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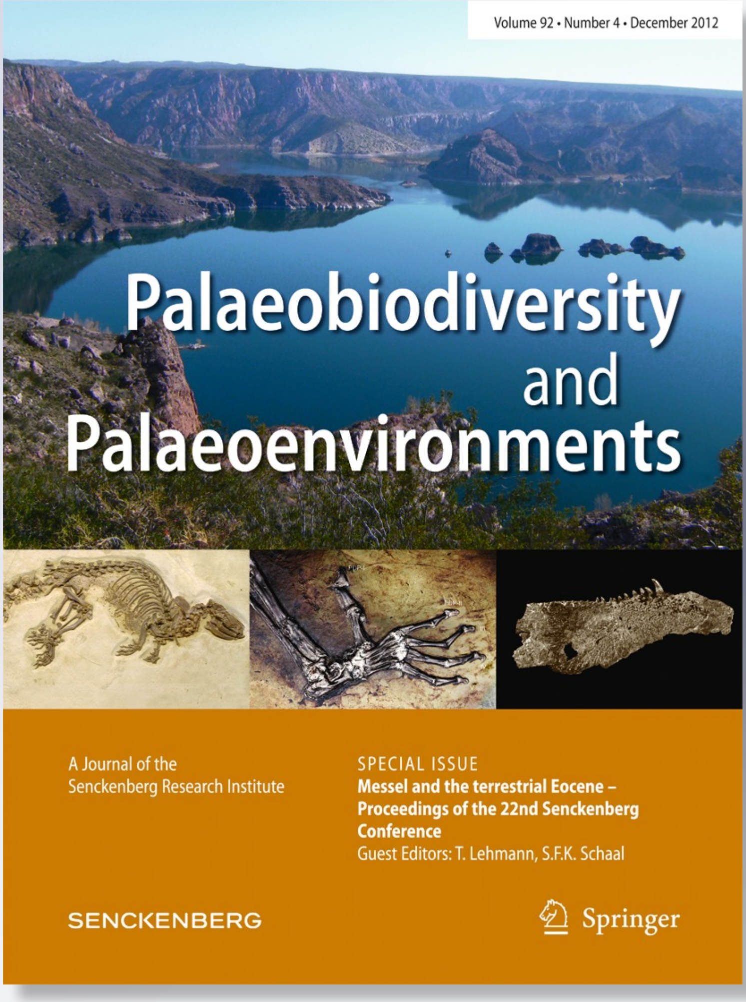

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Evolutionary morphology, cranial biomechanics and the origins of tarsiers and anthropoids

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Abstract During the Time of Messel, the dominant groups of primates were the adapiform strepsirhines and the tarsiiform haplorhines, both important in discussions of anthropoid origins. Living tarsiers are at the centre of these ideas as one school of thought, representing the Tarsier-Anthropoid Hypothesis, holds they are the sister-group of Anthropoidea. The Tarsier-Tarsiiform Hypothesis, however, maintains that tarsiers are phyletically nested among the (paraphyletic) fossil tarsiiforms (~omomyids). Orbital morphology is crucial to this debate: the possibility that the postorbital septa of tarsiers and anthropoids are synapomorphic and that it evolved in their last common ancestor to insulate the eyeballs from muscular interference. Our biomechanical model of forces acting on the enormous eyeballs and orbits of tarsiers especially *during locomotion* provides a strong counterargument to this proposition. The uniquely specialised orbita of *Tarsius*, which include prominent circumorbital flanges that are continuous with the postorbital septum, are designed to sustain enormous inertial loads transmitted by the eyeballs during the acceleration and deceleration phases of powerful leaping, for which *Tarsius* is also famous. The eyeballs are thus secured, and pressure absorbed by the retina during acceleration is minimised, by enlarging its surface area of contact with a "walled socket", i.e., by the extra-fossa expansion of these flanges. The tarsier septum is, therefore, a form–function convergence on the small-eyed anthropoid condition. Several related Eocene tarsiiforms exhibit a precisely *Tarsius*-like morphology of the rostrum relating to eyeball hypertrophy, although they lack the exaggerated circumorbital and septal morphology and only rarely exhibit postcranial features indicative of super leaping abilities.

Keywords Tarsiers · Anthropoids · Biomechanics · Postorbital septum · Phylogeny · Adaptation

Introduction

The Eocene Epoch, which encompasses the "Time of Messel" 47 million years ago, holds a special status as the period when recognisable close relatives, and perhaps ancestors, of the surviving mammalian orders begin to appear in the fossil record. The description of the fossil primate *Darwinius masillae* from Grube Messel in Germany (Franzen et al. 2009) has rekindled a debate central to the history of the Order Primates and the origins of its ecologically dominant group. Are anthropoids descendants from

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adapiform primates resembling *Darwinius*, which were then widespread? Are they descended from a contemporaneous, hard-to-identify haplorhine group? Or, are anthropoids the product of an ancestor shared exclusively with the living genus *Tarsius*? The intensity of this discussion is evidenced by the rapid publication of papers by several teams of scientists written explicitly to present alternative views regarding *Darwinius* interrelationships (Gingerich et al. 2012; Maiolino et al. 2012; Williams et al. 2010). Yet, because this growing body of work is focused principally on assessing this one remarkable fossil, which all agree bears resemblances to living strepsirhine (lemuriform, lorisiform and adapiform) primates, its position with respect to anthropoids cannot be adequately understood without considering the affinities of anthropoids and living tarsiers, as the latter are central to both of the other cladistic hypotheses. This, too, is a contested matter. There is no consensus on the phylogenetic affinities of *Tarsius* with respect to the fossil tarsiiform primates, generally known as omomyids, which were also plentiful during the Eocene Time of Messel. So, the debate concerning *Darwinius* is companion to a larger controversy on the origins of Anthropoidea that encompasses the fossil and the recent records.

There are currently two competing views of the cladistic affinities of *Tarsius*, a relict genus currently found on the islands of Sumatra, Borneo, Sulawesi and the Philippines. One holds that tarsiers are most closely related to living anthropoids, platyrrhines and catarrhines—the Tarsier-Anthropoid Hypothesis. The other is that tarsiers are more closely related to the fossil tarsiiforms—the Tarsier-Tarsiiform Hypothesis.

In this report, we examine aspects of the osteological evidence of the rostrum and the orbit pertinent to establishing the phylogenetic position of *Tarsius*, and remark on relevant fossil tarsiiforms where some of the critical anatomy can also be observed. We stress the systematic value of understanding the functional morphology of characters as part of the phylogeny reconstruction process, intentionally, in order to contrast this approach with the more popular methodology of analysing cladistic relationships by algorithm, which is intended to minimise or eliminate a priori interpretations of (not only!) morphological evolution. We use the concept of "evolutionary morphology" as a holistic, dynamic notion (e.g. Bock 1990; Rosenberger 2011a) that attempts to account for functional morphology (e.g. studies of biomechanics and adaptation), character transformation, anatomical patterns and integration, and the concept of preadaptation. All of these concepts can contribute to assessing homology, and therefore phylogeny. In an effort to untangle the phylogenesis of tarsiers, our strategy is to first isolate and explain its most unusual anatomical and behavioural characteristics, those that define its unique adaptive nature, focusing on the cranium. These features are considered to be of highest value in assessing fossils that are possibly related to tarsiers because of their powerful phenetic, and presumed genetic, integration, which means they offer a solid perspective for recognising homological continuity. Our view is that robust polarity hypotheses emerge by explaining anatomical novelties when their ties to challenging characteristic behaviours of the animals themselves can be established, as opposed to relying too heavily on taxonomic distributional information (i.e. the commonality principles as implemented by parsimony analyses) that has nothing directly to do with natural selection.

Who is *Tarsius*?

For context, a brief summary of the biology of tarsiers is in order. It should be noted that *Tarsius* (Fig. 1) has been the focus of several important edited volumes, monographs and a recent journal special issue (Hill 1955; Gursky 2007; Niemitz 1984a; Shekelle and Gursky-Doyen 2010; Wright et al. 2010). Niemitz (2010), a long-established authority on the biology and natural history of *Tarsius*, has also written an excellent research synopsis. Taxonomically, there has been a broad consensus, held for decades, that only one genus is represented (e.g. Le Gros Clark 1934, 1959; Hershkovitz 1977; Hill 1955; Napier and Napier 1967; Wilson and Reeder 1993), although the number of species is a difficult matter, especially as several new populations have recently been contacted and investigated in the field. Groves and Shekelle (2010), however, recognise three genera, a scheme that is not followed here. Regarding species, Hill (1955) maintained there are three (also Szalay and Delson 1979); Groves (in Wilson and Reeder 1993) listed five, which is basically the sense of most active primatologists (e.g. Fleagle 1999; Gursky 2007); Groves and Shekelle (2010) recognised eight or nine; and Merker and Groves (2010) identify ten. The careful systematics account of Musser and Dagosto (1987) found four species, which they divided into two species groups: the Celebesian *T. spectrum* and *T. pumilus*, and the Sundaic and Philippine species *T. bancanus* and *T. syrichta*.

All these animals live in varieties of rain forest habitat (see Musser and Dagosto 1987). They are all nocturnal and exceptionally predaceous. Their habit of vertical-clinging-and-leaping (VCL), and the hindlimb adaptations enabling it, has been employed as a model for springing locomotion among primates (e.g. Napier and Walker 1968; Napier and Napier 1967). Details of leaping behaviour have been related to hindlimb biomechanics and morphology in the study of Peters and Preuschoft (1984). However, Rosenberger (2010b) also suggested the way in which this adaptation is manifest in *Tarsius* is far more extensive than supposed up to now, for it also appears to involve widespread modifications of the

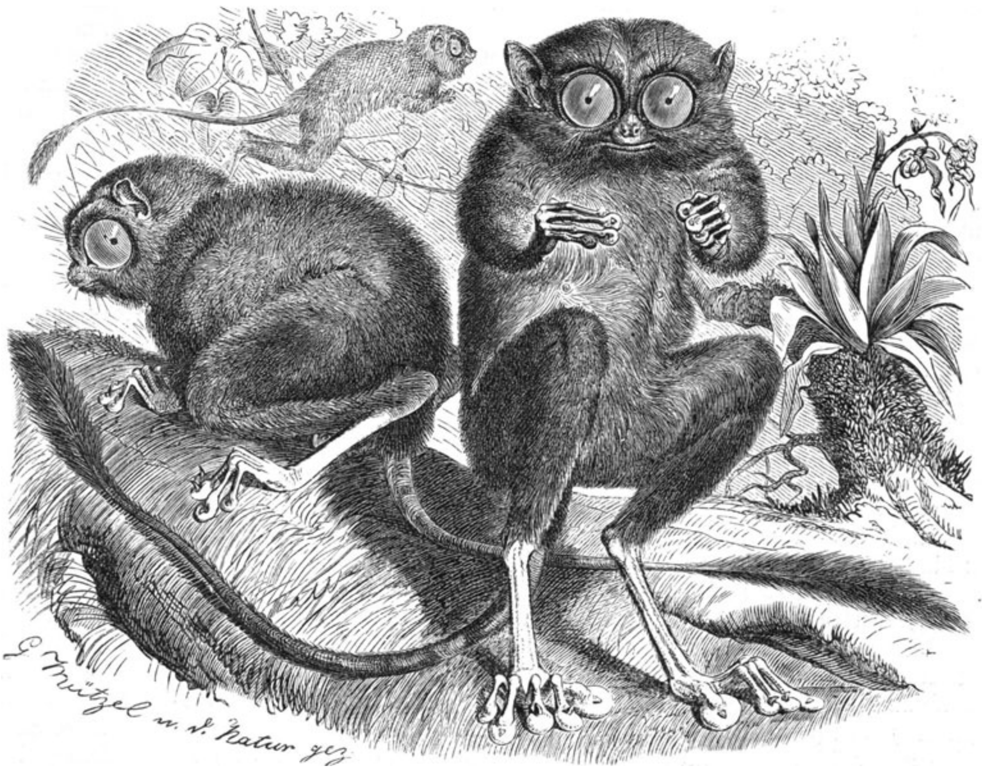

Fig. 1 *Tarsius*, the Koboldmaki. From Strassen (1877)

cranium, related functionally to carrying a heavy, eccentrically loaded head that is overbalanced by the huge eyeballs. He proposed to call this system XVCL (extreme VCL) to distinguish it from the less elaborate VCL system of strepsirhines such as galagos and indriids, which appears to be largely restricted to the postcranium as far as we now know. Because the tarsier eyeball lacks a tapetum lucidum, it has long been thought the animal evolved from a foveate, diurnal ancestor, and that their hypertrophic eyes are a novel consequence of this biorhythmic shift for which the retina is not well suited (e.g. Martin 1990; see also Rosenberger 2010b).

Fossils allocated to genus *Tarsius* are rare. Specimens have been recovered from the middle Eocene of China (Rossie et al. 2006) and the early and middle Miocene of Thailand (Chaimanee et al. 2011; Ginsburg and Mein 1987). On the other hand, the Eocene fossils known as tarsiiforms that have sometimes been regarded as close relatives of *Tarsius* are an abundant and geographically wide-ranging group, consisting of several dozens of genera (Gunnell and Rose 2002; Szalay 1976). Often called omomyids, the systematics and taxonomy of this group is now very much in flux (e.g. Rosenberger et al. 2008; Rosenberger 2011b) and needs to be revised. As will be seen below, an important aspect of this process would be to determine with confidence which genera are cladistically closest to *Tarsius*, or not.

Gursky-Doyen (2010; see also Gursky 2007) summarises the behavioral ecology and conservation of tarsiers. This context is vitally important to interpreting the history of the animal's evolutionary adaptations because it has the potential to supply information about biological roles pertaining to anatomical structure (see Bock 1990). Four of the species she recognises (*T. bancanus, T. dianae, T. spectrum, T. syrichta*) range in weight from about 100 to 140 g, while the fifth (*T. pumilus*) weighs only 58 g. Approximately half the tarsier's time budget is spent foraging, a quarter traveling, and the remainder resting and socialising. There are differences in group sizes among the species but they typically include no more than 1–3 adults. Home range size also varies, but most studies report no more than a few hectares (<1–3 ha; some *T. bancanus* reportedly use 4.5–11.3 ha) are used regularly. Tarsiers eat no vegetation; the closest Gursky reports to a "normal" primate diet relates to rare sightings in which individuals bit, *but did not chew or ingest*, leaves. Food is exclusively comprised of arthropods and vertebrates, including moths, crickets, beetles, ants, locusts, cicadas, cockroaches, spiders, lizards, poisonous snakes, birds and fruit bats. The mean body length of insects taken by the medium-sized *T. spectrum* is 1–6 cm, thus large insects are roughly a fifth the size of adult body length and twice the length of the hands. Some 35 % of its prey items are captured in flight, 43 % is taken on or under a leaf, 13 % are from branches, and 9 % are obtained from the ground by pouncing on the target. Rosenberger (1985, 2010b) described tarsiers as sit-and-wait predators. Roberts and Kohn (1993) aptly called them ambush predators.

The most prominent gross anatomical features of tarsiers that can potentially be traced in the fossil record are the inordinately large eyes and extremely long hindlimbs. The latter are exaggerated by a greatly lengthened hindfoot (calcaneus and navicular) and are also noteworthy for the fusion of the tibia and fibula over most of the lower leg's length. Regarding the distinctions of the postcranium, metrics compiled by Dagosto (1993) indicate an Intermembral Index [(humerus + radius length)/(femur + tibia length) × 100] of 55 and a Navicular Length Index [(navicular length/navicular width) × 100] of 500, indicating an exceptionally elongate hindlimb. The nearest values for other living nonhuman primates are found in *Galago*: 62 and 401, respectively. The hands are also large and the forearms long (see Dagosto 1993; Gursky 2007). Other postcranial details concerning the hip, knee and tarsal joints have been documented (e.g. Dagosto 1993; Gebo 1998; Grand and Lorenz 1968).

The biomechanical advantage of extreme hindlimb elongation has been shown to be the enhanced capacity to apply muscular force over a prolonged phase of takeoff (Demes and Günther 1989a, b; Peters and Preuschoft 1984). During landing, where substrate reaction forces are even greater than during takeoff, the length of the hindlimb also permits braking during an extended period of time, which serves to keep the substrate reaction forces at a tolerable level. Using the legs and feet for takeoff and landing requires, as a prerequisite, a rotation to reorient them from a trailing into a leading position in relation to the trunk. To accomplish this, the small-bodied tarsiers use their tails (Peters and Preuschoft 1984), thus keeping their long-fingered hands free for capturing swift and evasive prey while in flight (Niemitz 1977, 1979, 1984b). In contrast, the large-bodied indriids are compelled to use their forelimbs during landing (Demes and Günther 1989a, b).

Tarsier teeth are also distinctive, especially in the configuration of the reduced anterior dentition (2.1.3.3/1.1.3.3), with pronounced, spiky crowns presumably designed to disable and render prey (Fig. 2a). But the fossil record, while prolific and exhibiting anatomically varied postcanines morphologies—most with the stamp of insectivory—presents little for comparison with *Tarsius* as far as incisors and canines are concerned.

The tarsier skull: gross morphology

Figure 2 presents several views of the tarsier head to illustrate the remarkable size and disposition of the eyeballs, the most consequential feature of its unusual cranial morphology. Spatz (1965; see also Castenholtz 1984; Cummings et al. 2012; Jeffery et al. 2007) determined from four wet specimens, including a subadult, that individual eye size was 80–120 % of the volume of the brain. In shape, the eye appears to be irregular: it has been termed tubular and may also be called gourd-shaped, much wider posteriorly and constricted anteriorly near the base of the cornea. The eyeball and orbit continue to grow and change shape postnatally (Cummings et al. 2012; Rosenberger AL, Smith TD, Deleon VB, in preparation) and eventually most of the eyeball comes to lie outside the eyecup, as shown by Schultz (1940). This ectopic arrangement is evident in Fig. 2, which also shows how the superficial morphology of the rostrum and orbital flanges (the orbital surround) are modified to accommodate the eye's enormous size. Note the dotted line in Fig. 2b delimiting the inferior orbital margin. It extends far laterally beyond the dental arcade, thus providing a large paralveolar shelf to increase the surface area of the orbital floor (see also Fig. 2a). This is effected (Rosenberger 2011b) by having a relatively very wide posterior dental arcade (bi-molar breadth) and a correspondingly wide (lower) facial breadth, as measured conservatively across the roots of the zygomatic arches at the origin of the superficial masseter muscle (in order to apply the measure to damaged fossils).

Also evident (Fig. 2b) is the flaring osseous plate that walls off the orbital fossa from the temporal fossa. This feature is actually a bridge of bone formed by several elements (Fig. 3). A narrow vertical process of the zygomatic meets with an

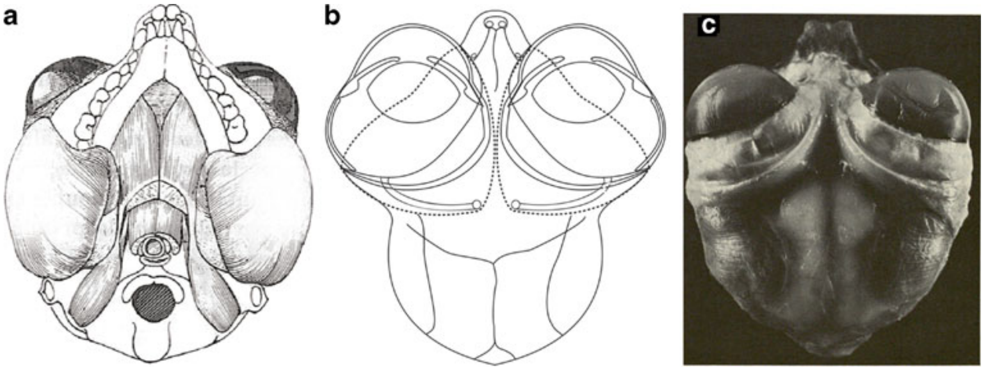

Fig. 2 Three views of the tarsier skull (**b** and **c** are *T. bancanus*) illustrating the shape of the hypertrophic eyeballs, their ectopic position in the orbital fossa, and functionally associated osseous and soft tissue specialisations. These include the antero-laterally expanded maxilla, enlarged orbital floor, lip-like everted superior orbital margins, laterally expanded partial postorbital septum, and tough periorbital ligament. **a** after Grassé (1968); **b** after Castenholtz (1984); **c** after Sprankel (1965)

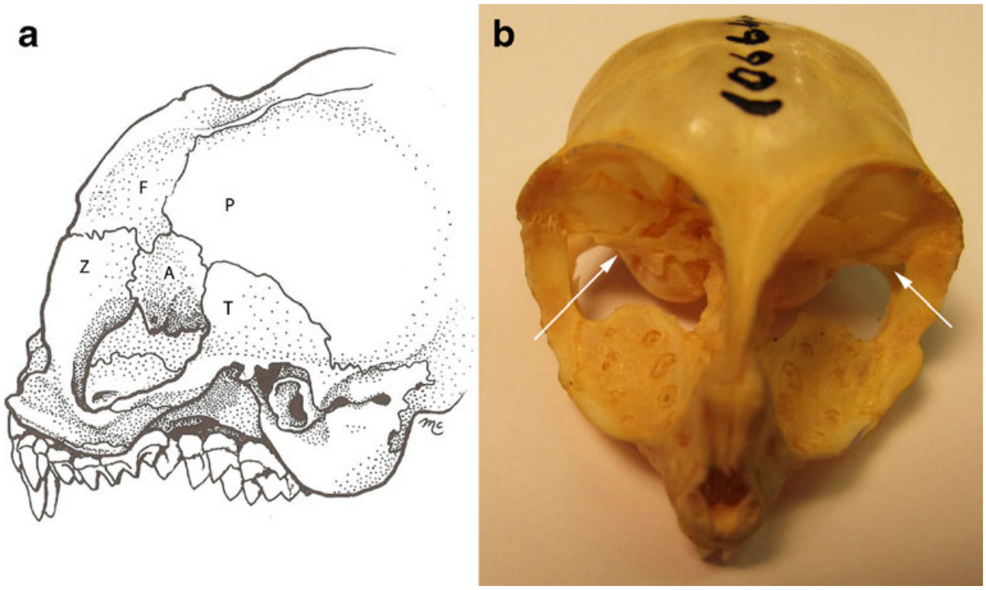

Fig. 3 **a** Posterolateral view of the partial postorbital septum of *Tarsius* (after Cartmill 1980); *Z* zygomatic, *F* frontal, *P* parietal, *A* alisphenoid. **b** Anteriodorsal view of a tarsier skull with alisphenoid indicated by *arrows*. The drawing should not be taken as "typical" of the bony proportions of the tarsier septum. Note, for example, the narrow bar-like alisphenoid ramus in the right orbit in the photograph. Its lateral end is slightly broken but in the left orbit the alisphenoid barely contacts the zygomatic near the zygomatic-frontal suture in this subadult individual. Compare with the younger individual in Fig. 6a

expanded lateral process of the frontal. Sutured to both is a small lamina that has been regarded an outgrowth of the alisphenoid (e.g. Cartmill 1980). While we refer to this element as an alisphenoid process, it appears to have a different ontogeny than its presumed equivalent in anthropoids (Rosenberger AL, Smith TD, Deleon VB, in preparation) and may thus be a neomorph. The three-bone wall has often been called a "postorbital septum", an allusion to the derived, posteriorly sealed eye socket of anthropoids. This is a controversial point, however, as it has also been argued that the septa of tarsiers and anthropoids are analogies. In this view, the anthropoid septum is seen more or less as a single unit, formed by a uniquely enlarged zygomatic bone with no substantive contributions from the frontal and alisphenoid even though these bones do meet (with the parietal) to close the lateral braincase of anthropoids (e.g. Simons and Russell 1960; Simons and Rasmussen 1989; Rosenberger et al. 2008; Rosenberger AL, Smith TD, Deleon VB, in preparation) as the pterion region. The septa of *Tarsius* and Anthropoidea may also have evolved under different selective pressures and may not subserve the same function (Rosenberger et al. 2008; Rosenberger 2010b), for the tarsier septum appears to be continuous with the everted dorsal margins of the orbital fossa, which suggests it is also a developmental phenomenon linked with orbital hypertrophy. Thus a functional interpretation, as discussed below, of the tarsier morphology becomes a priority in considering the Tarsier-Anthropoid Hypothesis.

The powerful influence of eyeball hypertrophy is evident in a variety of other features of the rostrum unique to tarsiers among living primates, such as the extreme reduction in the size of the nasal fossa and the olfactory scroll system, extensive fusion of the medial walls of the orbits, and development of a tubular channel that wires the olfactory nerves to the nose by coursing above the interorbital septum (e.g. Starck 1975). Rosenberger (2010b) has suggested that many other parts of the head, involving neurocranium, basicranium and the cranio-facial junction, are also influenced by eyeball hypertrophy. Regarding the orbits, as noted, the anterior edge of the frontal flares upward and the zygomatic flares inward to form a prominent circum-orbital margin superiorly and laterally. This pattern is extended to include the maxilla below, which is everted to widen the transverse span between postorbital bar and calvarium, and thus enlarge the orbital floor. Deep within the eyecup, a novel, upwardly directed posterior process of the maxilla also juts into the orbito-temporal fossa. The size, shape and disposition of these surrounding structures, including the units described as a postorbital septum, all appear to be integrated aspects associated with postnatal growth of the eyes (Rosenberger AL, Smith TD, Deleon VB, in preparation), indicating that they are supporting members that evolved specifically to accommodate the tremendous eyeballs (see Rosenberger et al. 2008). But there is also another interpretation available for the septum, most forcefully advocated by Cartmill (1980). He and colleagues (e.g. Cartmill 1980, 1994; Cartmill and Kay 1978; Ross 1994) argue that the septum itself has nothing to do adaptively with eyeball hypertrophy. Instead, they maintain it evolved in tarsiers and anthropoids to separate the contents of the orbital and temporal fossae so that the eyes would be shielded from mechanical interference while the *temporalis* muscles contract during feeding. This functional interpretation is a key feature of the Tarsier-Anthropoid Hypothesis.

Functional morphology of the tarsier postorbital septum

Rosenberger (2010b) proposed a basic biomechanical model of the tarsier skull that takes into account many of its structural peculiarities. The underlying hypothesis is twofold. One aspect explains detailed features, several noted above, that are specific structural evolutionary adjustments relating to the sheer size of the eyeballs. The second aspect explains the reorganisation of neurocranial and basicranial components. This involves adaptations to minimise the potential imbalance that would be produced when carrying a large head whose enormous summed eyeball mass is situated far forward of the cranio-vertebral joint. These accommodations may be seen as a spatial re-packaging of various anatomical features. It involves changes in the orientation of calvarium and the nuchal region, a shift in the location of the foramen magnum/occipital condyle complex, and adjustments to the ear region. The upshot is that the tarsier skull is highly influenced by head carriage, meaning its anatomy is an extension of the VCL positional behavior system driven by the profound consequences of enormous eyes; head and body together comprise the XVCL pattern. Here, we extend this analysis to show that this system is influenced even more by the enormous inertial forces that a tarsier experiences during leaping and landing, which have equally profound consequences for the mechanics of the postorbital surround, particularly the septum. The general model for this interpretation has been previously established by Preuschoft and colleagues (e.g. Preuschoft and Witzel 2004, 2005; Witzel and Preschoft 2002) who used finite element analysis to show that skull shape in primates and other vertebrates is directly dependent on mechanical stresses, just like the postcranium.

The forces affecting the eye are truly massive during rapid movement as a function of gravity and inertia. At *rest*, the weight of each eye (like that of the brain) pushes downward in the sitting tarsier, exerting permanently a force

$$F_g = \text{mass}*\text{gravity}.$$

In addition, if the tarsier *takes off* for a leap, the eye (and the brain, respectively) exert a force

$$F_i = \text{mass}*\text{acceleration}.$$

This force F_i is oriented against the trajectory of takeoff, at an angle oblique to the force of gravity F_g and the craniocaudal axis of the resting skeleton (Fig. 4a). The magnitude of F_i commonly is several times the force of gravity F_g. The calculations of Peters and Preuschoft (1984), which were based on movie films taken by C. Niemitz, assumed accelerations of 2–7 times earth gravity, but the realistic values may well be considerably greater. Data on *Galago moholi* (similar in size to a tarsier and jumping similar distances; see Demes and Günther 1989a, b; Günther 1989; Günther et al. 1992) show that in acceleration the animal reaches up to 12 times gravity. In the larger *Galago garnetti*, the body is propelled with 8 times the acceleration of gravity; in *Lemur catta*, it can be 4–5 times gravity. For comparison, human high-jumpers reach 4 times gravity (Demes and Günther 1989a, b).

The force F_g forms, together with F_i, a resultant (F_r) that presses the eyeball into its socket. According to film recordings of tarsiers (Niemitz 1984b; see also Peters and Preuschoft 1984), the head during takeoff is usually kept at an angle of about 20–30° between the nose and the trajectory, so that the force F_r indeed acts more or less perpendicular to the plane of the orbital margin (Fig. 4a). This means that the enormous resultant force must evoke in the orbital surround a counter pressure that stabilises the

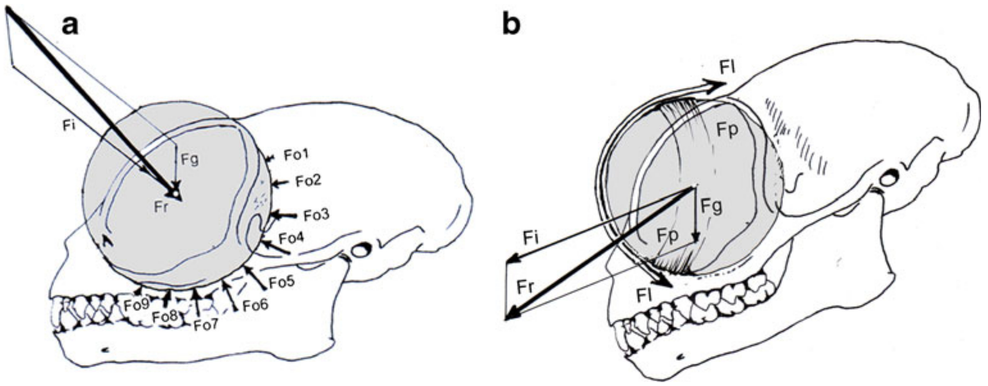

Fig. 4 Lateral views of a tarsier skull with their huge eyes under the influence of acceleration and deceleration. **a** During leaping takeoff; **b** during landing (braking and touchdown) after a leap. Aside from weight (*Fg*), the inertia of the eyeballs (*Fi*) exerts forces on the eyeballs. Both forces combine to a resultant (*Fr*), the direction of which depends upon the direction of the leap as well as on the posture of the head. The head positions assumed here are selected in accordance with Niemitz (1984b). While acceleration presses the eyeballs into their sockets with the forces *Fo1–Fo9*, deceleration pulls the eyeballs outward from the orbits (Fr directed forward). The orbito-temporal septum provides a reaction force Fo during acceleration, which is in the illustration is split into 9 components (*Fo1–Fo9*). Tension-resistant structures, such as the eyelids, are held taut by the force Fl during deceleration

eyeball in place. The novel features of the tarsier posterior orbital compartment, such as the enlarged frontal and alisphenoid process contributing to the widened postorbital bar and the upwardly directed posterior maxillary process, form a supporting framework positioned to secure the eyeball during a biomechanically challenging situation, acceleration during take-off for a leap. Because of the expansion of the bony elements behind and under the eyeball, the compressive forces are distributed over a large area. This reduces the danger of damaging the very sensitive structures of the eye, perhaps also including the optic nerve which has a long traverse within the orbit due to the eye's lateral position relative to the optic canal that is situated medially (see Fig. 2b).

Several other morphological details fit this picture. Dorsally, around much of the orbit the margin is everted. This rim is not a normal edge where the inner and outer surfaces around the orbital fossa converge. Rather, by extending as a flange, they produce a further "enlargement" of the orbital fossa's diameter. Thus, the eyeball is allowed to press more deeply into the fossa during acceleration, because the largest diameter of the ectopic eye actually lies far forward of the rim while static conditions prevail. So, more room (for both eyeball and periorbital ligament?) may be required as the eyeball moves backward under acceleration, and the support area is consequently enlarged by the expanded brim.

Any acceleration of an animal's body is inevitably followed by a deceleration, physically a "negative acceleration". These have turned out to be even more challenging and therefore more consequential biomechanically than positive accelerations, as the forces exerted during the first phase, braking, before contact with the substrate, are extremely high (because an impulse passes quickly through the skeletal elements). During landing phases, as the animal decelerates, the inertia of the tarsier's enormous eyeball mass would tend to pull them forward out of the orbital fossae (Fig. 5). The effect is profound since tarsiers seem to direct their nose toward the landing site during the deceleration phase of a leap (Niemitz 1984b). Tension-resistant structures, such as the strong periorbital ligament (see Fig. 2c), are thus a necessary adaptation to maintain the position (and shape?) of the eyeball within the orbital fossa. Shutting the eyelids, as reported by Niemitz (1984b), may be an additional safety measure employed by tarsiers to secure eyeball mass upon landing.

In considering a dorsal projection of the head, if a mediolateral component comes into play during an oblique jump, as per the example given in Fig. 5a, the rear walls of the orbits are loaded in different ways. On the left side, the forces act nearly normal to the "socket" and are distributed over a large bony surface (Fo1–6). On the right side, the components of the force F_r at the lateral margin of the fossa, at the extensions of the frontal, alisphenoid and zygomatic processes, produce higher partial forces (Fo2–6) than at the medial surfaces of the orbit. The more lateral force components exert bending moments against the lateral margin, exerting a rearward rotational torque. This part of the orbit can resist rather high bending moments because the frontal

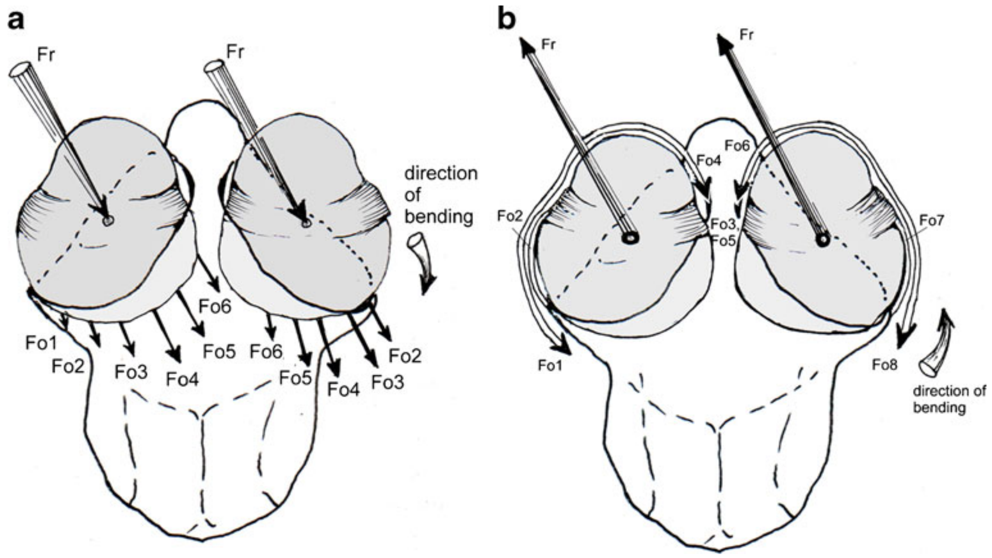

Fig. 5 Top views of the skull and eyeballs under the conditions of takeoff (**a**) and braking (**b**) show the resultant forces (*Fr*) acting on the eyeballs. A deviation between the skull's sagittal plane and the direction of Fr is assumed in order to show the potential variation. The inertial forces evoke in the orbita reaction forces *Fo*. During takeoff, these are distributed evenly over the entire floor of the orbits (including the posterior maxillary process) and simplified as a series of partial forces *Fo1–Fo6*, from lateral to medial. During braking, mass inertia tends to pull the eyeballs away from the orbital fossae. Connective tissue (*Fo2*, *Fo3* on the *left* side and *Fo5*, *Fo7* on the *right*) and the musculature of the eyelids (*Fo1*, *Fo4* on the *left* side, *Fo6*, *Fo8* on the *right*) keep them in place. Takeoff and braking thus bend the lateral margins of the orbits rearward or forward (*curved arrows*)

bone at the roof and the zygomatic and maxillary bones at the bottom function as ties where bending moments are sustained by braces. It is also possible that the tension-resistant structures of the eyelid reduce the bending moments acting on the lateral margin.

Because of the large diameter of the orbit's circumference, the postorbital septum presents a dangerously long lever arm for the high tensile forces exerted by tension-resistant structures, which would produce a tendency to bend it forward on the alisphenoid (curved arrow in Fig. 5). This may be counteracted, in part, by the masseter muscle, which has a marked horizontal component of force at its origin at the base of the vertical process of the zygomatic, more than is typical of primates with smaller orbits and a primitive postorbital bar (Fig. 6). This strong horizontal component, in the antero-posterior and medio-lateral planes, is produced by the novel geometry of *Tarsius*: (1) the extremely wide palate (and orbital floor) and everted maxilla, which displaces the origin of masseter far laterally; and (2) the extremely shallow mandibular angle for the muscle's distal insertion, on the (derivedly) reduced gonial angle of the tarsier jaw. This arrangement minimises the torques at the zygomatic-frontal suture and at the contact with the alisphenoid. These complex forces may also be balanced by musculature, as Witzel and Preschoft (2004) found in their finite element analysis of hominoids, where fibres of anterior temporalis inserting onto the postorbital septum and temporal fascia attaching to the zygomatic arch had a strong influence on the forces transmitted by the zygomatic and into the frontal region. The same effect seems to be exerted by the superficial temporal fascia, which obviously is of great importance in keeping the thin zygomatic arch in balance against the pull exerted by the *m. masseter* in hominoids (Witzel et al. 2004) as well as in monkeys (Curtis et al. 2011).

Form, function and phylogenetics: the postorbital septum

This functional model has phylogenetic consequences. On the one hand, it provides a rationale for interpreting similar features in the fossil record as structural–functional homologies, with a high likelihood of also establishing correct polarities, thus also providing a sound basis for assessing possible cladistic connections. For example, finding everted supraorbital margins among large-eyed fossils thought (for other reasons) to be tarsier relatives would imply that they, too, are adapted to secure the eye against massive acceleration forces, thus corroborating the phylogenetic hypothesis on the basis of both structural and behavioral continuity. On the other, our biomechanical model of the orbital surround offers a rationale for refuting the homology of descriptively similar traits alleged to be derivedly shared with anthropoids because their functions and bioroles—thus their initial, selectively causal determinants—differ, i.e. they evolved for different reasons.

This goes to the heart of the argument about the postorbital septa of tarsiers and anthropoids. As noted, it has long been seen as a possible synapomorphy linking tarsiers and anthropoids to the exclusion of any tarsiiform fossils. In recent decades, this idea was most forcefully advocated by Hershkovitz (1977), Cartmill and Kay (1978), Cartmill (1980) and Ross (1994). Cartmill (1980) provided the most

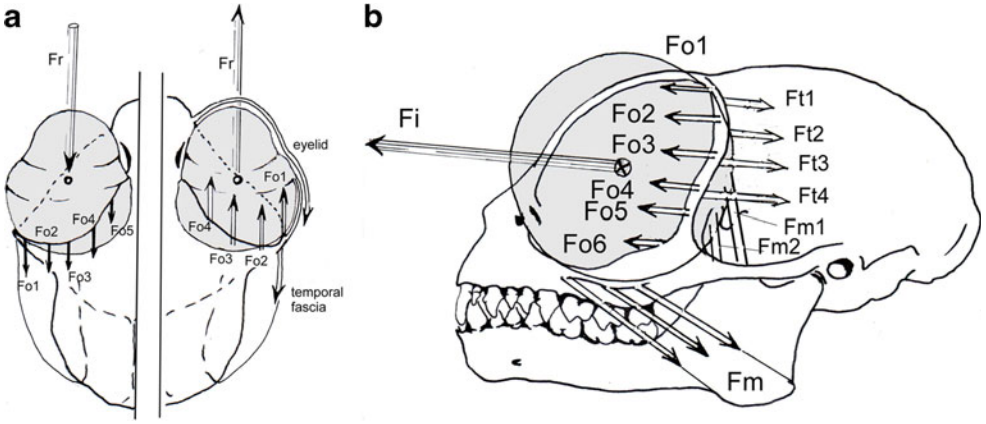

Fig. 6 **a** Top views of the tarsier skull cut into two independent halves along the midsagittal plane. During acceleration, the resultant force *Fr* pushes the eyeball into its socket (parallel to the midsagittal plane), where it evokes the reaction forces *Fo1–Fo5*. Because of slight deformation of the vitreus body, the connective tissue between orbital margins and periorbital ligament may be stretched (not shown) on the lateral side. *Right side* The resultant force Fr pulls the eyeball away from its socket, and the connective tissue between periorbital ligament (*Fo1–Fo4*) plus the eyelid keep it in place. As in Fig. 5, the lateral margin of the orbit is moved rearward (*left*) or forward (*right*). **b** Lateral view corresponding to the right side of (**a**), during deceleration. The resultant force F_i is directed forward and reaction forces *Fo1–Fo6* are applied to the lateral margin of the orbita. The zygomatic bone is kept in its place by the superficial fibres of the *m. masseter* (*Fm*), by fibres of the temporal fascia *Ft1–Ft4*, and perhaps also by fibres of the temporalis muscle, which originate on the rear wall of the orbit

detailed argument, including a functional hypothesis that explained the full septum of anthropoids and the partial septum of tarsiers as a jointly inherited adaptation designed to insulate the eyeball from movement that would be introduced by the contraction of the *anterior temporalis* if it were separated from the eyeball only by soft tissue. The underlying homology hypothesis has been debated strenuously (e.g. Rosenberger et al. 2008; Simons and Rasmussen 1989) on anatomical (and systematics) grounds, and also because mechanical support for hypertrophic eyeballs—in contrast to the small eyeballs of anthropoids—seemed like a better explanation for the specific features of *Tarsius.* In other words, the tarsier condition was interpreted as a convergent autapomorphy.

One aspect stressed by Simons, Rasmussen and Rosenberger as a basic challenge to the homology hypothesis of Cartmill and co-workers is that there is actually very limited morphological continuity between the postorbital walls of tarsiers and anthropoids. In higher primates, it is formed by a very much enlarged, spoon-like zygomatic that wraps around the side (and back) of the orbital fossa as a large lamina extending from the zygomatic's forward edge. It is largely situated in a parasagittal plane. In tarsiers, the wall is little more than a flattened, still quite narrow zygomatic (in comparison with anthropoids) that fuses with a lateral outgrowth of the frontal and the alisphenoid processes. The septum is positioned entirely in the coronal plane and closes off the temporal fossa from above, leaving a large gap below. Furthermore, most of the physical separation between temporal muscles and eyeballs in tarsiers (Fig. 2b) exists because the orbit fossae are shifted medially and posteriorly reset up against the wide anterior calvarium, which is raised relative to the rostrum for biomechanical reasons (Rosenberger et al. 2008).

From an anatomical view, the insulating effect of the composite postorbital wall in tarsiers is thus limited, as the wide anterior cranial fossa backs up most of the eyeball and the temporal fossa is adjacent to only a small lateral portion of the globe (Rosenberger et al. 2008). Experimentally, there is no empirical evidence supporting the insulation hypothesis, although there is indirect evidence suggesting it is plausible, as discussed by Heesy et al. (2007). When there is a continuous orbito-temporal fossa, as in galagos and cats, electrical stimulation of the *temporalis* muscle can produce sufficient eyeball movement to expect interference with vision. As these authors also note, the medial pterygoid can have a similar influence on eyeball stability, and it is well developed and inserts deeply into the orbital fossa in *Tarsius* (Cartmill 1980), uniquely among primates. If so, one wonders why, if selection saw advantages in shutting off the eyeballs from muscular interference as a prerequisite for a foveate retina, tarsiers have opted to elaborate a medial pterygoid which is not shielded from the orbital contents.

Cartmill (1980) also emphasised the presence of an alisphenoid contribution to the postorbital wall in tarsiers and anthropoids as a pivotal homology. But this, too, carries little weight as the anatomy is hardly similar. As shown in Fig. 7, the proportions of these various septal elements differ markedly in young individuals of *Tarsius* and the small anthropoid *Callithrix*, and these proportions remain quite similar as they grow into adulthood. In the marmoset, the zygomatic is always large and the alisphenoid is very large. In a perinatal tarsier, the zygomatic is ribbon-like and the alisphenoid may be so poorly differentiated that it cannot be identified (Rosenberger AL, Smith TD, Deleon VB, in preparation). Certainly, at this stage, it shows no lateral process

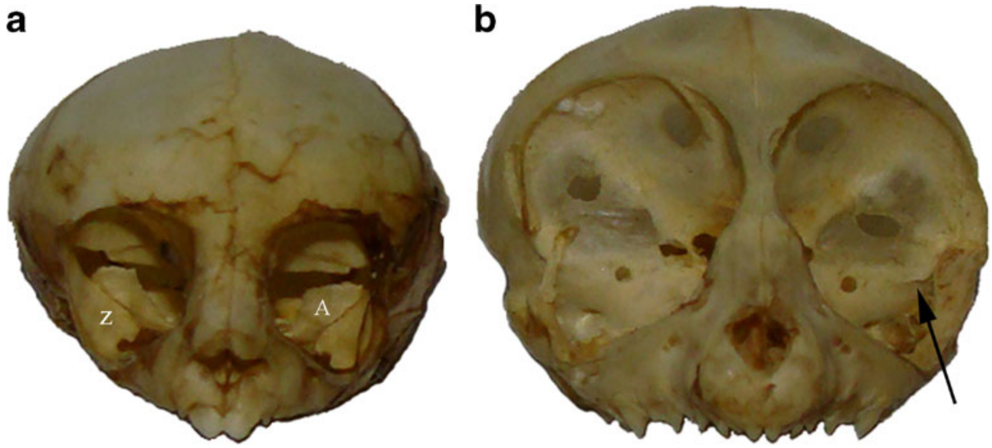

Fig. 7 **a** Perinatal or infant skulls of a marmoset (*Callithrix* sp.) and **b** a tarsier (*Tarsius* sp.), not to same scale. *A* alisphenoid, *Z* zygomatic. At this stage, *Tarsius* clearly does not exhibit circumorbital flanges or the laterally expansive frontal or alisphenoid processes that contribute to the postorbital septum, all of which develop postnatally. *Tarsius* also lacks an enlarged zygomatic, while the large orbital surfaces of the zygomatic (rotated out of position in this preparation) and alisphenoid are already visible in the marmoset. The *black arrow* points to what may be the beginnings of extra-orbital alisphenoid lamina in the tarsier. The marked contrast in development is consistent with the notion that postorbital closure in tarsiers and anthropoids evolved convergently, in response to eyeball hypertrophy in tarsiers but in a different, small-eyed context in anthropoids

approaching the ascending ramus of the zygomatic. Thus, the "eye funnel" configuration that defines anthropoids is hardly emergent in young tarsiers.

Additionally, to follow Cartmill's logic (1980) implies an unanticipated equivalence of tarsiers and modern catarrhines, for it would mean that *Tarsius* shares the same state in the bony mosaic of the pterion that distinguishes living catarrhine from living platyrrhine anthropoids. In the former, the alisphenoid sutures with the frontal and zygomatic, as in tarsiers. In the latter, the alisphenoid does not contact the frontal because it is separated from the alisphenoid by a zygomatic-parietal suture. This equivalence would further imply that the crown catarrhine condition is primitive for anthropoids, which is possible but contrary to what has been established for a large variety of craniodental and postcranial features, wherein platyrrhines are thought to be persistently primitive (see Fleagle 1999).

These examples of anatomical discord underpinning the Tarsier-Anthropoid Hypothesis means the "eyeball support" hypothesis we advocate to explain the novelties of *Tarsius* gains more power, increasing the likelihood that the posterior wall of its orbita involves a uniquely selected pattern unlike anything relating to the small-eyed, non-leaping anthropoids.

Large-eyed Eocene tarsiiforms linked with tarsiers

There are few Eocene tarsiiform genera for which there is cranial and/or facial evidence directly bearing of the phylogenetics of *Tarsius*, but the evidence is insufficient to attempt building a true phylogenetic branching sequence (see Gunnell and Rose 2002; Rosenberger et al. 2008). Yet enough is known to identify several forms with a high likelihood of belonging to a *Tarsius* clade based on derived features associated with eyeball hypertrophy, especially in light of the functional models presented above and in Rosenberger (2010b). However, it should be remembered that these fossils are of Eocene age. Many exhibit features far more primitive than *Tarsius* or features of indeterminate polarity. *Tetonius*, for example, lacks the highly compressed interorbital pillar; *Omomys* has an impressively large snout; *Necrolemur* has an unusual petromastoid morphology. And none exhibit the septal specialisation of the orbit's posterior compartment. But this in, and of, itself is instructive (Rosenberger 2010b): the North American fossils are not adapted postcranially to the XVCL pattern of locomotion, so an exhaustive complement of the modern features is not to be expected in the cranium either, especially following the above biomechanical analysis. In summarising this information, we begin with North American forms and follow with the European evidence.

Tetonius: The discovery and description of *Tetonius* (Cope 1882) created the original foundation of the Tarsier-Tarsiiform Hypothesis, as Cope drew a number of favorable comparisons between the fossil's cranium (Fig. 8) and *Tarsius*, especially concerning the large orbits of both. Later work cast doubt on this interpretation, as metrical studies did not support the notion that *Tetonius* has especially large orbital apertures relative to skull size or molar size (e.g. Heesy and Ross 2001; Kay and Kirk 2000; Martin 1990). However, this assessment should be regarded with caution. The primary variable used as a gauge of eyeball size in these studies was orbital aperture, but this may be of less significance among fossil tarsiiforms if the eyeballs were ectopic as in *Tarsius.* In that case, the circumference of the orbital margin compliments a line of latitude well below the eyeball's equator, thus it underestimates total eye size.

While there are several indicators that the cranium of *Tetonius* is not as advanced toward ocular hypertrophy as a tarsier's, the orbital floor is clearly capacious (Fig. 8). It deeply excavates the maxilla anteriorly, flares laterally beyond the dental arcade, and it is framed by a postorbital bar that is flattened and wide, ribbon- or spatula-like rather than rod-like —all indications that the eye was large and fit snugly in the orbital fossa. There is a marked ridge along the length of the dorsal orbital margin but no prominent flange is evident. The morphology may be indicative of attachments for strong tensile-resistant connective tissue, such as a tarsier-like periorbital ligament. Importantly, the posterior nasal aperture of *Tetonius* appears to be quite restricted in size, unlike the broad choanae seen in small-eyed *Rooneyia* and Eocene strepsirhines (Rosenberger 1985; Rosenberger et al. 2008). This means the posterior nasal fossa was reduced and the medial orbital walls were likely fused posteriorly (Rosenberger 2010b; Ross 1994), features also indicative of eyeball hypertrophy when found in combination. But *Tetonius* has a wide interorbitum anterosuperiorly, which immediately places constraints on how voluminous the eyeballs can be. The cranium also lacks the anterior shelving of the orbital floor and the dorsal orbital margins do not appear to be everted as in tarsiers. The orbital plane is laterally oriented because the postorbital bar is not displaced as far to the sides as in *Tarsius* (see Rosenberger et al. 2008), which produces a shallower angle, and the rostrum is not highly recessed below the forebrain. Overall, this pattern appears consistent with a much enlarged eyeball but its proportions would not have matched those of *Tarsius*.

Shoshonius: Recent discoveries of *Shoshonius* fossils present important information on the affinities of the genus, both cranial and postcranial (Beard et al. 1991; Beard and MacPhee 1994; Dagosto et al. 1999). These include anatomical studies that closely associate *Shoshonius* and *Tarsius* cladistically. Beard et al. indicated that the relative size of the orbital aperture was larger in *Shoshonius* than in *Necrolemur* and *Tetonius*, although smaller than in *Tarsius*. This view is not fully supported by Rosenberger's (2011b) analysis, where it is shown that when relative bi-molar

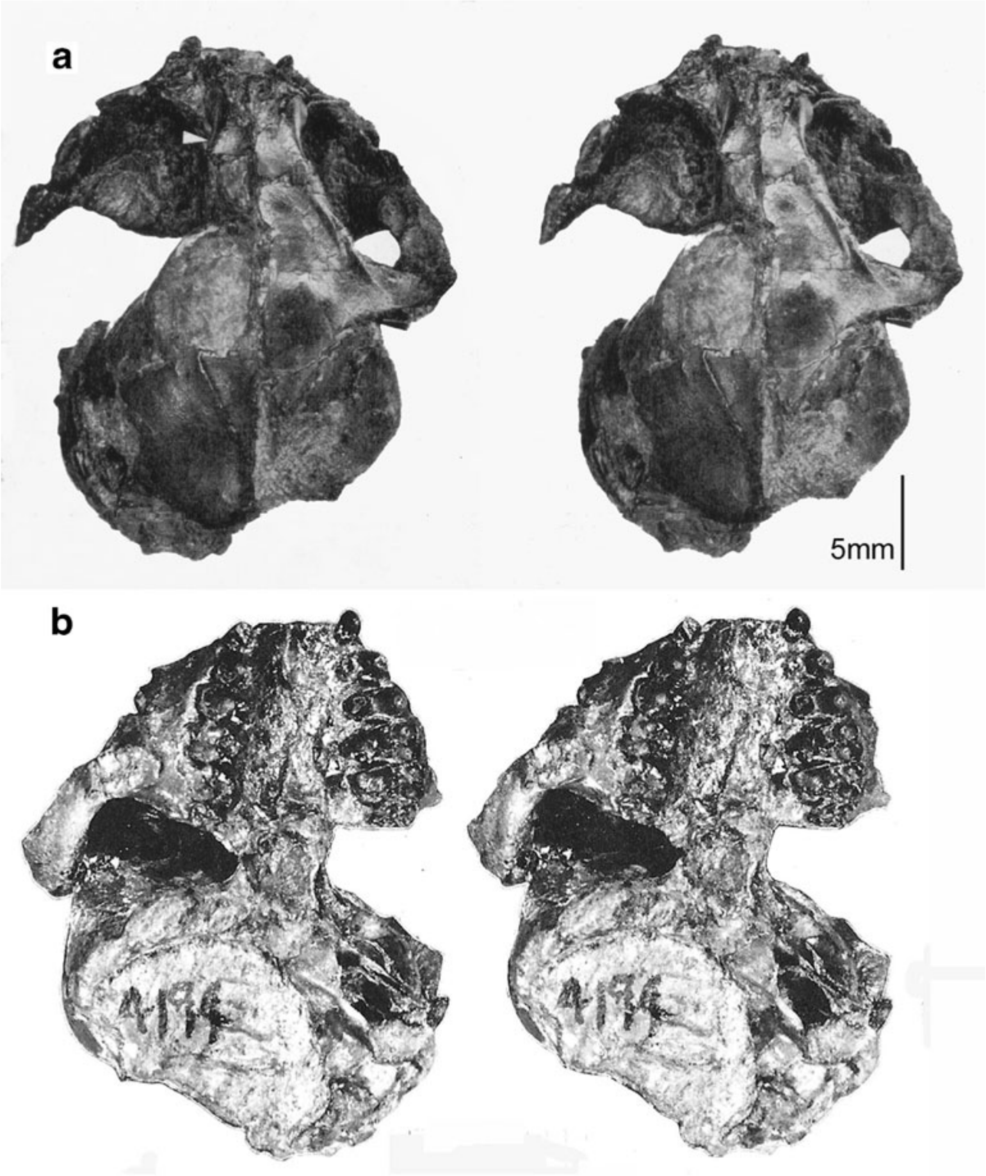

Fig. 8 Stereo pairs of the skull of *Tetonius* (**a** after Radinsky 1967; **b** after Szalay 1976) showing the large, deep, transversely expanded orbital floor, marked ridge along the superior orbital margin of the right orbit, wide postorbital bar, and laterally directed plane of the orbital aperture (**a**). Palatal view (**b**) shows the narrow choanae and wide paralveolar extension on the essentially intact right side

breadth is used as a proxy for orbital fossa size, *Shoshonius*, *Necrolemur* and *Tarsius* all plot well above galagos and anthropoids of comparable body mass, with the latter pair essentially enjoying over-plotting proportions. It remains to be seen if this is a more sensitive measure of eyeball size than orbital aperture in view of the potential discord between aperture and globe diameter when the eyeballs are ectopic. In any case, like *Tetonius*, *Shoshonius* also had narrow choanae, a laterally facing orbital aperture, a relatively wide interorbitum, and a ridged superior orbital margin but no flange.

Strigorhysis: A maxillary specimen of *Strigorhysis* (Rosenberger 2011b) presents an essentially intact orbital floor indicating that its orbits were enlarged. The shape of the palate and dental arcade is stunningly similar to *Tarsius*, which is an important clue in, and of, itself. Quantitative comparisons of dental arcade width and paralveolar shelving indicate that the orbital fossa of *Strigorhysis* was enlarged, comparable in relative size to the smallest living tarsier, *T. pumilus*.

Hemiacodon: Hemiacodon deserves brief mention since Simons (1963:74) noted that this form shows "…unusually large orbits for an Eocene prosimian and…a raised circumorbital flange somewhat suggesting a condition antecedent to…living *Tarsius*". The specimen informing Simon's inference is a frontal bone (Fig. 9). The superior orbital margins of the one known frontal (USNM 21878) allocated to *Hemiacodon* appears to be well defined and prolonged upwards, flange-like. The orbits are also laterally oriented and the root of the interorbital region is relatively very wide. Overall, the morphology is not unlike *Tetonius* but the flange-like margin may be better developed.

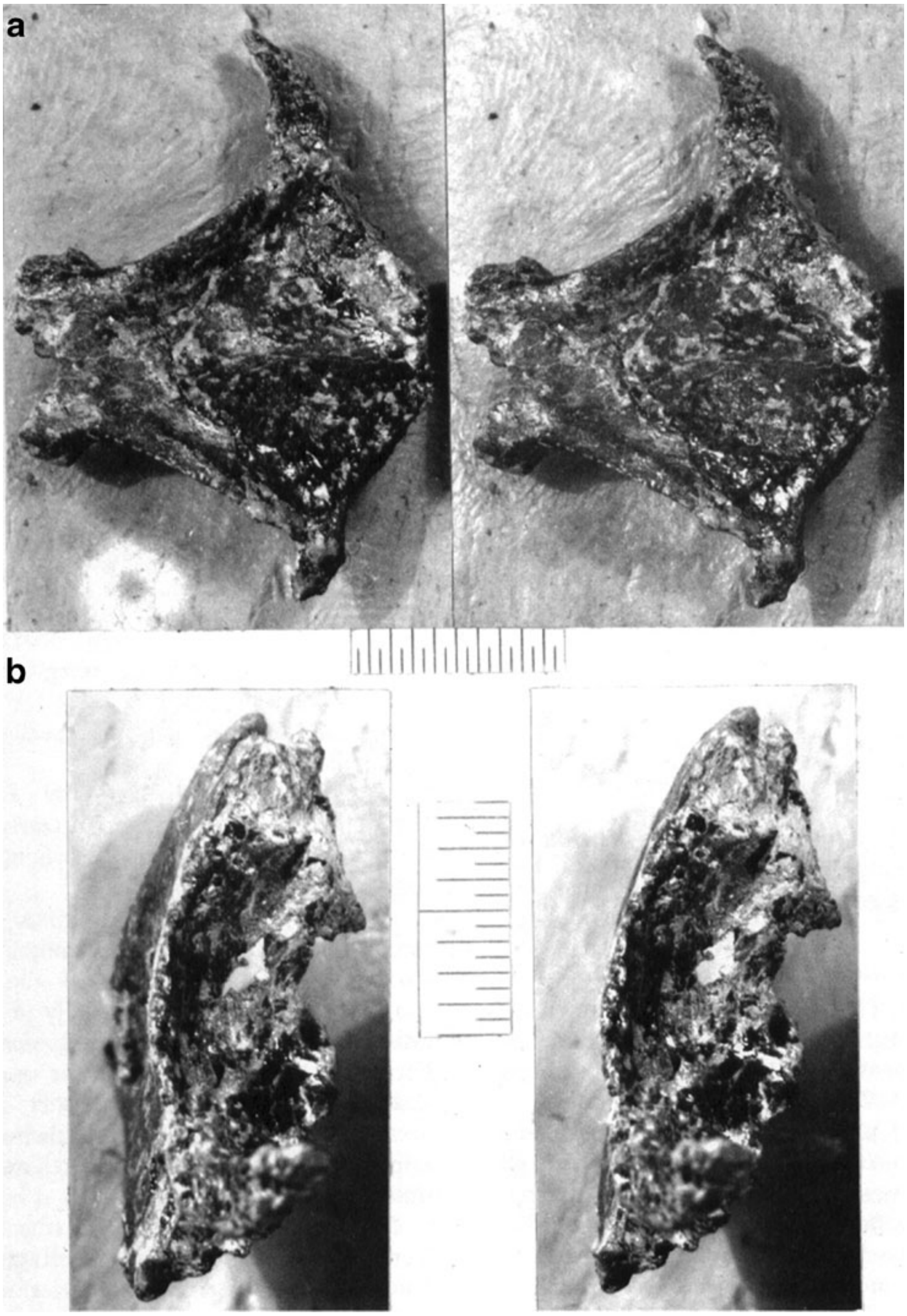

Fig. 9 Stereo pairs of the frontal bone of *Hemiacodon* (from Szalay 1976) in dorsal (**a**) (anterior to the left) and medial (**b**) (anterior to the bottom) views. Note the everted lip-like ridge, or flange, along the superior orbital margins and the deeply concave medial walls below the raised orbital margin

Omomys: In *Omomys*, incomplete orbital apertures make it impossible to determine actual diameters, but Heesy and Ross (2001) have calculated a projected width based on a segment of the inferior margin in one specimen. They infer that eye size may have been larger in *Omomys* than in *Shoshonius*. The description of a new partial cranium (Burger 2010) of *Omomys* may add more here. It makes the interpretation of the orbits more complex as the specimen shows that *Omomys* had a massive snout, which may not be consistent with very large orbits and appears not to be in accord anatomically with any of the other tarsiiforms discussed here as being large-eyed. So, the Ross and Heesy interpretation should be viewed cautiously.

Necrolemur and Microchoerus: Necrolemur is better known by cranial material than any Eocene tarsiiform but there is no recent comprehensive synthesis of its morphology and variation, which deserves monographic treatment. Important cranial features have been noted as possible synapomorphies shared with tarsiers (e.g. Rosenberger 1985; Rosenberger et al. 2008; Ross 1994; Simons 1960, 1972; Simons and Russell

1960). These include: at least partial fusion of the medial orbital walls, narrow choanae and a narrow basioccipital; overlap of the lateral pterygoid plates onto medial bullar wall; and, a narrow, trough-like glenoid fossa. As measured by aperture diameter, the eyes may not have been exceptionally enlarged (e.g. Kirk 2006). However, using bimolar breadth as a proxy for orbit floor size indicates that *Necrolemur* had proportions comparable to modern tarsiers (Rosenberger 2011b). *Microchoerus*, probably a sister-genus of *Necrolemur*, is fairly well known cranially, and essentially similar in the details bearing on this discussion.

Nannopithex: Known mostly by crushed, but informative, cranioskeletal material (see Thalmann 1994), Simons (1963) concluded that the orbits of the European *Nannopithex* were very large (see also Rosenberger et al. 2008), based on its narrow choanal region and apparent degree of paralveolar extension of the maxilla. Little more can be said at this time.

Pseudoloris: The cranial remains of *Pseudoloris* (Fig. 10) have not been well studied since Simons' early reviews (Simons 1960; Simons and Russell 1960) of the European fossil tarsiiforms, which basically carried forward the interpretations of Teilhard de Chardin (1921) and Le Gros Clark (e.g. Le Gros Clark 1934, 1959). Simons (1972:168) noted specific resemblances shared with tarsiers: "…relatively enlarged orbits, bell-shaped margin of palate with circular terminal nares, a short compressed snout, and flaring orbital margins, as well as similar frontals…". He (Simons 2003) later noted that a tarsier-like interorbital septum was also likely present and that the eyes of *Pseudoloris* were comparable in size to *Tarsius*. Rosenberger et al. (2008) complimented this argument by further contextualizing features associated with the ultra-large eyeball pattern from a functional perspective.

In summary, a variety of North American and European fossil tarsiiforms exhibit synapomorphies in the skull shared exclusively with tarsiers, involving features associated with moderately enlarged to relatively very large eyes. Exhibiting large orbital floors, paralveolar shelving, laterally facing orbita and ridged superior margins, it seems likely that this group had a least minimally ectopic eyeballs foreshowing tarsian hypertrophy. But none have distinctly flaring, marked, everted orbital margins, which are developmentally linked with rapid, hypertrophic postnatal growth of the eyeball (Rosenberger AL, Smith TD, Deleon VB, in preparation). Nor do any show indications of a postorbital septum, which we interpret here as a correlate to the XVCL locomotor complex. When preserved, the interorbital region of these fossils tends to be relatively wider than the narrow pillar found in *Tarsius*. This makes it likely that the tubus olfactorius, that in tarsiers carries the olfactory nerve to the

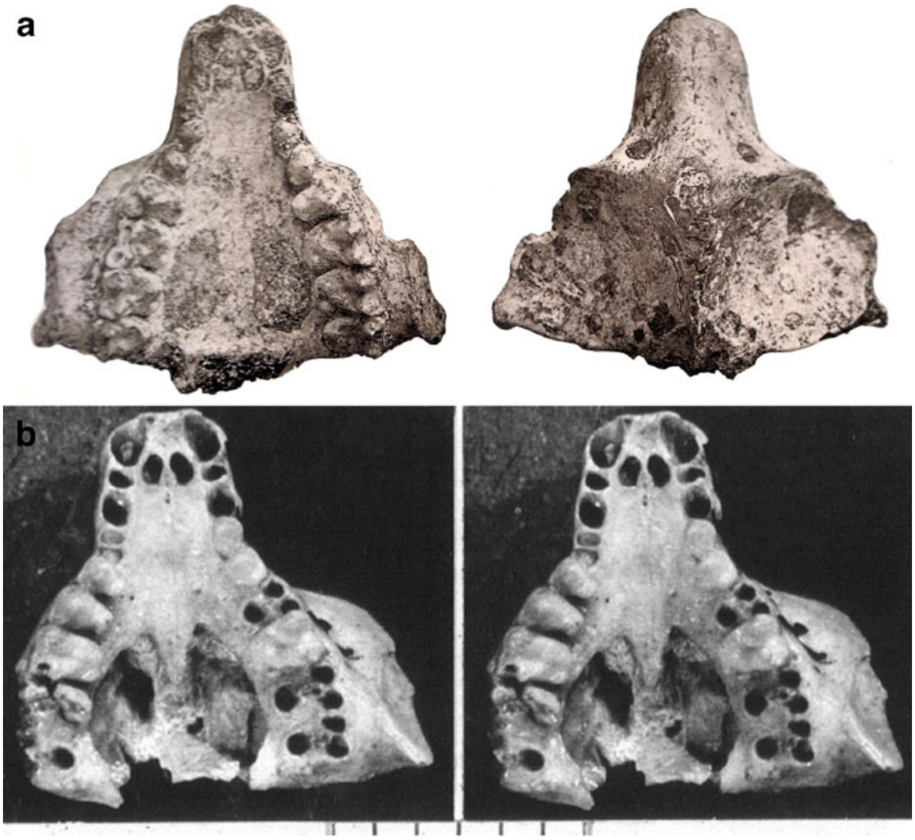

Fig. 10 **a** Palatal (*left*) and dorsal (*right*) views of a facial specimen of *Pseudoloris* (from Teilhard de Chardin 1921). **b** Stereoscopic image of *Pseudoloris* palate (from Szalay 1976). A combination of features indicates the eyeballs were quite enlarged, including the marked, tarsier-like width differential between anterior and posterior snout and the everted maxillae

anteriorly displaced nasal fossa, had not yet evolved. This, too, is associated with the massive hypertrophy of the eyes in *Tarsius*. Among the fossils discussed, the two genera with most potential to approximate the large-eyed anatomy of tarsiers are *Strigorhysis* and *Pseudoloris*, although they are still represented only by material illustrating the morphology of the orbital floor and face, not the orbit's posterior compartment. So, this notion must also be treated with caution.

While the available data are limited, there is an overarching hypothesis that may help explain the mosaic patterns exhibited by the fossil evidence, although many details need to be filled in. A key part of the hypotheses relates to locomotion. It appears that two patterns of locomotion can be delineated among fossil tarsiiforms, one that is primitively galago-like, i.e. emphasising a blend of leaping and quadrupedalism, and another that is derivedly more tarsier-like, i.e. a highly modified leaping specialisation (e.g. Anemone and Covert 2000; Dagosto 1993; Gebo 1998). The taxonomic distribution of the latter form among fossil tarsiiforms is not well understood, but it is demonstrated by the presence in *Necrolemur* and/or *Microchoerus* of super-elongated tarsals and, in the former at least, a fused tibio-fibula (Fig. 11). Known to lack one or both of these traits, the more primitive locomotor type is evident among all North American tarsiiforms for which comparable material exists, which includes several genera discussed above (*Tetonius*, *Shoshonius, Omomys, Hemiacodon*). Cranially, none of them have orbits designed to accommodate the massive inertial loads experienced by tarsier-sized eyeballs under extreme leaping conditions. This makes the cases of *Necrolemur* and *Microchoerus* interesting as they appear to have the more advanced tarsal and/or tibio-fibular specialisations, while their dentitions may suggest a secondary shift away from tarsier-like predation, which seems widespread among fossil tarsiiforms (Rosenberger 2011b). This presents a complex scenario requiring further investigation. It suggests the cranial anatomy of *Necrolemur* and *Microchoerus* may have retained aspects of the primitive pattern even after the more advanced hindlimb morphology evolved.

Discussion

The northern parts of the world at the Time of Messel were inhabited by two major groups of primates which have left an ample record of biodiversity, the adapiforms and tarsiiforms. Both groups have long been central to discussions of the origins of higher primates, the Anthropoidea. The recent discovery of *Darwinius masillae* at Grubbe Messel (Franzen et al. 2009) will no doubt generate new information bearing on anthropoid origins, for it is a remarkably complete fossil and it has already attracted considerable attention. On the other hand, the Messel site has not yet produced any fossil tarsiiforms. Is this a matter of ecology or chance? One expects the latter, and that eventually Messel will reveal more secrets about this branch of primate evolution. For the nearby Geiseltal site, which overlaps in time and faunal composition (e.g. Haubold and Hellmund 1998), has yielded both groups, including one of the fossils discussed above, *Nannopithex*.

Nannopithex is one of several European and North American fossil tarsiiforms which may have a direct bearing on the origins of tarsiers, and therefore on the origins of Anthropoidea. The reason for this is that tarsiers have long been understood to be closely related to anthropoids, but

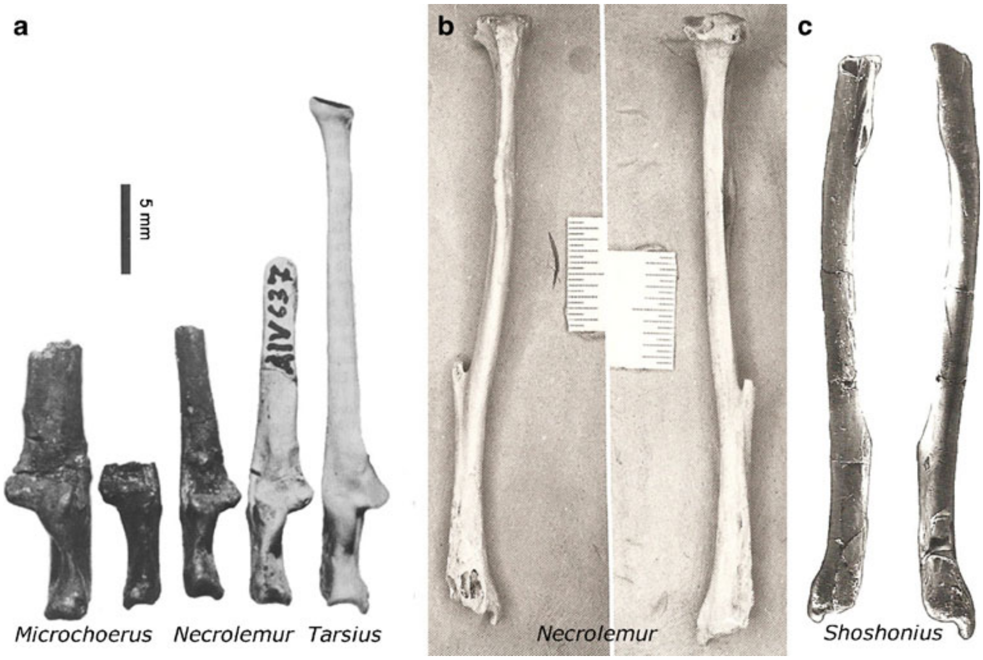

Fig. 11 **a** Calcanea of *Microchoerus*, *Necrolemur* and *Tarsius* (from Schmid 1979) showing massive elongation of the distal portion, far exceeding the proportions of North American fossil tarsiiforms despite all being broken distally. **b** Tibio-fibula of *Necrolemur* (anterior on left side). **c** Tibia of *Shoshonius* (anterior on right side; reproduced at same tibial length as *Necrolemur*). The unfused condition of *Shoshonius* anticipates fusion in *Necrolemur* and *Tarsius*. *Shoshonius* is an example of the more primitive galago-like style of VCL, while *Necrolemur* is more tarsier-like, although cranial morphology indicates the XVCL pattern had not yet emerged in *Necrolemur* or *Microchoerus*

just how close continues to be a matter of debate. Advocates of the Tarsier-Anthropoid Hypothesis maintain there are no fossils among the Eocene tarsiiforms with closer cladistic ties to *Tarsius* than the phylogenetic linkage between *Tarsius* and Anthropoidea. In addition to attempting to falsify core (but not all) anatomical and functional features of the Tarsier-Anthropoid Hypothesis, we have tried to show the contrary, that the cranium (and postcranium) presents cogent evidence of closer phylogenetic ties between various fossil tarsiiforms and *Tarsius*, although we find the taxa still too poorly known anatomically to generate a robust phylogenetic tree that connects the dots in any detail.

The features linking *Tarsius* with fossils such as *Tetonius* and *Shoshonius* and *Strigorhysis* are functionally integral to the design of the tarsier head, one of the most highly modified adaptive complexes found among primates and centred on the packaging, support, biomechanical and physiological function of what appears to be the largest sets of eyeballs, relatively, found among mammals. It is difficult, therefore, to see these patterned resemblances as anything but derived homologies. The Darwinian null hypothesis, that synapomorphies associated with this system are shared by tarsiers and assorted fossil tarsiiforms by virtue of common descent, places the burden of disproof, in our view, on advocates of the Tarsier-Anthropoid Hypotheses to demonstrate these features are convergent. No one that we are aware of has ever explicitly put forward such an argument in order to reject the Tarsier-Tarsiiform Hypothesis. The position of the tarsier-anthropoid school of thought would appear to counter this argument by (1) implying that the notion of parallelism or convergence can explain them away, but without articulating evidence to substantiate such a claim for any given set of resemblances, or (2) promoting an alternative cladistic model, but without falsifying the null.

The Tarsier-Tarsiiform Hypothesis is anything but new. It was forged during the nineteenth century based on the combination of reproductive and neontological evidence tying *Tarsius* to anthropoids (e.g. Burmeister 1846; Hubrecht 1897) and paleontological evidence that began with discovery of *Tetonius* (Cope 1882). The idea also had its champions during the twentieth century, among them primatologists such as Simons (e.g. Simons and Russell 1960; Simons 1972), who followed many of the ideas of Le Gros Clark (1934, 1959), Teilhard de Chardin (1921) and others about tarsiers having close ties with European tarsiiforms such as *Necrolemur* and *Pseudoloris*.

During the second half of the twentieth century, interpretations seemed to swing in the other direction. One reason for this was the demand for better resolution, articulation and documentation of phylogenetic proposals. Fuzzy hypotheses, often involving loosely defined higher level taxa that we would now call paraphyletic, and statements about ancestry and descent that we now recognise are difficult to corroborate in principle, began to be rejected outright. Still, other fuzzy notions continued to be part of the dialogue. Thus, Szalay (1976) abandoned the idea that *Tarsius* was connected to *Necrolemur*, *Microchoerus* and *Pseudoloris* because, among other things, he could not reconcile their dentitions as being of a sufficiently similar pattern. In the most influential studies, Cartmill, Kay and colleagues (Cartmill 1980; Cartmill and Kay 1978; Cartmill et al. 1981; MacPhee and Cartmill 1986) argued that fossil tarsiiforms shared none of the orbital and otic features they identified as synapomorphies exhibited by tarsiers and anthropoids. Scepticism arising from the craniodental evidence probably encouraged those interpreting the postcranium to see parallelism and convergence (e.g. Dagosto and Gebo 1994; Dagosto et al. 1999) in hindlimb characters that encouraged others to support the Tarsier-Tarsiiform Hypothesis, such as the presence of greatly elongate tarsals and a fused tibiofibula in *Necrolemur* (e.g. Schlosser 1907; Stehlin 1912; see also Godinot and Dagosto 1983; Schmid 1982). As noted, however, these counter-arguments have been proposed without falsifying the alternatives—*conjecture without refutation*.

The most recent challenge to the Tarsier-Tarsiiform Hypothesis also comes in the form of an impressively large series of algorithmic cladistic studies that consistently fix *Tarsius* as sharing a node exclusively with anthropoids (e.g. Kay et al. 1997; Marivaux et al. 2005; Seiffert et al. 2005). It should be noted, however, that these studies are codependent. They are based on a single but expanding matrix shared among colleagues and formulated with a particular method of highly suspect character coding. They are not independent blind tests coming from separate laboratories, and their matrices are replete with correlated characters, redundancies and admitted homoplasies (see Rosenberger 2010a, 2011a for critiques of related studies focused on platyrrhines, and citations therein). Recent examples that highlight the incredulity of such a parsimony-based approach are the mutually exclusive results obtained in studies concerning the affinities of *Darwinius.* Williams et al. (2010) identified it as a strepsirhine, Gingerich et al. (2012) interpreted it as a haplorhine, while Maiolino et al. (2012) nested it among strepsirhines but with a third topology. Another case involves the claim that the earliest anthropoid has been discovered from the early Eocene of India (Bajpai et al. 2008). This was based on a parsimony analysis of, essentially, a single isolated molar tooth said to be a first molar. The same tooth was also identified by others (Rose et al. 2009) as possibly an M3 and, more clearly, as the strepsirhine *Marcgodinotius* from the same Vastan locality.

What is evident from these exercises is that, as the number of characters and taxa increase along with the unknowns—missing data in the form of anatomical parts and taxa not sampled for various reasons—while character redundancy increases because anatomy is artificially segmented and atomized, the results become increasingly driven by phenetic similarity. Fundamentally, the numerical cladistic approach is an optimisation routine that effectively imposes a "neutral mutation" theory of change upon morphology, especially when homologies are not predetermined and characters are not ordered, or polarised. While not immaterial with regard to certain questions (e.g. validating drift), and probably useful as a heuristic tool, this approach is of limited practical utility for supraspecific cladistic questions. In theory, it also conflicts with, or at least ignores, the accepted model that evolutionary adaptation drives supraspecific evolution.

The approach we have taken differs substantially. Our view is that phylogenetic hypotheses can be built robustly within a functional–evolutionary context. In osteological (or dental) studies, the value or weight of characters relating to a specific hypothesis can be judged best when we have a solid idea as to what those characters mean to the animal, biologically and biomechanically, i.e. adaptively. This means that research on the meaning of characters must be undertaken a priori or simultaneously, and in the context of a phylogenetic framework. The latter must be flexible, of course, as less informative hypotheses are normally discarded in the process of building the most robust interpretation of the evidence. With regard to the fossil record of tarsiiforms, we thus consider the functional morphological evidence indicating advances toward eyeball hypertrophy as powerful phylogenetic and behavioural indicators when it aligns precisely with the anatomical design of *Tarsius*, or the logical precursors to the tarsier pattern. This perspective is not altogether different from one powerful aspect of the Tarsier-Anthropoid Hypothesis. For its attractiveness is also rooted in the notion that the same functional interpretation of the postorbital septum as an eyeball insulator, important during mastication, holds for both groups. But the logic and reasoning behind this supposition is flawed.

The morphology is not equivalent. If function follows form, the contrasts in structure suggest non-comparable functions. Put simply, the partial wall in tarsiers is a lateral, extra-fossa expansion of multiple bones that situates the wall in the coronal plane, whereas the septum in anthropoids is comprised essentially of one crucial bone suturing to the braincase and oriented in a parasagittal plane, which converts the fossa into a funnel. One lies behind an otherwise partly exposed eyeball; the other encloses the eyeball laterally, and completely. The tarsier septum appears to be inextricably linked functionally and developmentally with circumorbital flanges whose explanation (1) must be attributed to massive eyeballs, and (2) is likely to be a correlative biomechanical accommodation of radically modified locomotor dynamics. There is no equivalence among anthropoids. They are small-eyed, modest quadrupeds for the most part.

Nonetheless, if these form–function differences are held to be inconsequential and the essence of the septum is interpreted as nothing more than the bony surface to which the *m. temporalis* attaches, as is Cartmill's view (1994), in the absence of a tarsier–anthropoid morphotype reconstruction for this region the insulation hypothesis is devoid of content. Was the morphotype small-eyed or large-eyed? The existing morphology—all we know empirically—contrasts two states: a small-eyed condition with full closure, and a large-eyed condition lacking full closure. Without a covering explanation, neither of these seems suitable, heuristically, as the ancestral condition of the other. The presumption has been that tarsier-like partial closure preceded full closure, but the existing model for this in the current context also involves a large-eyed orbit, while there is no evidence that anthropoids evolved from a large-eyed ancestor. In this vein, it should be noted that the recent claim of an early anthropoid, *Biretia*, having hypertrophic eyeballs (Seiffert et al. 2005) is likely to be a misinterpretation of the anatomical implications of a very shallow suborbital dimension of the maxilla (Rosenberger 2011b). If the small-eyed condition is deemed ancestral in the Tarsier-Anthropoid Hypothesis, no cogent rationale has been given to explain why its correlate, full closure, which would seem to be most advantageous in terms of insulation, reverted to partial closure in the living tarsier. One possibility might be that re-opening the septum would allow the orbital head of the medial pterygoid access to an attachment site within the orbit, but that nullifies the argument that the tarsier's foveate eye must be shielded from interference by contracting masticatory muscles.

It is also illogical to presume that the septum in either tarsiers or anthropoids has only one potential adaptive explanation. We suggest important roles for it in non-masticatory and masticatory activities in *Tarsius* relevant to locomotion and load bearing. This does not falsify the insulation hypothesis but it begs the question as to which, if any, of several theoretical, jointly serving functions and roles should be favoured as the primary causal explanation, or the best working hypothesis. And it generates a cascade of questions and inconsistencies. For example, as noted, not all of these functional–adaptive interpretations have equivalencies in anthropoids. The locomotor option as a driving factor is surely irrelevant. As for masticatory load bearing, the biomechanical patterns of tarsiers and anthropoids must be profoundly different, if only because the orbits of anthropoids are small, the postorbital septum is broadly sutured directly to the cranium, and the zygomatic bone that forms it is enormous by comparison with *Tarsius* and oriented in a parasagittal plane. Without experimental evidence, this leaves the insulation idea to rise or fall on the degree to which the animals exhibit osseous continuity as a barrier dividing the orbito-temporal fossa. Evidently, this becomes highly problematic. As to the insulation hypothesis considered in the abstract, ignoring the osseous anatomical differences: how are we to reconcile the non-equivalence of the objects being protected—small eyes in anthropoids and large eyes in tarsiers?

In comparing the robustness of the insulation hypothesis versus the eyeball loading hypothesis we put forward, one must also account for the larger phenomenon of skull design, which has been found to be exquisitely and pervasively adapted to mechanical stresses precisely as is the locomotor skeleton (Preuschoft and Witzel 2004, 2005). Thus, the meaning of the null adaptational hypothesis of a specialised cranial structure is that it is functionally integrated with the existing mechanics of the skull and arises from it. Our interpretation places the tarsier septum squarely within that framework. It can be explained as a structural unit designed to transmit and endure external forces, of the feeding mechanism and also of the exceptionally derived, massive eyeballs. Additionally, it is the loads produced by this arrangement which are also responsible for stimulating production of bone and the shapes they take up. While it is possible that the *Tarsius* septum can be partly explained as the influence of bending stress imposed by the tensile forces of the temporal muscle attaching behind it, the specificity of the insulation hypothesis does not account for this as a primary adaptation of the structure, nor does it recognise the mechanical implications of eyeball mass as a contributing factor.

In conclusion, we re-emphasise the vital role of functional morphology and biomechanics in phylogenetic studies. The adaptively and anatomically bizarre tarsiers present a rich case study in how such principles can be applied to elucidate the evolutionary meaning of characters, how they make the unusual lifestyle of tarsiers possible, and how those characters may have evolved in a taxonomic context. What we find evident is that tarsiers have essentially a whole-body adaptation to their predatory foraging and feeding strategy, with the postcranial skeleton and cranium integrated biomechanically to power and sustain this system, which is ultimately predicated on enormously specialised, hypertrophic eyes. Thus, the skull is not only modified to house the overly large eyeballs and maintain head balance in response to an increased load that is equivalent to adding the mass of two more brains, eccentrically positioned with respect to the vertebral column. It is also designed to sustain and protect the eyes from the physical consequences of massive accelerations and decelerations that are experienced by the animal during high g-force locomotion. Seen in this context, it is difficult to equate the orbital morphology and adaptations of tarsiers and anthropoids, and this undermines support for the Tarsier-Anthropoid Hypothesis. In contrast, the identification in several fossils tarsiiforms of unusual anatomical features repeated as the same suite of cranial (and postcranial) features exhibited by tarsiers is strong evidence that *Tarsius* is more closely related to a network of Eocene tarsiiforms than it is to Anthropoidea.

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