic cavity. I consider this combination of local factors more likely than MacPhee and Cartmill's (1986) suggestion that migration of the posterior carotid foramen was influenced by the extreme narrowing of the basioccipital.

Discussion

Cranioskeletal Adaptations and Evolutionary History

The skull of *Tarsius* is arguably the most modified of any euprimate, save perhaps *Homo*. No other living genus has such a spectacularly unusual facial skull: virtually all eyes and hardly any nose at all, bony or soft. No other primate has such an enlarged and oddly shaped auditory bulla, nor a nuchal region and foramen magnum whose overall anatomy is more reminiscent of modern bipedal primates than of anything else. In addition, this characterization says nothing about the way tarsier teeth are arranged in the face: a set of vertical daggers, triangular in cross section, posted up in front of a peaked bell-curve arcade of cheek teeth, which flares widely in the rear because the maxillary bones carrying the molars have flanged out laterally to build the platform that undergirds the eyeballs. How and why these features evolved into a pattern is difficult to reconstruct without a good morphological record of closely related fossils, but our information is severely limited in that regard. Nevertheless, as a starting point for considering the mutual influences and integration of cranial components that are hypothesized to be responses to eyeball hypertrophy, I present the model shown in Fig. 5.

There may be a combination of benefits that explains why selection has transformed the shape of the tarsier cranium in the manner described. A principle one is the improved mechanical advantage of the nuchal muscles that allow their mass to be effective at a minimal size, which would save weight and also lessen the energetic costs of growth and maintenance. Lightness, especially at the head end of the body, is at a premium in a VCL primate such a *Tarsius*, benefiting liftoff and aerodynamic control. Increased sphericity of the skull, which is a combined effect of various changes but owes much to the unusually wide, truncated, rounded shape of the brain (Fig. 6), as well as its tilted disposition, may also be beneficial in that it adds structural strength with a minimal amount of weight. However, this biomechanical design built in bone may not be sufficient to balance the combined load of the paired eyes and brain in all respects. Osman Hill noted that some of the muscles involved in head carriage are hypertrophied, saying that the suboccipitals (1955, p. 164) "…are relatively enormous in proportion to the total body bulk…" He attributed this to the wide range of head turning that is required in tarsiers to compensate for their immobile eyes. This notion is consistent with the preceding analysis.

As is well known, the forward chamber of the auditory bullae of tarsiers is very large relative to skull size, and it is tempting to seek a unique acoustic explanation for this phenomenon and the abbreviated external auditory meatus, another tarsier novelty. However, some nuances of bullar morphology may be secondary consequences of the complex spatial packaging of the basicranium, especially

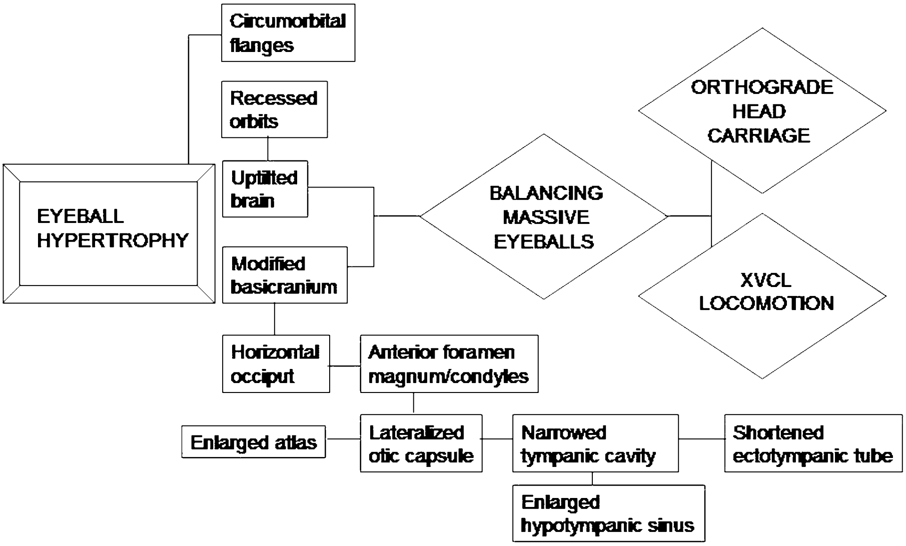
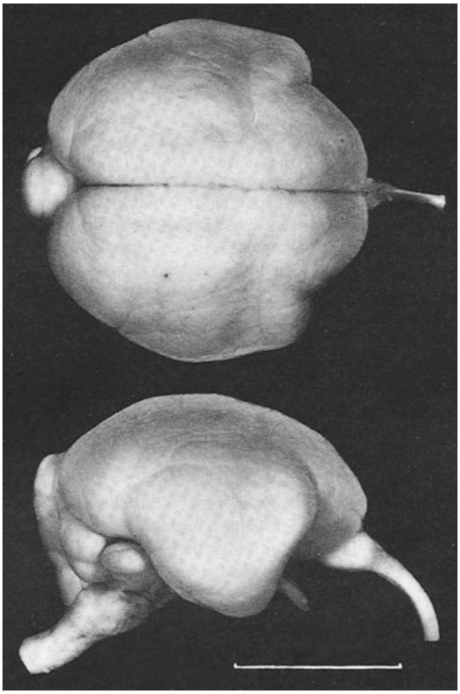


Fig. 5 A model of the transformational, functional, and adaptive interconnections among cranial components of the tarsier skull discussed in the text, hypothesized to be fundamentally driven by selection for hypertrophic eyeballs. The biomechanical reshaping of the skull, required by eyeball hypertrophy, influenced the evolution of an orthograde head posture as well as the evolution of the XVCL pattern of positional behavior, involving sit-and-wait predation and an overall ecological strategy that minimizes energy expenditure.

Fig. 6 Dorsal and lateral views of the brain of *Tarsius* showing its broad, rounded, foreshortened shape, related to uptilt of brain and recession of the orbital fossa beneath the forebrain. The anterior stalk on the right is the olfactory nerve. (Modified from Stephan 1984).



constraints on the volume of its posterior compartment, a tympanic cavity that is laterally shifted to accommodate the spread of the occipital condyles, and transverse processes of the atlas as the foramen magnum moved forward to a position between the bullae. In other words, the hypotympanic sinus may have increased in volume to compensate for the reduced volume of the tympanic cavity proper, which is spatially constrained. Similarly, the inflated petromastoids of *Necrolemur*, which has a differently shaped hypotympanic sinus, may reflect an alternative way to add intrabullar volume to the middle ear as well as enlarged attachment sites for prevertebral muscles to counterbalance the heavily loaded rostrum. Another consequence of laterally shifting the tympanic cavity toward the sidewall of the skull in tarsiers is that the length of the external auditory meatus is correspondingly reduced; *Necrolemur* still retains a lengthy tube.

Clearly, the enormous eyes profoundly influence cranial packaging and localized epigenetic processes, like the development of circumorbital flanges. But it is preferable to recognize the historical interplay of 2 major domains interacting with selection to produce the tarsier's specialized cranial morphology, the visual and positional behavior systems. As indicated, head carriage and control are probably fundamentally behind various novelties that contribute to the extensively modified neurocranium and basicranium. But these are specifically designed to function with the neutral position of the head set in an upright posture, as in VCL mode, not in a quadrupedal position. The precocious evolution of eyeball hypertrophy was thus first made possible by a VCL mode of head carriage and locomotion in early tarsiiforms. Once accomplished, the coordination of hypertrophic eyes and efficient head balance become core features of a new adaptive zone in primates occupied only by tarsiers, based on a set of radically new sensory capabilities that extend the VCL pattern.

This is not to say that facultative, pronograde head and body postures would be anomalous in *Tarsius*: quadrupedalism is an empirically documented aspect of its repertoire. Only that once the eyeballs hypertrophied in the tarsier lineage, certain biomechanical efficiencies would be virtually required and others could be gained while maintaining the head and trunk in orthogrady, obligatorily. Nor does this hypothesis suppose that small VCL strepsirhines like galagos, who frequently engage in quadrupedalism, are unable to hold their heads with eyes facing forward while clinging because they lack the same mechanism. But no form other than *Tarsius* has modified the head so extensively, or so radically altered the postcranial skeleton throughout to sustain a fully new manner of foraging. To emphasize this commitment, its uniqueness and adaptive pervasiveness across anatomical systems, I distinguish the tarsier mode of posture and locomotion as extreme VCL, or XVCL. To be clear, XVCL is not meant to emphasize either the leaping or the clinging, but to allude to an extensive suite of adaptations within and outside the locomotor skeleton that enables tarsiers to be successful at finding food without hunting actively and extensively for it: the nonpursuit predatory strategy.

The comparative evidence from modern primates suggests that a fundamentally orthograde style of head carriage based on intrinsic biomechanical adaptations of the head and postcranium is the distinctive skeletal basis of XVCL. I am aware of no reports that state that other VCL primates, such as galagos and indriids, have modified the skull to affect a comparable head carriage. Though there is no reason why the smaller-bodied VCL galagos could not be found to parallel tarsiers in this regard, galagos are also more persistent quadrupedal foragers. Nor have those strepsirhines with the largest eyes next to *Tarsius*, lorises, adopted a similar pattern; to the contrary, loris skulls are modified to enable them to stalk quadrupedally, with uptilted large eyes directed horizontally as they walk nose-to-the-branch. Thus the best explanation of the tarsier is that its skull is modified to direct the eyes horizontally while the head is perched vertically, and to swivel the head, instead of translating the whole body through space, as its scans for prey and initiates liftoff.

Although tarsiers have extensive, dramatic adaptations for saltation, they actually move little as part of the XVCL paradigm. The frequencies of positional behavior or support use have been documented for four species (Crompton and Andau 1986; Dagosto *et al.* 2001; MacKinnon and MacKinnon 1980; Niemitz 1984; Tremble *et al.* 1993). VCL and climbing, and usage of vertical and oblique supports, dominate the profiles in all studies. Quadrupedalism and horizontal support use is rare in the wild studies, with the highest frequencies of observations amounting to 11% and 21% in *Tarsius syrichta*, respectively, and locomotor bouts averaging only *ca.* 0.5 m in length (Dagosto *et al.* 2001). Clearly, living largely in the understory, the tarsiers eschew the branch networks, travel pathways, and behaviors that make roaming effective. The distances covered in leaps are small, averaging 1.3 m among *Tarsius bancanus, T. spectrum*, *T. syrichta,* and, according to Dagosto *et al*., bouts of climbing up and down averaged only *ca.* 0.4 m.

While measurements vary among the species and studies (Gursky 2007a), the home ranges of tarsiers, which usually amount to a small few hectares, compare well with the most predaceous galagines and lorisines (Nekaris and Bearder 2007). In some studies, tarsier home ranges are smaller, approaching that of the smallest primate gumivore, *Cebuella pygmaea* (Digby *et al.* 2007), whose life is tied to a small number of sessile trees. With regard to finding food, stealth, in this case cryptic non-motion, is the tarsier *modus operandi*. While being coy has obvious benefits for a predator as a form of concealment, its energetic returns would be vast if a semisedentary prey detection system could substitute for mobile prey foraging. As tarsiers have evolved a generally conservative energy expenditure strategy (Niemitz 1984), the prodigious leaping abilities of tarsiers are better understood as benefiting prey-capture accuracy and efficiency rather than a method for traveling large distances. In a small primate such as the tarsier, prone via ancestry to some form of VCL habit, the price of dragging around a massive head quadrupedally may be a costly limiting factor, as would lifting off and maneuvering a body with a massive ocular bulk added to the head end. Gursky (2007b, p. 121) argues similarly that tarsier mothers switch their locomotor preferences to quadrupedalism when carrying infants in their mouths because "…it may not be biomechanically possible to utilize vertical clinging and leaping when transporting a large load anteriorly."

There are other reasons why a lifestyle selected for overall energetic efficiency would be under strong selection in tarsiers for, as a derivative of neural tissue, maintaining the 2 enormous eyes metabolically is also likely to be very expensive. As noted by Wangsa-Wirwan and Linsenmeier (2003, p. 547; see also Nivens and Laughin 2004), "The retina is one of the most metabolically active tissues, consuming O_2 more rapidly than many other tissues, including the brain." This large combined caloric overhead can be offset by moving little to forage and by having small home ranges, i.e., forsaking plant foods that need to be collected by shopping and, alternatively, assuming a lamppost scanning and ambush strategy, where the prey comes to you. Roberts and Kohn (1993) emphasized the efficiency of this manner of prey selectivity in their study of a colony of captive *Tarsius bancanus*, where the capture success rate of adults was 88%.

Obviously, this would be best accomplished if prey detection methods are finely tuned. Though the specialized eyes of tarsiers have received much attention, hearing is likely to be equally important (Stephan 1984), and certainly the 2 senses are powerfully integrated (Niemitz 1985). The wide head and laterally displaced eardrums of tarsiers may augment prey detection by making the ears more adept at localizing sound though the binaural time delay principle. Thus it would be shortsighted to presume that the only advantage of tarsiers being able to swivel the head in a large arc is to adjust the gaze because the ocular muscles are weakly developed, as tradition has it. Head movements likewise position the ears for hearing. Perhaps freezing the eyeballs and moving the head instead is a way of accurately synchronizing the localizing functions of eyes and ears in high-resolution prey detection, as an alternative to hunting noisily and expensively through the forest via locomotion. An added benefit to nonpursuit predation is that tarsier mothers can be watchfully close to their parked infants (Gursky 2007a,b), whose eyes, spatial sense and limb coordination, one imagines, would be awkwardly slow in developing.

Eyeball Hypertrophy: Why?

Recent contributions to the basic form and function of the tarsier eye and visual cortex have been given by Castenholtz (1984), Hendrickson *et al.* (2000), Collins *et al.* (2005), and others (Martin and Ross 2005, and reference cited therein) have provided an evolutionary and ecological context for assessing tarsier vision in broad surveys of the primate visual system. These articles discuss various novelties of *Tarsius*, provide updates on fuzzy anatomical issues, and demonstrate newly found characteristics covering a range of topics, including among other features a finer characterization of the retinal fovea; demonstration and quantification of both rods and cones in the retina; descriptions of cornea size and pupil dilation; affirmation that the eyeballs are intrinsically immoveable; and characterization of the cell types in the lateral geniculate nucleus, the processing center and relay station joining the retina with the cortex. The emphasis arising from the physiological studies in particular is that tarsier eyes, in spite of being nocturnally adapted, are capable of high visual acuity and the perception of color (Collins *et al.* 2005), in keeping with its phylogenetic roots as a haplorhine. However, it is evident that much still needs to be learned about the functionality of tarsier eyes.

Of course, eyeball hypertrophy is almost always part of the discussion. The enormity of tarsier eyes has been explained as compensation for the lack of a tapetum lucidum, which is typical of nocturnal strepsirhine primates, in an animal that has reentered a nighttime niche but without the original, necessary optic equipment (Cartmill 1980; Martin 1973; Martin and Ross 2005). Martin (1990, p. 664) provided a concise statement of the hypothesis, saying that "…in comparison to the eyes of strepsirhines primates, those of tarsiers seem to have become adapted in a difference [sic] way for nocturnal vision—namely, through a radical increase in the size of the retina (and hence in the number if photoreceptors) well beyond the level of nocturnal strepsirhines." To explain why the convergent, secondarily nocturnal *Aotus* has experienced less eyeball hypertrophy, he notes that tarsiers have had a longer time to evolve their big eyes than owl monkeys did.

Though generally acknowledging that tarsier eyes are adapted to predation, these studies do not address how generalized interpretations such as "visual acuity" may actually confer selective benefits. The tarsier eye may be hypertrophied and photoreceptor cell count may be augmented and sight may be better than previously expected of a nocturnal haplorhine primate, but to what end? For what purpose is the receptor rich retina of a tarsier optimized: huge eyes and good nighttime vision to do what, exactly? Though the core idea has merit, the full hypothesis falls short as an explanation for the grotesquely large size of tarsier eyes, obviously the starting point for understanding what a tarsier is in essence. It does little to integrate eye size with other unique, and probably contingent features, such as the immobile eyeballs —is this really an anomalous consequence of supersized eyeballs?— or, with our improved understanding of the physiological capacities of the retina. In addition, these notions seem to exaggerate the negative, anticipated optical difficulties encountered by the tapetum-less, foveate visual system operating in low light, for the central retina of haplorhines is typically stocked with cones that rely on high levels of luminance to focus an image onto a large field of these color-sensitive cells. While such a "deficit" may be real in terms of a tarsier's ability to discriminate the shape and orientation of an object-image, which is exacerbated by the loss of color information when light is insufficient and constrained by a relatively small field of cone receptors, it need not be true for the other major function of the visual system, to detect, localize, and guide movement. This involves a different cortical pathway but is nonetheless predicated on the same fundamental purpose of the visual system, to map and interpret object information onto the retina and cortex (Morgan 2003).

I suggest the unique specializations of the tarsier eye are the basis of an adaptive complex that maximizes the visual system's spatial mapping properties, as opposed to a system designed for object identification. In other words, tarsiers may be more adept at finding prey and plotting a course to capture than knowing at first what it is. Visual acuity to a tarsier means being an excellent cartographer. It is not equivalent to "acute eyesight" in the human sense of being able to spot and encode the identifying features of objects, which to us seems more important cognitively than finding it in the first place. As an early branch of the haplorhine stock, tarsiers are not even expected to have either the same anatomical configuration of the central retina as anthropoids or the same kind of keen eyesight.

Regarding the extreme size, it is likely that tarsiers benefit in several ways from the geometry of outsized eyes such that selection eventually maximized this quantity until it became limited by some basic physiological threshold, or by simply relaxing selection. A key to the beginnings of hypertrophy may have been the development of an ectopic eye, for tarsiers have eyeballs that have largely escaped the osseous confines of the orbital fossa. Schultz (1940) pointed out long ago that more than half of the globe is located outside the margins of the orbital aperture, and Rosenberger *et al.* (2008) discussed anatomical evidence that may relate to this phenomenon among several Eocene fossil tarsiiforms in the form of supraorbital flanges, among other features. Castenholtz (1984) provided the following ratios of eyeball volume: orbital volume to provide perspective on how much the eye of *Tarsius* bulges out beyond the eyecup. The values are: tarsiers, 1.79; nocturnal strepsirhines, *ca.* 1.0; chimpanzees, 0.26; orangutans, 0.17; humans, 0.32.

Whereas the anthropoid eye is an organ whose core ecological adaptations may be understood to be concentrated near the center of the retina where the fovea is located and the color-sensitive cone receptors are densely distributed, tarsier retinas show evidence of specialization in the retinal periphery. This may be critical to explaining eyeball hyperetrophy. Given the fundamental topographic organization of the retina about a center, while cell populations near the central fovea could grow in number and density as tarsier eyes evolved to enormous size, the largest potential for adaptations relating to surface area increase can be expected to occur in the periphery, off center, where surface is more plentiful. The periphery is where rods are concentrated. Collins *et al.* (2005) reported that tarsiers have *ca.* 135,000,000 rods in the periphery of the retina, distributed in a density of *ca.* 300,000/mm^2. Humans, by comparison, have *ca.* 120,000,000 peripheral rod cells, at a density of 95,000/mm^2 (Curcio *et al.* 1991). Dichromatic ground squirrels have *ca.* 1,270,000 rods, with a peak density of 13,000/mm^2 (Kryger *et al.* 1998). This comparison suggests the possibility of capturing a larger and more finely grained image in the retinal periphery of tarsiers, all else being equal. Because in humans, and presumably in tarsiers, different populations of the rods are optimized for the luminance levels of starlight, dawn and twilight (Sterling 2004), this advantage in cell count is likely to be a specifically nocturnal adaptation, perhaps even tuned to different phases in the light-dark continuum.

Collins *et al.* (2005) also suggest another unusual feature in a peripheral retina of tarsiers, a wide band of cones at the rim of the photoreceptor array that is sensitive to ultraviolet light. They suggest these S-cones are useful for detecting prey that fluoresces in UV light. Their location contrasts with the M- and L-cones of tarsiers, which are not UV sensitive and occur in the central retina. If Collins and colleagues are correct, this means a specialized encoding feature of the tarsier night vision system is located in the retinal periphery, not in the central retina where the diurnal haplorhines appear to have specialized with their large populations of cones. Why?

A key benefit may derive from spatial factors that are a consequence of eyeball size. The enormity of tarsier eyes exaggerates point separations within and between the eyes, of the nasal (medial) and temporal (lateral) aspects within each retina and also in the position of the eyes with respect to one another: Their optical axes are spread apart as the diameters of the two eyeballs increase. Tarsiers are small bodied and would normally thus have absolutely small eyes. For a variety of structural and phylogenetic reasons (Rosenberger *et al.* 2008) probably linked with a diminution of olfaction and the nasal fossa in ancestral haplorhines, they also have orbits more closely spaced near the midline than strepsirhines or plesiadapiforms, whose orbital fossae are widely separated by the interorbital pillar. So, there are inherent hard tissue constraints that would otherwise keep tarsier eyes positioned very close together. Separating the eyes, or more properly their optical axes, while maintaining a small body size can be accomplished by simply enlarging the spheres beyond the eyecups formed by the orbital fossae.

Separation of the eyes is the central anatomical feature behind binocular vision, and increasing the separation of forward facing eyes enhances depth perception

(Morgan 2003). The mechanism involved is stereopsis, which is a distinct property of binocular vision. Stereopsis is based on the differences in what each eye "sees" in space and time as a function of their different viewpoints, i.e., their spatial separation. It is exactly comparable to the interaural time delay between the 2 ears hearing a sound coming from some direction. This horizontal disparity means that complementary areas on each retina are mapping different versions of the target image in real time. The differences are resolved and integrated by the retina and the brain to produce the sensation of spatial depth. Greater disparity of the retinal maps (up to a point) can enable more precision in sensing the target with forward facing eyes, a calculation that is done by measuring the differentials between the amount and distribution of light falling on the complementary receptive fields of the 2 eyes. For tarsiers, the peripheral low-luminance rods and the UV-sensitive S-cone bands that are farthest out on the retinal periphery would be most affected functionally as the eyeball expands, not the cones of the central retina. These peripheral photoreceptors are not designed to assess color or edges, properties useful for classifying the nature of an object. The information they convey is simply the cartographic information derived from mapping the object's position and movement in space relative to the viewer.

Within the cortex, the tarsier visual system also suggests a priority for dynamic cartography, i.e., selection of motion detection functions. According to Collins *et al.* (2005), the lateral geniculate nucleus is dominated by magnocellular cells rather than parvocellular cells. The M-cells have a quicker response time, are best suited for spatial assessment and motion detection, and not for discriminating color. P-cells, in contrast, are slow to process and designed to discern color.

In humans, binocular parallax, which involves seeing an object from different viewpoints, is sensed before objects are recognized (Morgan 2003). This is a crucial distinction. To explain it, Morgan (pp. 56–57) gives an example of the functional implications of the retina as a spatial detector that is especially apt for tarsiers. He compares a random-dot stereogram with natural camouflage.

> The square in the random-dot stereogram is totally invisible to either eye's image alone…It exists only by virtue of the relationships between the two eyes…binocular vision allows us to see it. This idea of camouflage gives us a new evolutionary perspective on binocular vision. A moth might make its colour and texture match that of the bark on which it sits, but it is not able to make itself perfectly flat. Viewed with two eyes, the moth will leap out from the bark like the square from the random-dot stereogram.

With color information already reduced or absent in the tarsier's low light domain, an even greater selective premium would be placed on a parallax spatial and motion detector, as described, able to see the topography of a moth and its movement.

An additional advantage of having a wide transverse diameter of the eyeball consonant with hypertrophy is that it allows for a larger cornea and a pupil that is capable of opening very widely. Both of these features are adaptations to maximize the amount of light entering the tarsier eye (Castenholtz 1984), i.e., to increase the size of the mapped image. The benefit of a larger image is not that the eye "sees better." It is that more photoreceptors are excited, making it easier and faster to calculate and compare where the object is in space from instant to instant based on horizontal disparity (Morgan 2003). The panoramic effect of the large, maximally dilated pupil of a tarsier may also help stabilize the mapped object-image on the retina to permit calculations as the target moves infinitesimally small distances across the photoreceptor field from instant to instant.

In the long axis, the larger eyeball effectively becomes a telescopic lens, also increasing the size of the image mapped onto the retina, although the optics of tarsiers eyes, which also involve a large anterior chamber associated with the cornea (Castenholtz 1984), are likely to be complex. Ideally, the image should be as sharp as possible, i.e., focused, for the sake of accuracy. According to Collins *et al.* (2005, p. 1016), tarsiers are probably capable of projecting a focused image, as "…they are likely to have use of color vision, as well as the high visual acuity implied by the high receptor counts of rods and cones in the central retina and fovea." Though it is not understood how tarsiers may use the light-intensive central retina and fovea in darkness, it seems that the retina is potentially very efficient in mapping an image because it is capable of sensing a nodal point within the mapped field that can be used in calculations. Photosensors in the periphery may be mapped as vectors against the fovea, as in anthropoids (Morgan 2003).

Ironically, the immobile eyes may be another asset of the tarsier visual system that benefits motion detection. In the absence of localized motor control, one may presume that tarsiers suffer by not being able to efficiently manage their gaze, or track a target with minimal energy expenditure by using the eyes alone. On the other hand, fixing the eyes in the head means that the visual system is yoked to the vestibular-cochlear complex. It suggests a high level of cortical integration between these sensory systems. Thus, while a tarsier's eyes may not be moving independently of the head, its gaze may be precisely registered against the vestibular-cochlear mapping system, giving the a high-fidelity spatial recognition and tracking apparatus. Stephan (1984) noted that the vestibular system was highly developed even though cortical motor systems were not, by comparison to strepsirhines. He also indicated that, in the midbrain, the superior colliculus of *Tarsius* was very well developed. The latter is essentially a mirror of the retinal mapping field, from which it receives input. Its functions have been well studied in macaques (Walton *et al.* 2007). There the superior colliculus controls eye shifts during gaze and head movement, but Walton *et al.* theorized there is a large population of cells that may control head movement alone independent of eye shifts. How, precisely, these structures might work in tarsiers cannot be determined. But they imply a profound emphasis and coordination of detailed spatial mapping functions. If tarsier eyes are truly motionless as reported, it is likely this is an advantage for the tracking system rather than an anomaly. If anatomical studies confirm that frozen eyeballs relate both to eyeball size and their ectopic position, we may be able to trace the implied contingent behaviors in the fossil record.

Comparative behavioral information suggests other reasons why mapping space and movement may be more relevant to explaining tarsier eyeball specializations than feature detection. Predaceous lorises and galagos, both armed with a tapetum that scatters light, and both lacking a fovea where incoming light could be concentrated, also have impressively large eyes for their body and brain sizes, and by comparison with their more frugivorous relatives (Rosenberger *pers. obs.*). Yet their optics suggests an inability to produce a focused image. The coincidence of biological roles between lorisiforms and tarsiers does not negate the potential general benefits of increasing photoreceptor count by enlarging the retina, along the same lines originally proposed to explain tarsier hypertrophy (Cartmill 1980; Martin 1973), but it suggests the need for a more specific interpretation of the underlying functions that were selected. Increasing photoreceptor count in lorisiforms would not increase visual acuity in the haplorhine sense because the retinal image would not be a focused image. The form-function common denominator behind their shared specialization, eyeball enlargement, may be an enhanced spatial mapping and motion detection system that comes with increasing binocular disparity between peripheral retinal fields.

Conclusions

The tarsier cranium has been extensively redesigned to accommodate huge eyeballs, not only by making space for them but also by arranging cranial components to produce a biomechanical system capable of balancing and accurately moving a head that is massively eccentrically loaded. Its compact, roundish skull, with the nuchal region rotated into a ventral position, is organized to balance the head in the neutral position of the vertical clinging body posture while keeping the skull light in weight and structurally strong. The wide brain case and forward position of the foramen magnum set the ears and tympanic membranes widely spaced apart, which may enhance the localizing abilities of the auditory system, also an asset to predation as hearing and vision may be exceptionally integrated and equally important to the tarsier lifestyle. Many specializations of the tarsier eye, including eyeball hypertrophy and the eye's cortical representation, may also serve to optimize the visual system's ability to map space and detect motion, rather than to discriminate patterns for object identification, an aspect that may be under less selective pressure given the low light conditions of the animal's nocturnal manner. Seeing movement and navigating the body through space in order to intercept prey are functions critical to the tarsier's unique style of non-pursuit predation which, overall, is an energy-minimizing ecological strategy. The selective imperative to conserve locomotor energy may counterbalance the massively hypertrophic eyes, which are metabolically expensive. The exclusively animalivorous diet of *Tarsius* may also be a prerequisite to evolving such a costly visual system.

The derived functional morphology of the tarsier visual system and cranium probably evolved as the lineage shifted the emphasis of posture and locomotion from a pattern that involved a rather varied profile of biological roles, supporting a mobile hunting lifestyle that almost surely involved a significant amount of quadrupedalism, to one that became highly efficient in supporting a relatively sedentary, sit-and-wait mode of prey detection, punctuated by the prey capture pounce. The integration of specialized optic, auditory, cranial, and postcranial elements is the XVCL habit, evident only in tarsiers. None of the fossil tarsiiforms for which we have relevant evidence have hypertrophic eyeballs on the order of a tarsier's or the advanced biomechanical features related to head carriage and eccentrically loaded skulls, although several appear to have at least precociously developed ectopic eyeballs and some, such as *Necrolemur*, exhibit extensive tarsal elongation and tibio-fibular fusion, in the absence of greatly enlarged orbits. This indicates that VCL locomotion and insect foraging (as well as frugivory and/or soft-prey preferences, *viz. Necrolemur*) were central to a branch of the tarsiiform radiation, but none thus far known are likely to have practiced the nonpursuit, XVCL foraging method of modern *Tarsius*, which relies so heavily on sight, and probably sound. Taxonomically then, it remains to be seen if the fossil record reveals this unique lifestyle to be anything more than a genus-specific phenomenon, which would perhaps be another cause to draw similarities between the evolutionary histories of 2 of the odder primates, *Tarsius* and *Homo*.

Acknowledgments The research was partially supported by grants from PSC-CUNY and the Tow Travel Research Fund, Brooklyn College. For access to collections I thank authorities and colleagues at the American Museum of Natural History; the United States National Museum; the San Diego Museum of Man; Yale Peabody Museum; Museum of Comparative Zoology, University of California, Berkeley; Museum National d'Histoire Naturelle, Paris; British Museum, London. I express special thanks to Emily Rosenberger for scientific assistance, Julia Zichello for help with illustration, Mark Dow for developing and producing Fig. 1, and to Carsten Neimitz. I thank Siobhan Cooke and anonymous reviewers with deep expertise in tarsier biology for thoughtful comments that improved the manuscript.

References

Ankel-Simons, F. (1999). *Primate anatomy: An introduction*. San Diego: Academic.

Beard, K. C., & MacPhee, R. D. E. (1994). Cranial anatomy of *Shoshonius* and the antiquity of Anthropoidea. In J. G. Fleagle & R. F. Kay (Eds.), *Anthropoid origins*. New York: Plenum.

Beard, K. C., Krishtalka, L., & Stucky, R. K. (1991). First skulls of the early Eocene primate *Shoshonius cooperi* and the anthropoid-tarsier dichotomy. *Nature, 349*, 64–67.

Biegert, J. (1963). The evaluation of characteristics of the skull, hands and feet for primate taxonomy, classification and human evolution. In S. L. Washburn (Ed.), *Classification and human evolution* (pp. 116–145). Chicago: Aldine.

Cartmill, M. (1972). Arboreal adaptations and the origin of the order Primates. In R. H. Tuttle (Ed.), *The functional and evolutionary biology of primates* (pp. 97–122). Chicago: Aldine.

Cartmill, M. (1974). *Daubentonia*, *Dactylopsila*, woodpeckers and klinorhynchy. In R. D. Martin & G. A. Doyle (Eds.), *Prosimian biology* (pp. 655–670). London: Duckworth.

Cartmill, M. (1980). Morphology, function, and evolution of the anthropoid postorbital septum. In R. L. Ciochon & A. B. Chiarelli (Eds.), *Evolutionary biology of New World Monkeys and continental drift* (pp. 243–274). New York: Plenum Press, New York.

Castenholtz, A. (1984). The eye of *Tarsius*. In C. Niemitz (Ed.), *Biology of tarsiers* (pp. 303–318). Stuttgart: Gustav-Fisher Verlag.

Cave, A. J. E. (1967). Observations on the platyrrhine nasal fossa. *American Journal of Physical Anthropology, 26*, 277–288.

Collins, C. E., Hendrickson, A., & Kass, J. H. (2005). Overview of the visual system of *Tarsius*. *Anatomical Record, 287A*, 1013–1025.

Crompton, R. H., & Andau, P. M. (1986). Ranging, activity rhythms, and sociality in free-ranging *Tarsius bancanus*: A preliminary report. *International Journal of Primatology, 8*, 43–71.

Curcio, C. A., Allen, K. A., Sloan, K. R., Lerea, C. L., Hurley, J. B., Klock, I. B., *et al.* (1991). Distribution and morphology of human cone photoreceptors stained with anti-blue opsin. *Journal of Comparative Neurology, 312*, 610–624.

Dagosto, M., Gebo, D. L., & Beard, K. C. (1999). Revision of the wind river faunas, early Eocene of central Wyoming. Part 14. Postcranium of *Shoshonius cooperi* (Mammalia: Primates). *Annals of the Carnegie Museum, 68*, 175–211.

Dagosto, M., Gebo, D. L., & Dolino, C. (2001). Positional behavior and social organization in the Philippine tarsier (*Tarsius syrichta*). *Primates, 42*, 233–243.

Digby, L. J., Ferrari, S. F., & Saltzman, W. (2007). Callitrichines. The role of competition in cooperatively breeding species. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, & S. K. Bearder (Eds.), *Primates in perspective* (pp. 85–105). Oxford: Oxford University Press.

Gurche, J. A. (1982). Early primate brain evolution. In E. Armstrong & D. Falk (Eds.), *Primate brain evolution* (pp. 227–246). New York: Plenum.

Gursky, S. L. (2007a). Tarsiiformes. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, & S. K. Bearder (Eds.), *Primates in perspective* (pp. 73–85). Oxford: Oxford University Press.

Gursky, S. L. (2007b). *The spectral tarsier*. Upper Saddle River: Pearson Prentice Hall.

Hendrickson, A., Djajadi, H. R., Nakamura, L., Possin, D. E., & Sajuthi, D. (2000). Nocturnal tarsier retina has both short and long/medium wavelength cones in an unusual topography. *Journal of Comparative Neurology, 424*, 718–730.

Hershkovitz, P. (1977). *Living New World monkeys (Platyrrhini) with an introduction to primates, vol 1*. Chicago: University of Chicago Press.

Hill, W. C. O. (1955). *Primates: Comparative anatomy and taxonomy. II. Haplorhini: Tarsioidea*. Edinburgh: Edinburgh University Press.

Jerison, H. J. (1979). Brain, body and encephalization in early primates. *Journal of Human Evolution*, 615–635.

Kay, R. F., & Kirk, E. C. (2000). Osteological evidence for the evolution of activity pattern and visual acuity in primates. *American Journal of Physical Anthropology, 113*, 235–262.

Kryger, L., Galli-Resta, L., Jacobs, G. H., & Reese, B. E. (1998). The topography of rod and cone photoreceptors in the retina of the ground squirrel. *Visual Neuroscience, 15*, 685–691.

MacKinnon, J., & MacKinnon, K. (1980). The behavior of the wild spectral tarsiers. *International Journal of Primatology, 1*, 361–379.

MacPhee, R. D. E., & Cartmill, M. (1986). Basicranial structures and primate systematics. In D. R. Swindler & J. Erwin (Eds.), *Comparative primate biology, vol 1. Systematics, evolution and anatomy* (pp. 219–275). New York: Alan R. Liss.

Martin, R. D. (1990). *Primate origins and evolution: A phylogenetic reconstruction*. Princeton: Princeton University Press.

Martin, R. D. (1973). Comparative anatomy and primate systematics. *Symposium of the Zoological Society of London, 33*, 301–337.

Martin, R. D., & Ross, C. F. (2005). The evolutionary and ecological context of primate vision. In J. Kremers (Ed.), *The primate visual system: A comparative approach* (pp. 1–36). New York: John Wiley & Sons.

Morgan, M. (2003). *The space between our ears*. Oxford: Oxford University Press.

Nekaris, K. A. I., & Bearder, S. K. (2007). The strepsirrhine primates of Asia and Mainland Africa: Diversity shrouded in darkness. In C. Campbell, A. Fuentes, K. MacKinnon, M. Panger, & S. K. Bearder (Eds.), *Primates in perspective* (pp. 24–45). Oxford: Oxford University Press.

Niemitz, C. (1984). Activity rhythms and use of space in semi-wild Borenean tarsiers, with remarks on wild spectral tarsiers. In C. Niemitz (Ed.), *Biology of tarsiers* (pp. 85–117). New York: Gustav-Fischer Verlag.

Niemitz, C. (1985). Can a primate be an owl? Convergences in the same ecological niche. *Fortschung Zoologie, 30*, 666–670.

Nivens, J. B., & Laughin, S. B. (2004). Energy limitation as a selective pressure on the evolution of sensory systems. *Journal of Experimental Biology, 211*, 1792–1804.

Plotnick, R. E., & Baumiller, T. K. (2000). Invention by evolution: Functional analysis in paleobiology. *Paleobiology, 26*(4, Supplement), 305–323.

Radinsky, L. B. (1967). The oldest primate endocast. *American Journal of Physical Anthropology, 27*, 385–388.

Radinsky, L. B. (1970). The fossil evidence of prosimian brain evolution. In C. R. Novack & W. Montagna (Eds.), *Advances in primatology, vol 1: The primate brain* (pp. 209–224). New York: Appleton-Century-Crofts.

Radinsky, L. B. (1977). Early primate brains: Facts and fiction. *Journal of Human Evolution, 6*, 79–86.

Roberts, M., & Kohn, F. (1993). Habitat use, foraging behavior, and activity patterns in reproducing Western tarsiers, *Tarsius bancanus,* in captivity: A management analysis. *Zoo Biology, 12*, 217–232.

Rosenberger, A. L. (1985). In favor of the necrolemur-tarsier hypothesis. *Folia Primatologica, 45*, 179–194.

Rosenberger, A. L., Hogg, R., & Wong, S. M. (2008). *Rooneyia*, postorbital closure, and the beginnings of the age of Anthropoidea. In E. J. Sargis & M. Dagosto (Eds.), *Mammalian evolutionary morphology: A tribute to Frederick S. Szalay* (pp. 325–346). Dordrecht: Springer.

Schultz, A. H. (1940). The size of the orbit and of the eye in primates. *American Journal of Physical Anthropology, 26*, 398–408.

Schultz, A. H. (1955). The position of the occipital condyles and of the face relative to the skull base in primates. *American Journal of Physical Anthropology, 13*, 97–120.

Simons, E. L., & Russell, D. E. (1960). Notes on the cranial anatomy of *Necrolemur*. *Breviora, 127*, 1–14.

Spatz, W. B. (1968). Dies bedeutung der augen fur die sagittale gestaltung des schadels von *Tarsius* (Prosimiae, Tarsiiformes). *Folia Primatologica, 9*, 22–40.

Spatz, W. B. (1969). An interpretation of the sagittal shape of the skull of higher primates, based on observations of the skull of *Tarsius*. *Proceedings of the 2nd International Congress on Primatology, 2*, 187–191.

Sprankel, H. (1965) Untersuchengen an *Tarsius*. I. Morphologie des schwanzes nebst ethologischen bemerkungen. *Folia primatologica, 3*, 153–188.

Starck, D. (1975). The development of the chondrocranium in primates. In W. P. Luckett & F. S. Szalay (Eds.), *Phylogeny of the primates: A multidisciplinary approach* (pp. 127–155). New York: Academic.

Starck, D. (1984). The nasal cavity and nasal skeleton of *Tarsius*. In C. Niemitz (Ed.), *Biology of tarsiers* (pp. 275–290). Stuttgart: Gustav Fischer Verlag.

Stephan, H. (1984). Morphology of the brain of *Tarsius*. In C. Niemetz (Ed.), *Biology of tarsiers* (pp. 319–344). Stuttgart: Gustav Fischer Verlag.

Sterling, P. (2004). How retinal circuits optimize the transfer of visual information. In J. S. Werner & L. M. Chalupa (Eds.), *The visual neurosciences* (pp. 234–259). Cambridge: MIT Press.

Szalay, F. S. (1976). Phylogeny, adaptations and dispersal of the tarsiiform primates. In W. P. Luckett & F. S. Szalay (Eds.), *Phylogeny of the primates: A multidisciplinary approach* (pp. 357–404). New York: Academic.

Tremble, M., Muskita, Y., & Supriatna, J. (1993). Field observations of *Tarsius dianae* at Lore Lindu National Park, Central Sulawesi, Indonesia. *Tropical Biodiversity, 1*, 67–76.

Walton, M. M. G., Bechara, B., & Gahndi, N. J. (2007). Role of the primate superior colliculus in the control of head movements. *Journal of Neurophysiology, 98*, 2022–2037.

Wangsa-Wirawan, N. D., & Linsenmeier, R. A. (2003). Retinal oxygen: fundamental and clinical aspects. *Archives of Ophthalmology, 121*, 547–557.

Weishampel, D. B. (1993). Beams as machines: Modeling approaches to the analysis of skull form and function. In J. Hanken & B. K. Hall (Eds.), *The skull, vol 3. Functional and evolutionary mechanisms* (pp. 303–344). Chicago: University of Chicago Press.