14. *Rooneyia*, Postorbital Closure, and the Beginnings of the Age of Anthropoidea

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> "…it is particularly striking that no fossil prosimians show postorbital closure, yet all early anthropoids show a walled-off orbit. Where did the anthropoid condition come from? Or the tarsier condition, for that matter?"
>
> Fleagle and Kay (1994:693)

> "If and when we are compelled to conclude that the two [septa] are not homologous, it will only be because a convincing analysis of haplorhine phylogeny has given us convincing reasons for thinking that the last common ancestor of tarsiers and anthropoids lacked a postorbital septum."
>
> Cartmill (1994:563)

> "A large flange of the frontal descends behind the orbits [of *Rooneyia*]. Judged from the postorbital constriction of the skull, part of the major mass of the temporalis muscle extended slightly anteriorly above the orbits. In the case of *Rooneyia* the orbital partition, perhaps the homologue of that part of the postorbital funnel in *Tarsius*, platyrrhines and catarrhines, appears to be the bony wall which kept the muscles from intruding into the orbit. Possibly this partition is the initial adaptation responsible for the role of protecting the eyeballs and associated structures from the contraction of the temporalis."
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> Szalay (1976:349).

14.1 Prologue

In the Age of Anthropoidea, the higher primates came to dominate primate evolution – at least since the Oligocene and probably even before that. In his research on the origins of anthropoids during the 1970s, F.S. Szalay set the stage for the present paper in three ways: he established its overarching

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phylogenetic framework; he promoted a methodology that emphasized the integration of phylogenetics and adaptational analysis in the reconstruction of evolutionary history; and, thankfully for us, he made a key morphological observation that produced the line of inquiry that this paper has followed up.

Regarding phylogeny, Szalay championed three big ideas that are crucial to an understanding of anthropoid origins. First, he helped convince primatologists to embrace the fossil record in applying Pocock's (1918) concept of Haplorhini (Szalay, 1975a), crafted originally in response to the phylogenetic puzzle of a single living genus, *Tarsius*. Second, he promoted the idea that anthropoids are monophyletic (Szalay, 1975b) at a time when the anatomical similarities between modern platyrrhines and catarrhines were seen by more senior authorities (e.g., Simpson, 1961; Gazin, 1958) as effects of parallel evolution and evidence of a dual origin. Third, Szalay developed the notion that omomyids are *the* model of pre-anthropoid anatomy (Szalay, 1976) while another equally authoritative school of thought (e.g., Gingerich, 1975, 1980) preferred adapids, a group with more obvious superficial morphological similarities to many anthropoids. Szalay thus established the modern version of the omomyid-anthropoid hypothesis (OAH), which remains the most widely accepted working hypothesis regarding the affinities and potential ancestry of higher primates (see Gregory, 1922; Le Gros Clark, 1934; Rosenberger and Szalay, 1980; Ross and Kay, 2004). The most viable single alternative to the OAH is the tarsier-anthropoid hypothesis (TAH; see Ross and Kay, 2004, for a brief history), which has strong promoters, too.

Szalay has advocated an approach to systematics – powerful and perhaps even more vital than the foregoing concepts because it is a tool – that builds on hypothetical *transformation series* of characters as phylogenetic evidence, which in turn generates readily testable hypotheses of the twin elements of phylogeny: sister-group (cladistic) and ancestral-descendant relationships (Szalay, 1977). His method for inferring a transformation series has been both dynamic and multifaceted, most often following a line of reasoning wherein character state A is posited to have evolved into state B because that is the most likely sequence suggested by the fossil record, and/or because that is the most logical direction selection would have taken to alter the evolutionary adaptation of a particular feature and its biological roles.

Also to influence this paper was the clue he left, buried in his seminal monograph on the systematics of the Omomyidae. Szalay (1976) elaborately confirmed Wilson's (1966) prior observation on the skull of the late Eocene fossil from Texas, *Rooneyia viejaensis* – it reveals an incipient form of postorbital closure. This passage, cited above, is a morphological keystone of our analysis.

We proceed by reopening questions of homology, phylogeny and classification that have critical bearing on the matter of anthropoid origins, followed by an examination of the morphology of the haplorhine skull as a context for interpreting the affinities of tarsiers and the enigmatic *Rooneyia*. Pursuing Szalay's lead (1976), and his interest in bringing classificatory rigor to higher phylogeny, we have identified several other features of the orbits which strongly indicate that *Rooneyia* belongs to a lineage that is the sister-group of Anthropoidea, a theory we have expressed by reclassifying *Rooneyia* and revising the higher classification of haplorhines (Rosenberger, 2006). In removing *Rooneyia* from the conventional grouping of Omomyidae, acknowledged by many to be paraphyletic (e.g., papers in Ross and Kay, 2004), the fossil tarsiiforms become somewhat more homogeneous in their morphology and adaptations, and more tarsier-like. This enables us to extend prior cranio-skeletal studies which show that some genera, European and North American, are cladistically allied with *Tarsius*, which again requires a rethinking of tarsiiform classification.

14.2 Setting the Agenda

14.2.1 Homology, Character Analysis, Adaptation and Origins of the Alisphenoid Septum

Simply put, anthropoids reinvented the primate skull. Because of the complexity of anatomical modifications this group experienced around its inception, apparently, researchers are bound to explain this reinvention in more ways than one. A cardinal feature of the anthropoid cranium, postorbital closure made possible by a highly modified postorbital septum, has attracted enormous attention in recent years as a phylogenetic character (e.g., Cartmill and Kay, 1978; Cartmill, 1980; Rosenberger, 1986; Ross, 1994; Ross et al., 1998, Ross, 2000; Kay and Kirk, 2000; Simons, 2003; Hogg et al., 2005; see also chapters in Ross and Kay, 2004). An equally important feature is orbital orientation, and this too has been intensively studied (Ross, 1993, 1994, 1995). In some quarters, particularly among advocates of the TAH, the results of these parallel inquiries are interestingly asymmetrical. While the occurrence of a septum in taxa outside Anthropoidea is held to be phylogenetically and functionally informative, similarities in orbital convergence and frontation tend to be seen as functionally significant but phylogenetically moot. This duality, labeling characters as to their "functional" or "phylogenetic" value, reflects another key facet of Szalay's philosophy (1981) – he finds the distinction overblown and artificial. It also speaks to the core inferential issues of phylogenetics that he advocates, the search for homologies and the importance of weighting characters. These factors are laced throughout this paper, and crucial to evaluating competing hypotheses about anthropoid interrelationships.

As our opening quotes from Cartmill, Fleagle and Kay suggest, understanding the evolution of the postorbital septum is not straightforward. There are two schools of thought regarding its origins. One regards it as a decisive homology linking anthropoids and tarsiers, whereas the other sees it as convergently evolved in anthropoids and tarsiers. Until the advent of computerized parsimony analyses based on superabundant samples of taxa and characters, the argument came to pivot increasingly on the homology of a slip of the alisphenoid bone which has been put forth as *the* defining attribute of the postorbital septum, unique to tarsiers and anthropoids. Only recently, Cartmill (1994), for example, continued to discuss the alisphenoid problem at great length, concluding that there was no logical way to employ conventional character analysis of the septum in order to resolve the matter "in advance of our phylogenetic analyses" (p. 563). Whether or not one agrees with Cartmill, it is evident that undue attention to the question of the alisphenoid poses a larger danger, for the faces of Anthropoidea and of tarsiers probably have longer, more complex, and potentially more informative histories than the story of the alisphenoid in and of itself. To be fair, advocates of the TAH, and the alisphenoid's role in supporting it, have also invoked the morphology of the auditory bulla as evidence of tarsier–anthropoid monophyly (see Cartmill and Kay, 1978; MacPhee and Cartmill, 1986). While this region is beyond the scope of our paper, we refer the reader to Beard and MacPhee (1994), wherein one of the architects of the bulla analysis retreats from his earlier position.

The surest way to test the homologies of the tarsier and anthropoid alisphenoid postorbital septa would be to find at least one transformation series through time which revealed directly how it evolved in one group or the other. This is the phylogenetic gauntlet that Cartmill (1994) laid out to resolve the alisphenoid debate. However, there are no euprimate fossils that present anything like an alisphenoid precursor to the septum, which greatly limits the ways in which the anatomy can be studied and assessed. On the other hand, there are more than a half-dozen tarsiiform genera that offer *other cranial features* amenable to character analysis and phylogeny reconstruction, of tarsiers explicitly and of anthropoids by implication. Based on these fossils and characters, as we discuss below, one can see that the assumption of the alisphenoid plate as the final arbiter in a tarsier-anthropoid comparison poses an uncalled-for risk; this tiny plate of bone does not pass the threshold of a high-weight character in this context.

Some may argue that the question of tarsier-anthropoid alisphenoid homology has already been well-tested cladistically by the extensive series of parsimony (PAUP*) studies of anthropoid interrelationships that have been conducted (see chapters in Ross and Kay, 2004). While we agree that such analyses are useful in some ways, their results have been notoriously inconsistent for particular questions (Rosenberger, 2005; see further below) – usually the hard ones – and they are replete with unresolved polytomies. Almost all of the various alternative cladograms generated in these studies (e.g., Ross et al., 1998) were unable to root and/or sort the relationships of fossil tarsiiforms. This raises severe questions about pivotal conclusions regarding *Tarsius*. For if tarsiers are not most closely related to anthropoids they must surely be related to some set of fossil tarsiiforms, yet the interrelationships of this group would appear to be the only haplorhines whose affinities cannot be adequately addressed by these data and methods. In other words, if the cladistic relationships of the animals most similar phenetically to tarsiers (all sharing a "tarsiiform morphology," for lack of any other useful generalization) prove to be utterly confounding as a research outcome, why believe the particular results spun out for one small sample of them – genus *Tarsius*? If these studies return suspect or irresolvable phylogenetic relationships, it follows that the homologies and polarities upon which those results are based must be equally dubious. But which ones?

While the phylogeny test can shed light on homologies *post hoc*, there are other pointed reasons why the homologization of tarsier and anthropoid alisphenoid septa is not to be trusted in advance of a cladistic result. After all, this is a two-point comparison conducted exclusively using morphologically derived terminal taxa. (Fayum anthropoids, notwithstanding their geological age, are utterly modern in this regard, making them essentially equivalent to a living *Saimiri* or *Cercopithecus* in this context.) There are no plesiomorphic fossils (ignoring *Rooneyia* for the moment; see Szalay, 1976; Rosenberger, 2006) with the requisite anatomy and there is no meaningful, detailed morphocline among the living forms, meaning the *a priori* risk of a homology error is quite high. As baseline conditions, this does not bode well for homology inferences involving a question of deep-time origins. This situation is exacerbated by the fact that tarsiers, no matter what opinion one has about their origins, remain a vestigial phylogenetic twig as well as a morphological outlier. The risk of homology error is compounded when the morphological congruence between presumptive homologues occurs in taxa that are so vastly different, objectively, that scholars universally agree to distinguish them taxonomically at near-ordinal levels for the morphology of the character complex in question – the orbits – in addition to a myriad of other phenetic issues. And the risk level rises higher still when the septum is assumed to serve the same functional adaptation – preventing mechanical interference from chewing muscles – as we know intuitively that hardly anything in the tiny tarsier head could avoid coming under the selective and morphogenetic regime dictated by eyesight and eyeballs. This evolutionary/anatomical milieu is certainly unlike that which propels the small-eyed anthropoids.

Thus it is not surprising that the proposed homologization has met strong criticism. While the focal point of today's debate centers around the case as it has been most fully fleshed out by Cartmill and colleagues (e.g., Cartmill, 1980, 1994; Cartmill and Kay, 1978; Kay et al., 1997, 2004; Ross, 1993, 1994, 1996), the essence of their point follows the reasoning of earlier workers articulated at a time when the morphology of fossil tarsiiforms was poorly sampled, when morphologists were quite limited in terms of justifiable comparisons, explanations and alternative hypotheses. For example, Duckworth (1915:104) noted, "…the postorbital wall (to which the alisphenoid makes a distinct contribution) constitutes a resemblance to the Anthropoidea, and severs *Tarsius* (*sic*) from the Lemurs." Pocock (1918:51) agreed but in more general terms, saying that for "…the presence of the postorbital partition, and other well-known features, it seems that Hubrecht was quite right in removing *Tarsius* from the Lemurs and placing it in the higher grade of Primates." Le Gros Clark (1934:64) essentially concurred: "The orbits of the pithecoid skull are…almost completely cut off from the temporal region by a bony wall formed by the malar and alisphenoid (an advanced character which, it has been seen, occurs to a slight degree in *Tarsius*)."

For the early advocates of this school of thought, tarsiers represent an intermediate state of a series leading to anthropoid closure wherein a postorbital septum, deriving from the still more primitive euprimate postorbital bar, is enlarged but does not fully seal off the orbital fossa behind the eyeball (see Hershkovitz, 1977). Adding modernity to the argument that the alisphenoid component of the septum "proves" that the partition is homologous with anthropoids, Cartmill (1980 *et seq.*) and his colleagues offered a covering adaptive explanation to enhance the logic of the case. They proposed that a single adaptive reason for compartmentalizing the orbit in the tarsier-anthropoid group, to protect its contents from mechanical interference originating in the adjacent temporal fossa, where contraction of the temporalis muscle would otherwise disrupt the vision of these animals that place a high premium on pinpoint visual acuity (but see Ross, 2004, on the moot homologies of haplorhine foveae). A sizable literature has sought to establish this hypothesis, a variant of the visual predation hypothesis (e.g., Cartmill, 1972), by examining allometric and masticatory contingencies relating to eye size, orbit size and biomechanics (see reviews in Ross and Kay, 2004; Ravosa and Hogue, 2004; Ross, 1994; Ross, 2000). While important in their own right, these studies seek to corroborate by correlation and association. They do not doubt the supposition that the postorbital septa of tarsiers and anthropoids are homologous, and rarely challenge the interference explanation.

An empirical behavioral test of the interference/visual predation hypotheses has not yet been conducted, to our knowledge. If the septum does successfully insulate the eyeball, do tarsier eyes not wobble when the temporalis is stimulated? Do their eyes wobble less than a galago's, where there is no postorbital septum? Can it be shown that tarsiers have, need, or benefit from foveal, pinpoint vision as a motion detection device? Or, does a foveal retina primarily benefit hand-eye coordination, i.e., prey capture and manipulation, which would be another form of the visual predation hypothesis? Do tarsiers actually scan for prey and calculate takeoff coordinates while masticating? They ought to if the interference hypothesis is correct. Or, do they finish a meal before hunting again? As hold-and-feed animals, doesn't the logic of the interference hypothesis suggest that selection for the septum in tarsier ancestors favored populations with the fickle habit of chewing a live victim while clutching it and also being able to *simultaneously* take off again in order to…drop the first and grab a new one? Testing hypotheses of functional evolutionary adaptation is always complex and none of these questions alone would prove much if they were answered individually. But solutions would probably advance our knowledge of the issues to a new state and perhaps challenge the functional rationale of the homology hypothesis, which is tied to the proposition of visual predation as a causal explanation.

Such difficulties notwithstanding, the primary morphological substance of the hypothesis has also been challenged by Simons and Russell (1960; see also Simons and Rasmussen, 1989; Simons, 2003) and Rosenberger and Szalay (1980), who independently argued it is more likely that the slips of alisphenoid contributing to the postorbital wall of tarsiers and anthropoids are not homologous. This means that the evolution of the anthropoid eye socket and the tarsier postorbital septum were coincidental, convergent events. The general hypothesis advanced by these authors is this: in tarsiers the small alisphenoid rampart belongs to a series of lip-like orbital superstructures that are correlated autapomorphies, none of which occur in anthropoids. In adult tarsiers, the constituents of this pattern are evident superiorly, in the form of an everted superior orbital margin; inferiorly, by a shelf-like posterior extension of the maxillary orbital floor; posteriorly, by a broadened wing of the frontal bone that is continuous with a narrow horizontal process of the alisphenoid; and, laterally, by an enlargement of the surface of the maxillary-zygomatic complex (see below). In this view there is no simple "tarsier postorbital septum." Rather, tarsiers have a periorbital structural system whose principal biological role is related to eyeball hypertrophy and position, again distinguishing it fundamentally from the smaller-eyed anthropoids where the major biological role of the alisphenoid is not related to enlarged eyeballs. Additional support for this notion can be found in their different ontogenies. In anthropoid neonates, the alisphenoid plate forms a readily visible, proportionately large "wing," while in tarsier newborns there is little more than a nubbin of bone evident where the alisphenoid process arises. It appears to develop postnatally, in concert with the other periorbital flanges. As discussed below, one part of this derived pattern is already evident among fossil tarsiiforms in a mosaic distribution that suggests the alisphenoid of the tarsier condition is a "final" element of the design uniquely evolved in the genus.

While descriptively dissecting anatomical parts in this way involves some arbitrariness, it is instructive to consider briefly another major facial element of the orbital surround, discussed further below. This is the laterally flaring and essentially horizontal paralveolar extension of the tarsier face, which encompasses the anterior root of the zygomatic arch and forms the lowest and most lateral portion of the bony ring around the eyeball. Enlargement of the surface of the maxillary-zygomatic complex in *Tarsius*, which essentially everts the lateral face of the maxilla, has not figured as a character in discussions of tarsier and anthropoid orbits, yet it seems to make the case emphatically that the periorbital components of tarsiers are all functionally tied to the large-eye syndrome. Its purpose must be to enlarge the orbital floor laterally, extending it beyond the margin of the toothrow in order to accommodate hypertrophic eyeballs in a skull where there is no place to grow bone but outward. Thus tarsier faces have enormous bony facial extensions anteriorly and laterally, displacing the lateral orbital margin away from the midline and braincase. With the obvious highly derived exception of *Aotus*, hardly at all a mirror for the pattern, anthropoid skulls are nothing like this.

The upshot of this extensive integration of unique tarsier features is that it becomes difficult to isolate the septum from the others and ascribe to it a unique functional explanation apart from the rest. Rather than being fundamentally related to closing off the eye from the temporal fossa as the interference hypothesis claims, for both large- and small-eyed haplorhines (i.e., anthropoids and by extension *Rooneyia*; see Rosenberger, 2006, and below), the tarsier septum appears to represent an entirely different adaptational history and transformation series. It is difficult to say if it is essential to mechanically supporting the eye and its attachments as opposed to being simply an epigenetic reflection of orbital hypertrophy, which may be a distinction without a difference. In any event, this does not negate the interpretation that the alisphenoid septum provides bony insulation from interference as preferred by Cartmill and colleagues. But if this is a secondarily acquired biological role of a larger morphological pattern related to eyeball enlargement, it means that the tarsier morphology is less likely to be a homology shared with anthropoids.

Simons and Rasmussen (1989) offered a second challenge to the premise that the evolutionary essentials of anthropoid postorbitum pivots on the alisphenoid element. They pointed out, instead, that in anthropoids the ascending ramus of the zygomatic is what provides the principle separation of orbital and temporal fossae, not the alisphenoid. This contrasts with the *Tarsius* condition, where the ascending frontal process of the zygomatic bone is not so enlarged. To the contrary, it may seem surprisingly narrow given the size of its zygomatic and frontal roots, and the other superstructures described above. In other words, tarsiers are seen as retaining a primitive albeit modified postorbital bar. Anthropoids, in contrast, show a dramatically transformed postorbital bar predicated on a unique size and shape of the ascending process of the zygomatic bone, which was modified into a spoon-like shape, to use Simons' terminology, from a bar-like process. In all anthropoid skulls this laterally positioned lamina of the zygomatic is what makes for postorbital closure, with only a small fraction of the partition being formed by alisphenoid medially. In this view, the tarsier-anthropoid alisphenoid comparison turns out to be a red herring.

Arguing from another perspective, Rosenberger (1985) opposed the phylogenetic aspect of the TAH and the homologization of the alisphenoid flange in tarsiers and anthropoids. Building on Simons and Russell (1960), he suggested there is a series of uniquely derived features of the basicranium that align *Tarsius* more closely with European microchoerine tarsiiforms, which we now regard as tarsiids (Table 14.1; see Simons, 1972). Beard et al. (1991) and Beard and MacPhee (1994) then showed that newly discovered skulls of the North American tarsiiform *Shoshonius* also present this same suite of features (see also Dagosto et al., 1999). These data and arguments, along with the presence of definite Eocene tarsiids (Beard, 1998; Rossie et al. 2006), indicates that tarsiers were part of a larger, tricontinental radiation already well

TABLE 14.1. A provisional classification of non-anthropoid haplorhines that forms the basis of this study. Tarsioids and tarsiids are distinguished from other tarsiiforms as likely monophyletic groups sharing a suite of cranial characters relating to relatively large and hypertrophic eyes, in conjunction with postcranial features related to leaping, such as extensive apposition of the tibiofibula (see review in Dagosto et al., 1999). Tarsiines and microchoerines are known to show highly advanced postcranial adaptations, such a tibiofibular fusion (*Tarsius, Necrolemur, Pseudoloris*) and enhanced anterior calcaneal elongation (*Tarsius, Necrolemur, Microchoerus*) as well as a derived tubular auditory meatus (*Tarsius, Necrolemur, Microchoerus*). The *incertae sedis* tarsiids are known to share mosaics of the primitive and derived cranio-skeletal states of these features, so they may be referable to either Tarsiinae or Microchoerinae on cladistic grounds upon further study. Some microchoerines, such as *Pseudoloris*, may prove to be justifiably included in the tarsiines. *Xanthorhysis* is allocated to Tarsiidae based on Beard's (1998) analysis of the dentition. It is likely that other genera now regarded as omomyids will be classified as tarsioids when they are reconsidered. *Teilhardina* is kept outside the tarsiid group, as an anaptomorphid, because of its primitive craniodental morphology. (With the nominate genus *Omomys* removed to the Tarsiidae, the family-level term Omomyidae cannot be applied to non-tarsiid tarsiiforms, and the first available name becomes Anaptomorphidae Cope, 1883 based on chronological priority.) The classification of Rooneyia is discussed further elsewhere (Rosenberger, 2006), where the new higher taxa are formally proposed based in part on the analysis presented herein.

- Suborder Haplorhini
- Semisuborder Tarsiiformes
  - Superfamily Tarsioidea
    - Family Tarsiidae
      - Subfamily Tarsiinae
        - *Tarsius*
      - Subfamily Microchoerinae
        - *Hemiacodon, Microchoerus, Nannopithex, Necrolemur, Pseudoloris*
    - Family Tarsiidae *incertae sedis*
      - *Absarokius, Omomys, Shoshonius, Tetonius, Xanthorhysis*
  - Superfamily *incertae sedis*
    - Family Anaptomorphidae
      - *Teilhardina*
- Semisuborder Simiiformes
- Hyporder Protoanthropoidea
  - Family Rooneyiidae
    - *Rooneyia*
- Hyporder Anthropoidea
  - Infraorder Platyrrhini
  - Infraorder Catarrhini

established in the Eocene (see also Rosenberger and Pagano, in press), which eliminates the genus from having a sister-group relationship with anthropoids.

While this particular phylogenetic point, which is further developed below, weakens the phylogenetics of the TAH and the underlying character analyses pertaining to the alisphenoid, it does not refute it entirely. The fallback position might be that anthropoids are still more closely related to a *greater tarsier clade* than to any other tarsiiforms (see Ross et al., 1998). While we consider this unlikely, it is worth noting that several variations of the cladistic interrelationships of tarsiers, "omomyids" and anthropoids may be said to be currently in play if one subscribes to the array of parsimony (PAUP*) analyses performed in the past decade by Kay and colleagues (e.g., Kay et al., 2004).

14.2.2 Toward A New Classification of Tarsiiforms

Thus in our view the alisphenoid postorbital septum has already been over-interpreted by those who regard it as a homology shared with anthropoids. But this does not explain why these points, several of which have been made before in other ways, have not sealed away the argument. We surmise that in a subtle way, this is because the problem has been cast too deeply in neontological terms, bound up in a heuristically outmoded taxonomy that fails to integrate paleontology. Cartmill (1994), for example, in his extended explication of the alisphenoid problem, makes almost no mention of fossil evidence. How is this possible in tracing the evolution of such a structure, or a lineage like Anthropoidea? Only part of the answer rests with the fact that an alisphenoid postorbital septum has not been observed in non-anthropoid fossils. But another part of the answer surely is that the *status quo* has long considered *Tarsius* a genus apart from fossil tarsiiforms, adaptationally and phylogenetically, and this, in turn, helped promote a limiting approach as to how tarsiers tend to be classified, compared and understood.

We would argue that the concept of Tarsiidae, as implemented in the literature in recent decades, has been too narrow. This is evident in formal classifications and the less formal ways that taxonomic terms are used and/or extended conceptually in various works. For instance, it has been rare for primate classifications published during the twentieth century to include any other genus besides *Tarsius* in the Tarsiidae. Osman Hill (1955) and Simons (1972) present the significant counterexamples. The only other case where this rule seems to have been broken recently involves the allocation of a new Chinese Eocene genus, *Xanthorhysis*, to Tarsiidae by Beard (1998); a bold move given today's aversion to recognizing modern primate families during epochs before the Miocene. It is noteworthy also that Simons, (1972; 2003), influenced by Teilhard de Chardin (1921), had previously discussed the genus *Pseudoloris* as the fossil most closely related to modern tarsiers and called it a tarsiid, but his argument has not been carefully assessed and so his reasoning has not been extended to other tarsiiform genera. A case in point: in placing *Xanthorhysis*, Beard (1998) did not consider Simon's points about *Pseudoloris*, which is also Eocene, nor did he integrate other highly pertinent phylogenetic analyses (e.g., Rosenberger, 1985; Beard et al, 1994; Dagosto et al., 1999) which suggest strongly that other tarsiiform genera are close cladistic relatives of modern *Tarsius* as well. Following from this, to present an illustration of a different sort, Jablonski (2003) discussed the origins of the tarsier ecological niche, specifying only *Xanthorhysis* and the Egyptian *Afrotarsius* (see Simons and Bown, 1985; Rasmussen et al., 1998) as fossil tarsiid genera and concluding that the animals must have originated in eastern Asia. There would be a far more complex case to be evaluated if one were to acknowledge European microchoerines and North American forms such as *Shoshonius* (see Beard et al., 1991) as being part of a monophyletic family of tarsiids. While Beard has motivated some welcome movement to expand the concept of Tarsiidae, as was the case with *Homo*/Hominidae for decades (see Simpson, 1961), the gradistic consensus of *Tarsius*/Tarsiidae as a category of its own has supported a reluctance to group tarsiers with potential or demonstrable cladistic relatives in an integrative way.

There is another set of forces at work which calls for a shift in how tarsiers, and tarsiiforms, ought to be classified. It begins with the gradual breakdown of Szalay's concept of Omomyidae (1976), which is steeped in a deeper history, most notably the synthetic works of Gregory (1922) and Le Gros Clark (1934), and his view that no fossil tarsiiforms are close enough to tarsiers phylogenetically to warrant expansion of the one-genus concept of Tarsiidae. In addition to the phyletic arguments already alluded to, fossil tarsiiforms are becoming better known adaptively. There is a host of genera for which we have information on cranial and postcranial morphology, as well as dentitions. Several show that advanced leaping adaptations *and* cranial features associated with relatively enormous eyes were present in combination, as we emphasize here. Thus the supposed ecomorphological differences between modern tarsiers and Eocene tarsiiforms is diminishing, and the facile argument that parallelism explains away suites of anatomical similarities between them is no longer compelling. As implied above, Beard et al. (1994) has even allocated an Eocene species, dentally similar and with good indications of having large eyes, to genus *Tarsius*.

For these reasons we provide a provisional classification that takes into account recent findings (Table 14.1), emphasizing the taxa that are relevant to our discussion of the postorbital septum. We recognize the incompleteness of this exercise and expect this iteration to be useful only as an interim step. However, to us it seems to be an effective way to promote necessary changes in the systematics and classification of Eocene tarsiiforms in particular, which holds the key to tarsier – and possibly anthropoid – origins. From a taxonomic standpoint, our intention is to maintain a monophyletic family Tarsiidae. Following Simons (1972), we keep *Tarsius* in a distinct subfamily and allocate other tarsiiforms that can be shown to be probably monophyletically related to it by cranial and/or postcranial characters to Subfamily Microchoerinae. This move was anticipated by Rosenberger (1985), who used the informal term "necrolemurs" to refer to this group, which then included only the classic microchoerines, *Necrolemur, Microchoerus, Nannopithex*, and *Pseudoloris*.

14.2.3 Questions and Goals

The forgoing should make it clear that, in our view, the structural antecedents of the transformed anthropoid skull is an unsettled matter in spite of a prodigious effort to understand the history of the postorbital septum and forward-facing orbits. The neontological work that has dominated debate must be extended more effectively to accommodate early relevant fossils if we are to get beyond the current stalemate of ideas. How anatomically, why adaptively, when temporally, and whom taxonomically was involved as the anthropoid orbital complex was reconfigured by natural selection? Even murkier is the question of phylogenetic transformation: what anatomical prelude was preadaptive to postorbital closure?

Our goal is to address the origins of the anthropoid skull by expanding the focus of inquiry, starting with a rethinking of the anatomical and spatial relationships of important components of the orbit relative to the face and neurocranium in early haplorhines, especially tarsiiforms. The skulls of pertinent Eocene tarsiiforms are still relatively scarce and understudied, but they are reasonably known in varying states of preservation from about seven genera: *Necrolemur, Microchoerus, Nannopithex, Pseudoloris, Shoshonius, Teilhardina* and *Tetonius*. Only a few of the important observations can be made on *Teilhardina*, which has been reconstructed via high resolution CT imaging (Ni et al., 2004).

In addition to these forms, we emphasize the late Eocene fossil from Texas, *Rooneyia viejaensis*, a controversial taxon (e.g., Szalay, 1976; Ross et al., 1998; Gunnell and Rose, 2002; Kay et al., 2004; Rosenberger, 2006) still known from only one relatively complete, undistorted and little damaged specimen (Wilson, 1966). The centrality of *Rooneyia* to the question of anthropoid origins is contextualized by the OAH: *Rooneyia* has most often been considered an omomyid for about 30 years now (see Gunnell and Rose, 2002, for a recent review). A different view promoted by some advocates of the TAH is that the systematics of *Rooneyia* is fundamentally un-interpretable in that there are several viable phylogenetic solutions. To wit, paraphrasing Ross et al. (1998:255) *Rooneyia* is: (1) not an omomyid; (2) related to extant strepsirhines; (3) related to an adapid/strepsirhine clade; (4) related to anthropoids; (5) the sister-taxon of all primates; (6) related to a parapithecine-*Aegyptopithecus* group; (7) the sister-taxon of an omomyid/tarsier/anthropoid clade. Here we consider *Rooneyia* a member of the Protoanthropoidea (Rosenberger, 2006), a group formally defined as a non-tarsiiform sister-group of Anthropoidea. The species has seldom been considered in detail in connection with anthropoid origins (e.g., Simons, 1972; Hogg et al., 2005; Rosenberger 2006) even though its skull stands well apart from fossil tarsiiforms in overall morphology, as shown by Fleagle (1999:376) in a rare comparative illustration. This is somewhat surprising given the clarity with which Szalay (1976), as quoted above, discussed the morphology of its postorbitum and the Cartmillian rationale he then offered to explain the adaptive benefits of postorbital closure.

14.3 Comparative Morphology

14.3.1 Haplorhines and *Rooneyia*

Using *Rooneyia* as a starting point, we draw on 3-D digitizations based on laser surface scanning to clarify how the orbits of haplorhines are packaged in the skull. *Notharctus* sp. was chosen as a comparative model for early strepsirhine cranial morphology (see Szalay and Delson, 1979; Gebo, 2002). As noted above, we attempt to refocus the discussion of the origins of the anthropoid orbit away from a narrow emphasis on the postorbital plate toward a balance of several factors. Our most important conclusions are these: (1) Haplorhine orbits are derived among primates in having a posterior-medially shifted orbital fossa and a mediolaterally extensive, relatively horizontal orbital floor. (2) The functional concern about spatial adjacency of the orbital and temporal fossae in foveate tarsiers and anthropoids is probably exaggerated. (3) *Rooneyia viejaensis* is unique among known Paleogene non-anthropoids in having a pattern of attributes that may foreshadow the evolution of an anthropoid eye socket, including: a funnel-shaped orbital fossa deeply recessed below the forebrain; a dorsoventrally and laterally extensive frontal process that forms a partial postorbital septum and implies, albeit tenuously, the existence of a relatively large ascending processes of the zygomatic bone (postorbital bar); a relatively large frontal bone with a fused metopic suture (see Figure 14.3), that extends roof-like above the orbit; highly convergent and frontated orbits. Simultaneously, *Rooneyia* is more primitive than fossil tarsiiforms for which skulls are known in having relatively small, anthropoid-sized eyeballs and in lacking numerous features that are correlated with eyeball hypertrophy, immediately around the orbital fossae, in the organization of the face, and in the morphology of the posterior palate and nasopharyngeal region that relates to enlarged eyes.

14.3.1.1 Orbital Fossa

There are profound differences in the size and placement of the orbital fossae in *Notharctus* and *Rooneyia* (Figure 14.1). We hypothesize that the *Notharctus* morphology represents the ancestral euprimate and strepsirhine pattern and that the *Rooneyia* arrangement models the ancestral condition of haplorhines. In the former, the orbital floor is situated far forward of the braincase and it is located quite laterally on the snout, nestled in the space formed by the junction of the anterior root of the zygomatic arch and the rostrum (Figure 14.1a). This is the common condition among mammals and must have been ancestral in euprimates. The orientation of the floor among strepsirhines can vary in the transverse plane. It may be horizontal or pitched upward, antero-dorsally, for example. However, the restricted size of the orbital floor is maintained among strepsirhines even in cases where the eyeballs are relatively large, as in lorises.

In contrast, in *Rooneyia* and other haplorhines, the orbital fossa is situated posteriorly in the face, essentially at the craniofacial junction (Figure 14.1b). The floor is greatly expanded, especially in its transverse dimension, and tends to be built largely from a horizontal lamina formed within the maxilla. The large size of the floor can be explained as the lamina's medial incursion into the space of the rostrum. In some cases, the floor is also enlarged laterally as a paralveolar expansion that is confluent with the root of the zygomatic (see below). In horizontal section (Figure 14.1c, d), the large orbital floor is clearly seen in connection with the typically haplorhine reduction of the nasal fossa in the transverse dimension, and approximation of the medial walls of the orbits. In superior view, the relatively large size of the orbital floor of haplorhines is also evident (Figure 14.2), whether the eyeballs are relatively large (e.g., *Necrolemur*) or small (*Rooneyia*).

14.3.1.2 Frontal Bone, Craniofacial Junction and Temporal Fossa

The complex morphology of the frontal bone and craniofacial junction is markedly different in *Rooneyia* and *Notharctus*. To begin with, the metopic suture is fused in *Rooneyia* (Figure 14.3; *contra* Ross et al., 1998). It tends to be fused in *Notharctus* and in the majority of living strepsirhines, contrary to conventional wisdom. (Rosenberger and Pagano, in press). The type specimen of *Rooneyia* is a young adult, judging by its little-worn molar teeth, suggesting that frontal fusion did not occur as bone was remodeled during aging. Unlike *Tarsius*, on the external surface of the frontal there is no indication of a longitudinal ridge or a sagittal canal (see Rosenberger and Pagano, in press). The frontal bone is also large in overall size and extends shelf-like above the orbital fossae (Rosenberger, 2006; Hogg et al., 2005). This is well illustrated by comparing the positions of the anterior margins relative to a line defining the transverse axis of postorbital constriction in *Rooneyia* and *Necrolemur* (Figure 14.2).

In *Notharctus*, the frontal bone is smaller and, because the degree of convergence and frontation is less and the orbital fossa is positioned further forward on the snout, the superior margin of the orbit does not overhang the orbital fossa (Figure 14.2). It is most likely that this typically strepsirhine condition is the primitive euprimate pattern. Tarsiiforms such as *Tetonius, Microchoerus*, and *Necrolemur* also tend to have laterally facing orbital margins rather than a forward-projecting superior rim. Thus their orbits are not roofed by the frontal, as in *Rooneyia*.

Ross (1995) has shown that the orientation of the orbital plane in *Rooneyia* is essentially anthropoid (Figure 14.4), i.e., its forward facing orbits just fall at the boundary (of a minimum convex polygon) of a bivariate plot of the angles of convergence and frontation, a geometry that is rare among non-anthropoids. Rosenberger (2006) argued that this is unlikely to be a homoplastic similarity shared with anthropoids; rather, it may be homologously derived. *Notharctus*, in presenting what must be the primitive condition for primates (e.g., Le Gros Clark, 1934), has laterally facing, relatively divergent orbits typical of most strepsirhines, fossil tarsiiforms, and modern tarsiers, quite unlike *Rooneyia* and anthropoids. It is the spread along the convergence axis of the bivariate plot describing the orbital plane (Figure 14.4) that most clearly distinguishes these forms from more primitive euprimates.

Regarding the vertical tilt of the plane, frontation, the anthropoids and *Rooneyia* accomplish this similarly by combining several factors: prolongation of the frontal to form a roof-like extension over the orbital fossae, combined with the deep recession of the orbits toward the braincase and a somewhat reduced interorbitum. This flattens the angle of tilt fixed by the upper and lower orbital margins in lateral view. Tarsiers may resemble *Rooneyia* and anthropoids in their metrics but not anatomically. The superior margin of the tarsier orbit is everted dorsally like a pitched awning rather than prolonged horizontally as a roof, and the inferior margin is extended anteriorly as part of the paralveolar expansion (see below). But their angles are similar because the tarsier facial skull is uniquely bent downward relative to the basicranial axis (Spatz, 1969; Starck, 1975), displacing the ventral margin of the orbit inferiorly and tilting the plane of the orbit into an anthropoid-like orientation.

An important consequence of the orbit's location within the cranium is the funnel-like shape of the orbital fossae in *Rooneyia*, as seen in the cutaway of Figure 14.5. This is a product of the subcerebral position of the orbit (which in turn contributes to the bony orbital roof), the medial incursion of the orbital floor and the convergence of the orbital apices toward the midline. That is, the anterior wall of the braincase effectively becomes part of the back wall of the orbital fossa, while angulation of the medial walls is conditioned by the width differential between the interorbitum and the span between the optic foramina. This pattern approximates the cone-shaped "eye socket" that defines Anthropoidea, differing

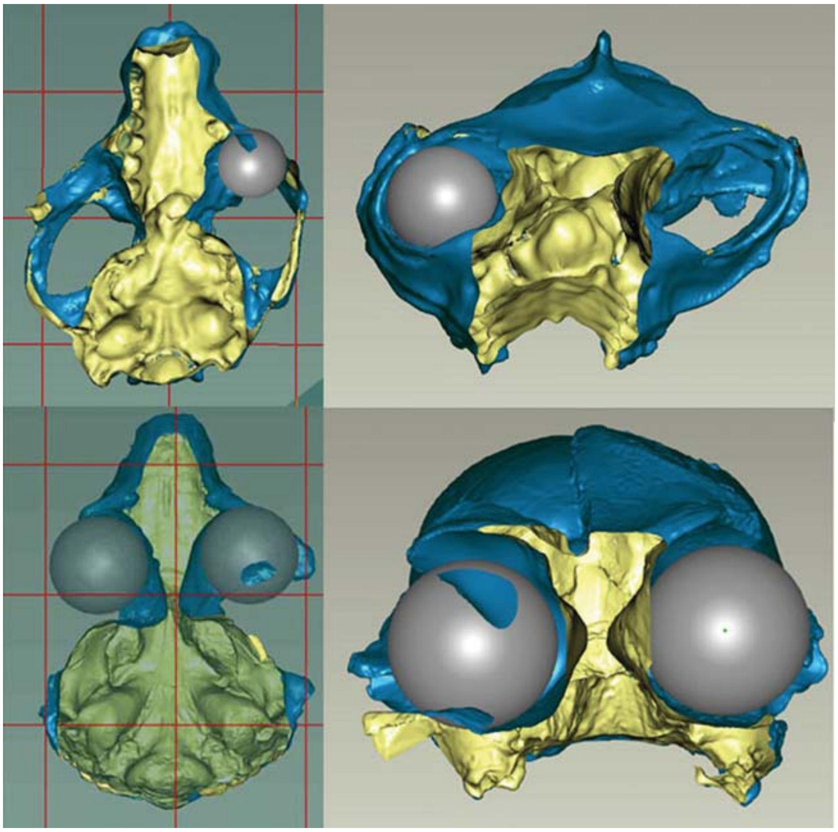

Figure 14.1. Images captured from three-dimensional laser scans of *Notharctus* (top) and *Rooneyia* (bottom) in horizontal and coronal sections taken near the lacrimal canal. The size and position of virtual eyeballs are based on contours of the orbital fossae, and are meant for illustrative purposes. Two alternatives are shown for *Rooneyia*, where the right eyeball is colliding (see irregular splotches) slightly with the back of the orbit and with matrix on the orbital floor. These images show the primitive antero-lateral placement of the orbital fossa in strepsirhines as compared with the derived postero-medial position in haplorhines, which is related to reduction of the posterior nasal fossa. The large size of the orbital floor in *Rooneyia*, like all haplorhines, is evident.

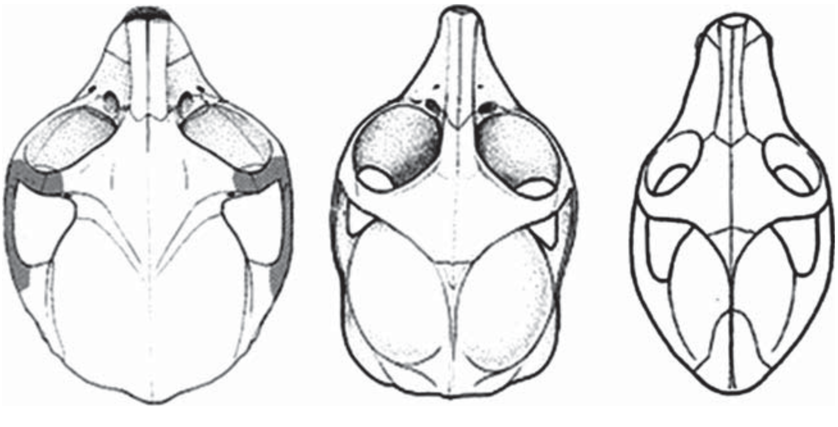

Figure 14.2. Dorsal views of *Rooneyia, Necrolemur* and *Notharctus*, left to right, brought to the same length (adapted from Szalay, 1976). The relatively large size of the haplorhine orbital floor is evident, as are recession of the orbits toward the braincase and the relatively wide shape of the braincase. Notice the relatively smaller size of the frontal bone in *Notharctus*, its intermediate size in *Necrolemur* and its relatively large size in *Rooneyia*, where the superior margin of the orbit is prolonged to partially roof over the fossa. In *Necrolemur*, the strongly tapering, concave profile of the snout and the relative narrowness of the interorbital region are aspects of eyeball enlargement and sagittally shifted medial orbital walls, part of the derived transformation series leading to the extensively modified arrangement of *Tarsius* where paralveolar expansion and fused medial orbital walls are part of the hypertrophic eyeball pattern.

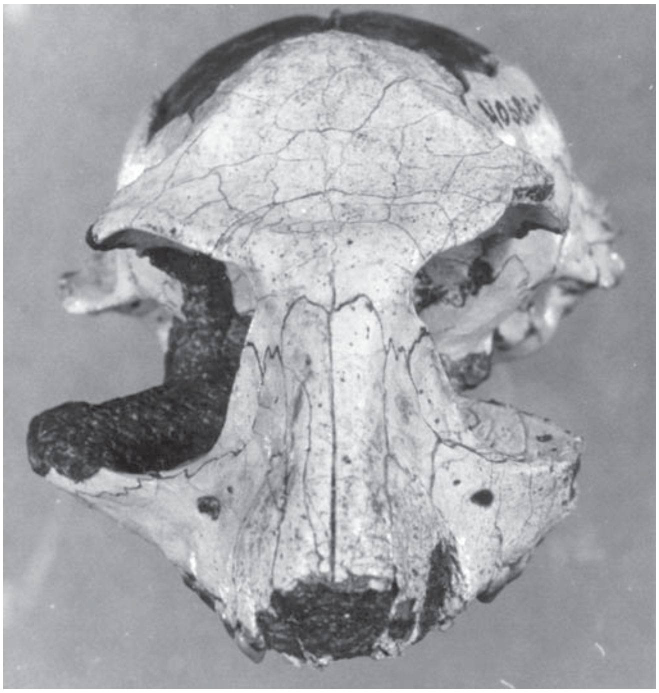

FIGURE 14.3. Anterodorsal view of *Rooneyia* (courtesy of Dr. Timothy Rowe, Vertebrate Paleontology Laboratory, Texas Memorial Museum, University of Texas at Austin) before the right side of the frontal bone was removed to expose the forebrain endocast. The metopic suture is fully fused and obliterated, except perhaps for a line of a few millimeters continuous with internasal suture, which is most likely a postmortem crack. The dorsal margins of the orbits are not everted and there are no anterior paralveolar extensions as in the large-eyed tarsiids.

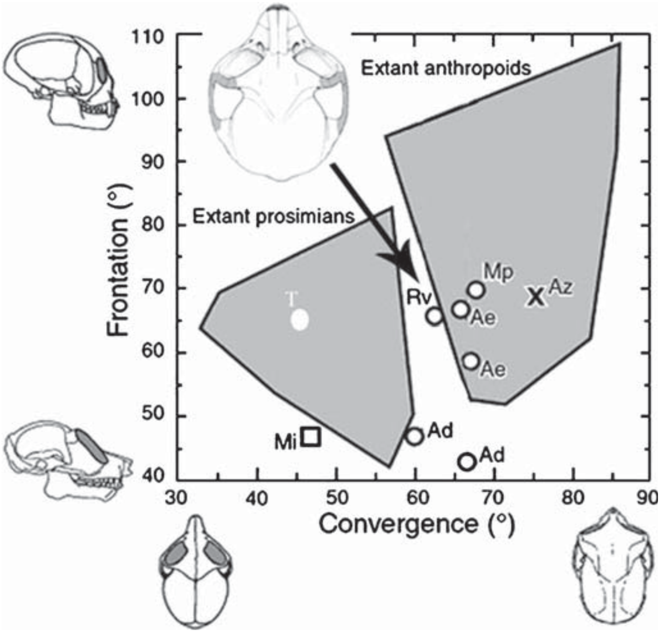

FIGURE 14.4. Orientation of the orbital plane in primates (modified from Ross, 2000, and Szalay, 1976). Minimum convex polygons outline the widest spatial distributions of points for extant species of anthropoids and non-anthropoids. Symbols: T, *Tarsius* spp.; Mi, *Microchoerus* sp.; Ad, *Adapis* sp.; Ae, *Archaeolemur edwardsi*; Az, *Aegyptopithecus zeuxis*; Mp. *Mesopropithecus pithecoides*; Rv, *Rooneyia viejaensis*. Approximate midpoint position of three *Tarsius* species based on plot in Ross (1995). In spite of differences in relative eye size, the orbital plane of *Tarsius* is laterally directed as in *Microchoerus*, both resembling strepsirhines. The higher degree of orbital frontation in *Tarsius* is a product of the unique downward tilting of the face on the neurocranium coupled with the extensively everted supraorbital flange, thus producing a superficial resemblance to anthropoids in this measure. Absent these specializations, and with a much more primitive overall cranial design, *Rooneyia* resembles higher primates more than any other non-anthropoids because of its prolonged frontal bone plane and recessed orbital fossae.

only in the absence of a structure that closes off the fossa laterally, i.e., the spoon-shaped zygomatic. Since the orbital fossae of *Notharctus* and other strepsirhines are placed so far forward on the snout, well away from the braincase, there is nothing comparable to this in their morphology (Figure 14.1a, b).

The posterior envelopment of the eye by the frontal-alisphenoid complex at the craniofacial junction is related to the width of the postorbital constriction, which tends to be larger relative to braincase width in modern haplorhines than in strepsirhines (Figure 14.6). With the exception of *Victoriapithecus*, all anthropoids in our plot fall above the slope of the line fit through our combined sample of strepsirhine and haplorhines. Another distinction is that the relationship between postorbital breadth and braincase width is somewhat more complex in strepsirhines than in haplorhines. In the strepsirhines, the correlation coefficient between these variables is 0.55, for an r^2 of only.31. In the haplorhines, the coefficient is 0.95, resulting in an r^2 of.90. Thus, among haplorhines the constriction is more tightly constrained by braincase width, and vice versa.

It is noteworthy that among the Eocene euprimates, *Notharctus* and the other adapids consistently fall well below the regression line. This corresponds with the notion that early strepsirhines are more primitive than early haplorhines in having a relatively narrow craniofacial junction, although this condition is probably exaggerated in the large-jawed, heavily muscled and small-brained (e.g., Martin, 1990) *Adapis* and *Leptadapis*. While the much wider postorbitum of *Tarsius* is also unusual for a haplorhine of its body size, this is undoubtedly a function of several associated features: hypertrophic eyeballs, an unusually wide forebrain (Starck, 1975), and the bent craniofacial axis (Spatz, 1969; Starck, 1975). When this outlier is eliminated, it is evident that the relatively wide postorbitum of typical haplorhines, which is also related to brain shape – their relatively broad frontal and temporal lobes (e.g., Radinsky, 1970) – is derived for euprimates.

When these features are considered together, a new picture of the spatial relationships of orbital and temporal fossae

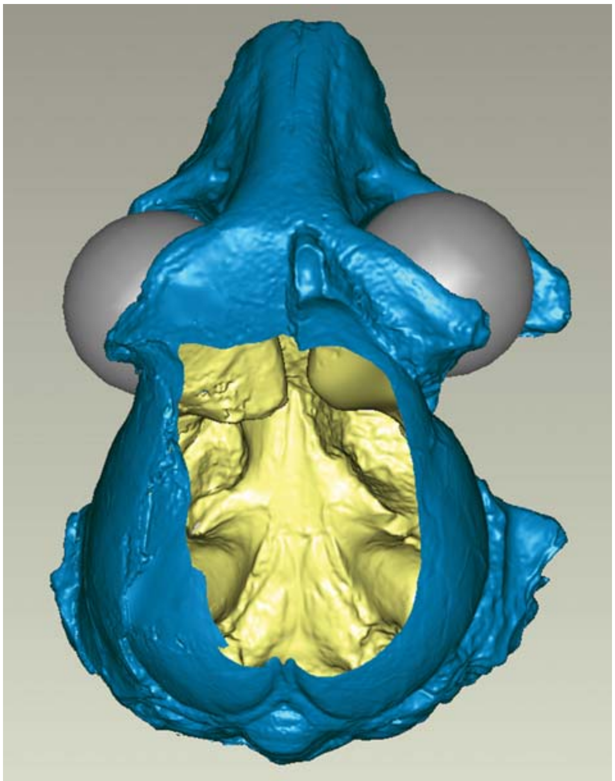

FIGURE 14.5. Cutaway of a three-dimensional model (same as in Figure 14.1) of the braincase of *Rooneyia*, with the basicranium shown in obverse for orientation. Note the V-shaped conformation of the orbital fossa, with it posterolateral wall formed by the braincase, the recessed virtual eyeballs, and the anterior overhang of the frontal bone.

emerges, different from that generally depicted in the literature. The chief determinants of their separation are the orbit's anteroposterior position relative to the braincase and the width differential between face and braincase as manifest by the degree of postorbital constriction at the craniofacial junction. Thus, as shown in Figure 14.1, in *Notharctus*, with eyes in the forward and lateral position and the constriction narrow, orbital and temporal fossae are adjacent. In *Rooneyia*, with the eyes pulled back toward the braincase and situated medially, and the constriction broad, a large part of the globe is shielded from the temporal fossae by the braincase. The literature (e.g., Cartmill, 1980; Ross 1993) seems to assert that these spaces would be broadly continuous in strepsirhines and haplorhines were it not for a *de novo* architectural partition formed of a bony screen, the postorbital plate. This view is at least partly inaccurate because it does not recognize that the temporal fossa has been lateralized in haplorhines by a broadening of the braincase, while eyeball position also differs from strepsirhines by having been shifted medially and posteriorly.

These fundamental differences hold even for larger-eyed strepsirhines and haplorhines. As shown in Figure 14.7, even though the orbits of the large-eyed loris have also shifted medially by virtue of the expanded transverse diameter of the eyeball, the narrow postorbital constriction is retained; therefore, much of the temporal fossa is located just behind a large segment of the eye. In *Tarsius*, on the other hand, the anteriorly wide braincase backs approximately half the diameter of the eyeball and displaces the temporal fossa far laterally as well. The small size of the tarsier temporal fossa is again evident Figure 14.7c, which also raises doubts about its physical impact on orbital contents.

14.3.1.3 Zygomatic

As the lateral segment of the postorbital bar is built from the ascending frontal process of the zygomatic (FPZ), this element is important to the interpretation of the early evolution of postorbital closure. Unfortunately, there is no way of making an accurate reconstruction of this feature in *Rooneyia*, for it is completely gone. Too much bone is also missing on both sides of the skull where the maxilla meets the root of the zygomatic, so the morphology cannot be established. However, the remains of the lateral process of the frontal (LPF) and comparisons with other primates enable us to clarify some details and propose several points for consideration.

Notharctus has a typical euprimate postorbital bar like that of most strepsirhines and fossil tarsiiforms: a uniformly narrow, flattened shaft of bone connecting the FPZ with the LPF. All the tarsiiforms are similar. However, as noted by Szalay (1976), the configuration of the LPF differs in *Rooneyia*, and this suggests that the "postorbital bar" of *Rooneyia* also differs. It is a large, flange-like process that we surmise is part and parcel of the overall enlargement of the frontal bone. However, in our view, Szalay's (1976) reconstruction of the postorbital bar and anterior zygomatic arch in *Rooneyia* is unnecessarily conservative. Figure 14.8 shows his diagrammatic reconstruction of this area and its appearance in two living strepsirhines, a galago and a loris. Szalay's *Rooneyia* differs little from the galago. But the clearly enlarged LPF would better match an equally well developed FPZ, perhaps as exemplified by the loris. While we do not suggest that the shape of the FPZ of *Rooneyia* was quite that similar to a loris, where hypertrophic eyeballs have played a large role in shaping this region, there are no obvious reasons requiring *Rooneyia* to have a slender postorbital bar as depicted. Rather, given the size of the LPF flange, it may have been considerably wider.

14.3.1.4 Frontal Process and Postorbital Flange

Figure 14.9 examines the dorsoventral extent of the LPF and its configuration as a postorbital flange. A partial, laterally broken flange with a distinct vertical lamina is present on both the right and left sides of the specimen. The right side probably preserves more of its bone overall but the left preserves undamaged the flange's inferior junction with the braincase. On the left side, the postorbital flange extends vertically downward until the line of the frontal-sphenoid suture, i.e.,

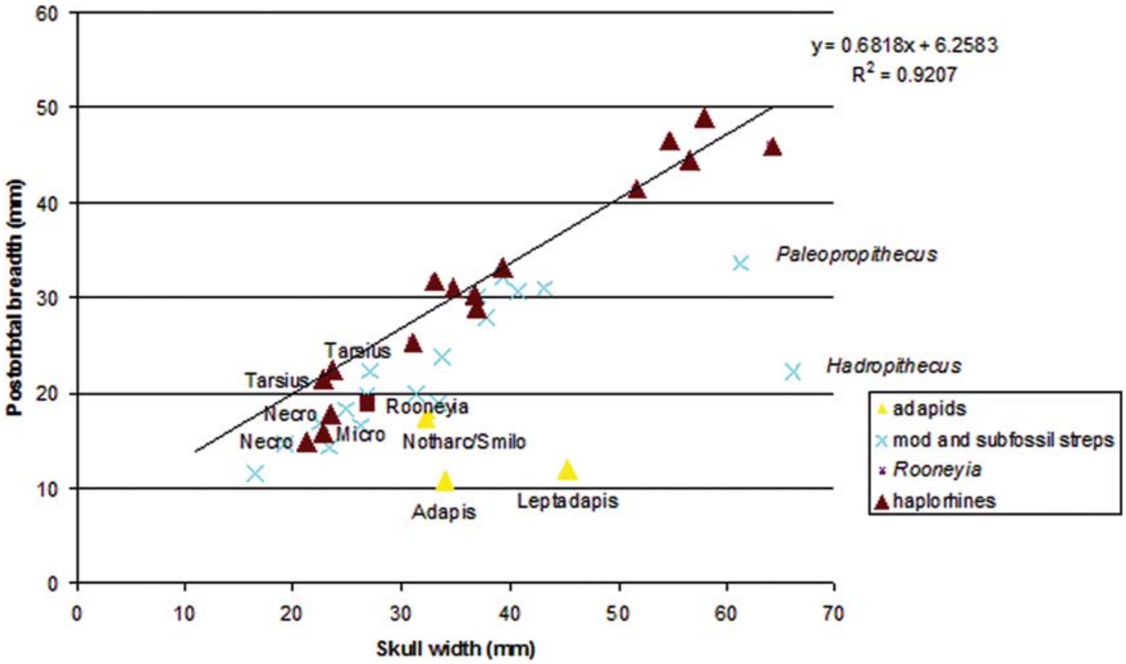

FIGURE 14.6. Bivariate plot of braincase width and postorbital breadth. Haplorhines have a relatively wider postorbitum than strepsirhines, and this holds true even for Eocene forms. Consequently, adjacency of temporal and orbital fossae is reduced since the orbits are situated at the craniofacial junction, and shielded medially, while the temporal fossa is located more laterally. Tarsiers have an unusually wide postorbitum, as their forebrains are distinctly broad, thus effecting the largest transverse spatial separation of orbital and temporal fossae. The regression is based on the anthropoid sample.

as far ventrally as possible without crossing a bone boundary. This is the area where in anthropoids the zygomatic sutures to the sidewall of the braincase. It is where in some platyrrhines there is a lateral orbital foramen (in *Saimiri* and *Cebus* possibly transmitting a branch of the superficial temporal artery, pers. obs.). In other words, the frontal process in *Rooneyia* is broadly similar in its spatial extent to the configuration of platyrrhines. Below this point, however, *Rooneyia* differs markedly for there is no alisphenoid component joining the frontal or zygomatic.

However, the ventral depth of the LPF in *Rooneyia* is extensive. In Figure 14.9b we have reoriented the skull of *Rooneyia* from the way it is usually depicted (e.g., Szalay, 1976) and into the Frankfurt plane, aligning it with *Necrolemur*, which tends to resemble *Notharctus* and other euprimates. Line “a” marks the lower horizon of the LPF in *Necrolemur*; line “b” marks it in *Rooneyia*. It is evident that the LPF in *Rooneyia*, as Szalay (1976) emphasized, partitions a proportionately larger amount of the orbital fossa from behind. Figure 14.9c makes this point by illustrating the right side, where the LPF is broken ventrally as well as laterally but still covers a proportionately large segment of a virtual eyeball fit into the orbit. We know of no other Eocene primate, strepsirhine or haplorhine, which matches this pattern.

14.3.2 Tarsiers and Tarsiids

There is an increasing body of evidence supporting the notion that tarsiers are most closely related to a collection of Eocene tarsiiform genera, which we have moved to classify as tarsiids (Table 14.1). Most active workers who disagree with this hypothesis believe that tarsiers are more closely related to anthropoids, the TAH (e.g., Cartmill and Kay, 1977; MacPhee and Cartmill, 1986; Ross, 1994; Kay et al. 1997; Ross et al., 1998; Kay et al., 2004; Ross and Kay, 2004). Therefore, placement of tarsiers is crucial to an understanding of the origins of anthropoids and the anthropoid orbit, as implied by the Cartmill (1994) quote that opens this paper. Of course, the proposed link between living tarsiers and fossils designated as tarsiiforms is not a novel hypothesis. It was widely (though not always dogmatically) assumed generations ago, albeit stated in less modern terms and argued without today’s cladistic formalisms (e.g., Gregory, 1922; Le Gros Clark, 1934, 1959; Simons, 1972). In the past, genera often singled out as having a close relationship with *Tarsius* included *Tetonius, Necrolemur* and *Pseudoloris*. For example, influenced by Teilhard de Chardin (1921), Le Gros Clark said (1934:269): “…it seems not unlikely that *Pseudoloris* represents the direct Eocene precursors of the modern *Tarsius*.” This roster of relatives has been enlarged recently following new character analyses of the skull and postcranium (Rosenberger, 1985; Beard et al., 1991; Beard and MacPhee 1994; MacPhee et al. 1995; Dagosto and Gebo, 1994; Dagosto et al., 1999), including some parsimony-based (PAUP*) studies. Among the postcranial synapomorphies identified in these studies as derived homologies shared by the fossils and *Tarsius* are features of the knee, calcaneus, tibio-fibula and, in the skull, several involving the basicranium and bulla, the glenoid fossa, pterygoid plates and the choanae (see summary in Dagosto et al., 1999).

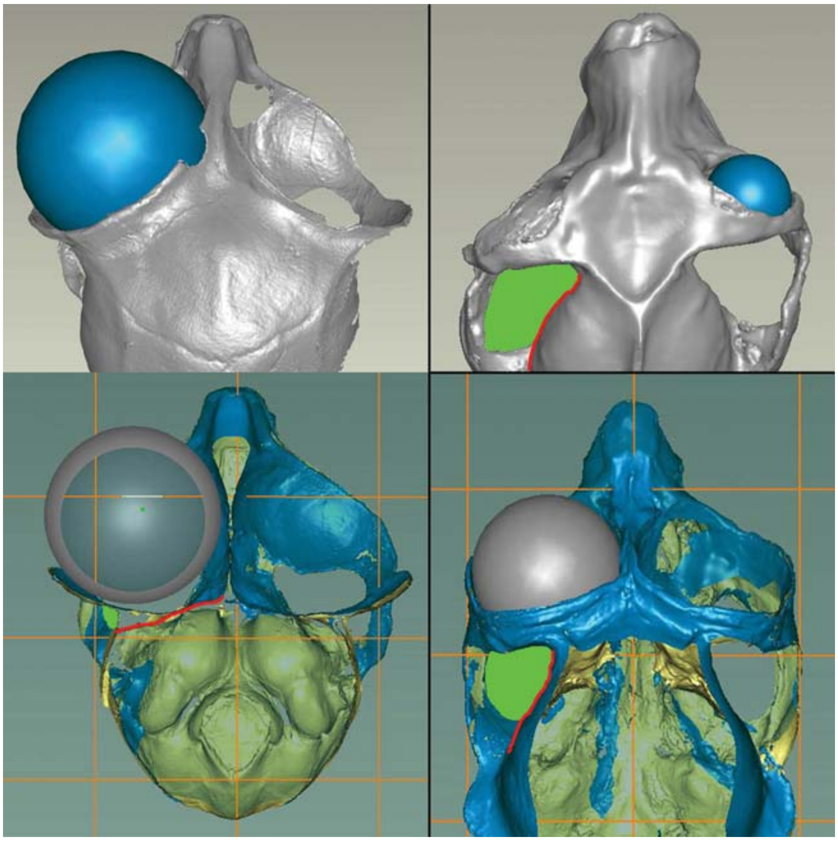

FIGURE 14.7. Images captured from three-dimensional laser scans of *Tarsius* (left top and bottom), *Notharctus* (top right) and *Loris* sp. (bottom right) to illustrate spatial relationships of orbital and temporal fossae and virtual eyeballs, and influence of postorbital breadth, with regard to the interference hypothesis of the postorbital septum. Rostrad placement of the orbital fossae in the strepsirhines is apparent irrespective of relative eyeball size. With a relatively wide anterior braincase, tarsiers have very small, laterally displaced temporal fossae. In dorsal view, the margin immediately surrounding the eyeball can be seen as an everted rim, continuous with the lateral process of the frontal. Fossil tarsiids with eyes that are probably roughly similar to *Tarsius* in their proportions, e.g., *Shoshonius*, and those with a less exaggerated size, e.g., *Necrolemur*, also show a superior everted margin, indicating this is a transformation series exclusive to the large-eyed tarsioids.

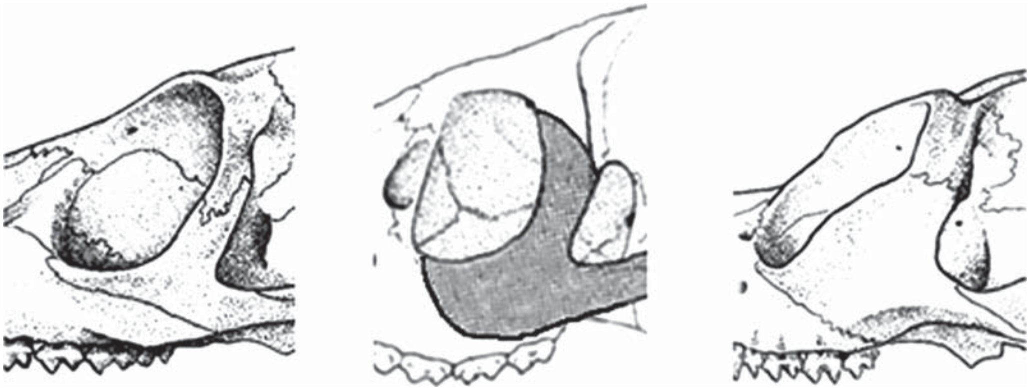

FIGURE 14.8. Lateral views of the postorbital bar in *Lemur* sp., *Rooneyia* and *Loris* sp. (left to right). The narrow ascending process of the zygomatic is the norm among strepsirhines while the loris condition illustrates how sizeable the zygomatic can become in response to eyeball enlargement. The small-eyed anthropoids are a different, parallel example of zygomatic hypertrophy. This portion of the *Rooneyia* postorbital bar may have been reconstructed too conservatively by Szalay (1976; see Figure 14.8), as its dorsal area of attachment in large, as depicted, raising the possibility that *Rooneyia* may have had a more loris-like pattern, predisposing it to a more extensive lateral closure of the orbit by the zygomatic that could approximate anthropoids. Note that the image of *Rooneyia* has been modified by stippling to better show the full extent of missing bone from the zygomatic/orbital region of the original, and to better reveal the conservatism of the original reconstruction. (Adapted from Szalay, 1976, Mahe, 1976).

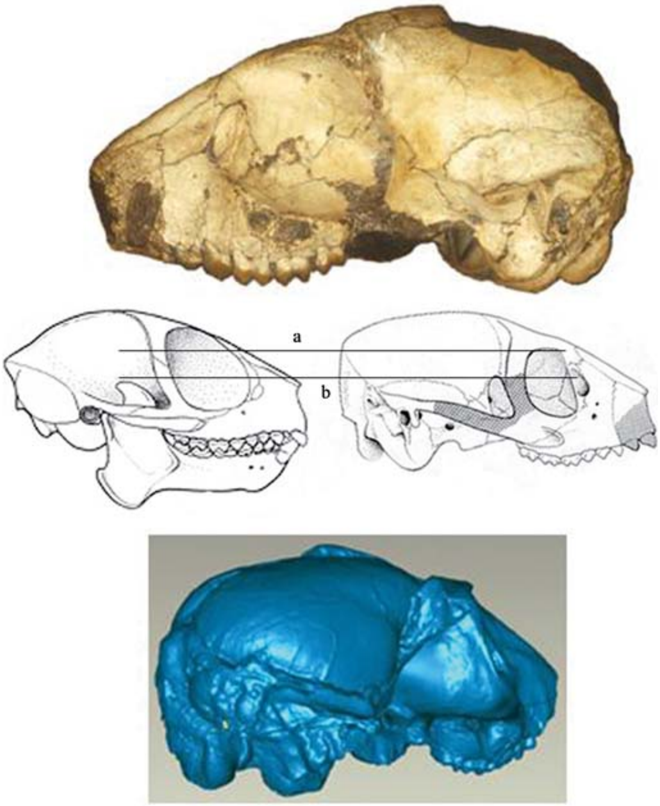

FIGURE 14.9. Top. Left lateral view of *Rooneyia* showing the great vertical depth of the lateral process of the frontal bone that forms the flange-like upper root of the postorbital bar, effecting partial postorbital closure superiorly (courtesy of Eric Delson). Middle. Lateral views of *Necrolemur* (left) and *Rooneyia* (right), drawn to same approximate cranial length and oriented on the Frankfurt plane, comparing the ventral horizon of the lateral frontal process in *Necrolemur* (line a) and *Rooneyia* (line b). Bottom. Posterior view of the broken frontal flange on the right side of *Rooneyia*, with a virtual eyeball set in place to illustrate how much of the eye is closed off from behind by the process and how relatively large the zygomatic process may have been in its area of attachment to the flange (middle and bottom adapted from Rosenberger, 2006).

It is rare for these studies to list cranial characters connected with the most striking morphological adaptation of the tarsier skull, the enormous orbits, as evidence of a phyletic link between fossil tarsiiforms and *Tarsius*. This is consistent with metric assessments that have attempted to infer relative orbit/eyes size among tarsiiforms and other fossil primates (e.g., Kay and Cartmill, 1977; Martin, 1990; Kay and Kirk, 2000). Although various Eocene tarsiiforms have relatively large eyes in the nocturnal euprimate range (e.g., Kay and Kirk, 2000; Heesy and Ross, 2001; Ravosa and Savakova, 2004), with the possible exception of one genus none of these studies have demonstrated that any fossils have eyes as anywhere nearly as large relatively as a tarsier's – "Most omomyiforms do not exhibit the enormously enlarged orbits (and thus eyes) characteristic of both extant tarsiers and owl monkeys…" (Kirk and Kay, 2004:582). This conclusion was wrought in consideration of Kay and Kirk's (2002) metric demonstration that orbits are relatively large in *Necrolemur, Microchoerus* and *Tetonius*, and unusually large relative to body size in *Shoshonius*.

Advocates of the TAH might explain the presence of large-eyed fossil tarsiiforms as evidence of parallelism, or a haplorhine last common ancestor which had large eyes that became reduced subsequently in anthropoids. Either way, it is reasonable for PAUP* users to code eye size in Eocene tarsiiforms and other euprimates (e.g., Ross et al., 1998 *et seq.*) in a three-state scheme as follows: "0" equals small; "1" equals large; "2" equals extremely large, the latter found only in *Tarsius. (Shoshonius* has only recently been added to the dataset used in the studies cited.) However, the morphological organization of tarsiid dentitions and skulls, as presented here, suggests that these necessarily reductionistic methods of metric assessment and parsimony analysis underestimate how relatively large the eyes of some fossil tarsiiforms actually are. Here we consider several cranial features belonging to a pattern which points to eyeball hypertrophy in many of them.

Before proceeding, however, we elect to elaborate on what should be obvious. Evolutionary biologists would probably all agree that there is no reason to expect that even a sister-genus of the tarsier *must* have an eye as large as a *Tarsius*. Meaning, even if its eyes were smaller, that would not negate a close phylogenetic relationship. To the contrary, it is expected. And that provides a rationale for homologizing and weighting heavily evidence of relatively large eyes in fossil tarsiiforms, although this is rarely done.

Sprankel's figures (1965) for juvenile *T. bancanus* indicate an eyeball:brain size weight ratio of 90%. While it is prudent to assume as a working hypothesis (but not an axiom) that this ratio is likely to be utterly unique among all primates living and extinct, as phylogenetic evidence the state coded (relatively) "large" in another taxon is fully acceptable as an "ordered" synapomorphy when the anatomical patterns associated with it suggests that the large-eyed similarity to *Tarsius* is homologous and that the ancestral condition of the larger group in question is thought to have unenlarged eyes and orbits. Thus, with reference to Kay and Kirk's (2002) careful metrical study, it becomes difficult to interpret their data on relative orbit size to reflect anything other than a phylogenetically meaningful transformation series, with *Necrolemur, Microchoerus* and *Tetonius* reflecting one shared, homologously derived state, large, relative to primitive euprimates; *Shoshonius* reflecting a more derived/more enlarged state; and, *Tarsius* reflecting the most modified state *if indeed its eyes were larger relative to body size than Shoshonius*. In the absence of a way to resolve this last caveat, the parsimonious interpretation would assume that *Tarsius* and *Shoshonius* share a derived version of the "large" condition. And, if it turns out that the living tarsier is a variant of that state, the tarsier condition would be seen as an autapomorphy derived from the *Shoshonius-Tarsius* condition. Lest the point not be clear, this mode of argument also implies that the other three genera mentioned share "large" as a derived state with *Shoshonius-Tarsius* as well, but one node removed from their common ancestor, which would have had the "small" condition.

What is vitally important here is that there are other features indicating that an advanced state of eyeball enlargement or hypertrophy obtained broadly among fossil tarsiids, especially for taxa lacking orbits sufficiently complete to be measured by conventional means. This reinforces the supposition that the derived metrics of the eyes in all these tarsiiforms is homologous. As a start, our anatomical perspective can be reduced to these points of reference: (1) arcade shape; (2) paralveolar morphology; (3) osseous interorbital septum; (4) choanal shape; and, (5) everted dorsal orbital margins.

14.3.2.1 Arcade Shape

Modern tarsiers tend to have what might be called a modified bell-shaped dental arcade (Figure 14.10). We add the qualifying term "modified," because it is best to look at this feature transformationally. This shape reflects an extreme narrowness of the anterior snout, i.e., closely set antemolar teeth, coupled with an exceptionally broad posterior palate, i.e., width across the molars. The postcanines diverge so dramatically toward the rear that bimolar breadth almost equals the maximum width of the braincase. The narrow anterior snout, sometimes described as tubular (e.g., Rosenberger, 1985), is not indicative of diminished function in the anterior teeth. Rather, it relates to a robust premaxilla with tall, stout, well rooted medial incisors and strong canines arranged in a particular way, which probably concentrates muscular force to enhance the efficacy of these teeth in puncturing prey while working against the lower anterior teeth (e.g., Thalmann, 1994). The posterior breadth of the arcade relates to megadontia and hypertrophic eyeballs. Tarsiers, and most likely some fossil tarsiiforms, also have large molars for their body size (Gingerich et al., 1982; Dagosto and Terranova, 1992). Additionally, with each eye approaching the volume of the whole brain, it stands to reason that the breadth of the orbital floor and the palate, to which the latter is fused, has been grossly modified to reflect transverse eyeball diameter.

In all fossil tarsiids for which the anatomy is known, in contrast to all anthropoids and strepsirhines, the arcade is pinched in the middle and even more precisely bell-shaped, more than in *Tarsius*. The anterior snout is narrow, the molars spaced far apart and the transition from premolar to molar is contoured to bridge the width differential. It is easy to visualize the differences between the fossil tarsiids and *Tarsius* as a transformation series where differences are related to simple contrasts in premolar-molar tooth widths, tooth proportions and, eventually, the massively enlarged molars in tarsiers. The bell-shaped silhouette is muted in some forms because the premolar-molar shape transition also conforms to another novelty of the tarsiiform face, the anteriorly extended paralveolar region of tarsiers as discussed below. Therefore, we interpret the formative bell-shaped arcade that is widespread

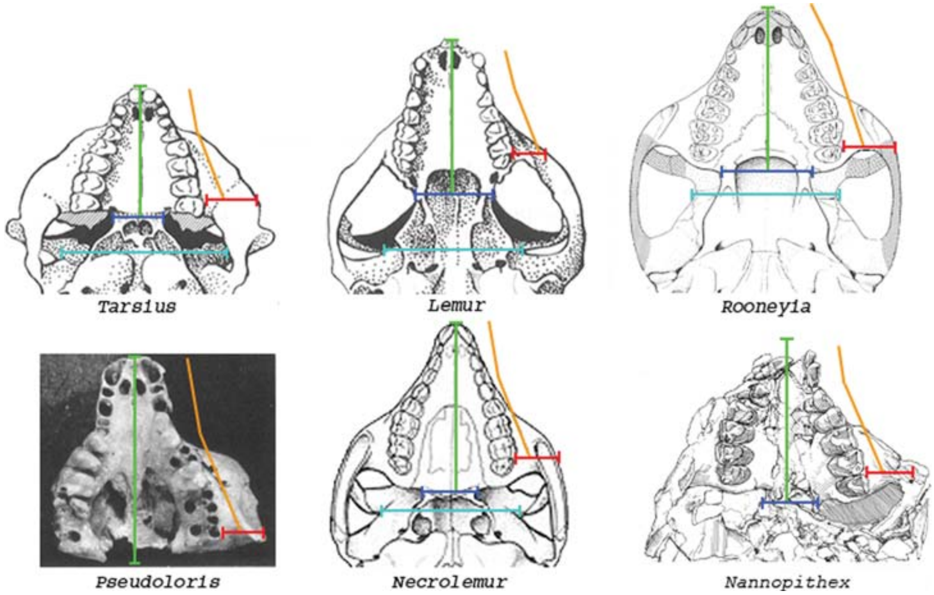

FIGURE 14.10. Basal views of (clockwise from top left) *Tarsius*, sp., *Lemur*, sp., *Rooneyia, Pseudoloris, Necrolemur*, and *Nannopithex* showing variations in the tarsiiform "bell-shaped" dental arcade, paralveolar extension of maxilla beyond the toothrow, relatively narrow choanal breadth and wide postorbital breadth. *Lemur* is typical of strepsirhines and taken to represent the ancestral euprimate pattern. *Rooneyia* retains the primitively wide choanae. Paralveolar extension and choanal narrowing are postero-lateral and postero-medial factors connected with eyeball hypertrophy, which is most exaggerated in *Tarsius, Pseudoloris* and perhaps *Nannopithex*. (Adapted from Cartmill, 1980, Szalay, 1976, Thalmann, 1994).

among tarsiids as a derived feature among euprimates relating to an increase in the transverse diameter of the orbits. As noted below, when the orbits become further exaggerated in genus *Tarsius*, the phenomenon is also played out in the anteroposterior axis in a localized way that makes the bell-shape less pronounced.

In *Rooneyia*, there is no sharp transition from premolar to molar so there is no indication of a bell-shaped arcade behind the canines. Since the tip very front of the snout is not preserved, we are limited in terms of what can be inferred about it. However, there is no reason to suppose it was narrow or tubular, as in the tarsiids. To the contrary, judging by the postcanine contour, and guided by the frugivorous cheek teeth, it would seem more likely that the snout was not set up to have tarsier-like piercing teeth and that it accommodated relatively wide incisors as Szalay (1976) believed. A wide anterior snout would resemble the condition of adapids, and is therefore likely to be ancestral in euprimates.

14.3.2.2 Paralveolar Morphology

As noted, a shape feature of *Tarsius* that is part of the bony underpinning of orbital hypertrophy involves the paralveolar surface of the face (Figure 14.10). To some degree, one might consider our delineation of this feature as a redundancy, a correspondent to the bell-shaped arcade. This may be a legitimate point, but we believe there is descriptive value in separating the two, which are surely functionally correlated – and that is our point: all five of the features discussed here are functionally correlated with one another and with hypertrophic eyes. But the anatomical expressions differ among the genera, and this permits and provokes evolutionary character analyses.

With the orbital floor grossly expanded transversely and fused to the hard palate medially, there is essentially no "suborbital" facial depth to speak of in *Tarsius* (see Seiffert et al., 2005). Rather, lateral to the dental arcade, the maxillary-zygomatic complex is extended anteriorly and transversely to form an enlarged overhanging plane which conforms to a massively expanded orbital floor (Figure 14.10). Since the equator of the eyeball lies high above the orbital floor, the line of maximum bi-orbital width actually lies well above the junction between zygomatic arch and maxilla, so that the surface of the latter has essentially become everted.

Fossil tarsiids do not uniformly present such an exaggerated condition (Figure 14.10) and none (as well as can be documented by measuring or estimating external orbital diameters) appear to have such hypertrophic orbits, except perhaps *Shoshonius* (see Beard et al., 1991; Kay and Kirk, 2000). However, the pattern is well developed in *Pseudoloris*, which genus may exhibit the closest resemblances to *Tarsius* in having an anteriorly and laterally expanded paralveolar shelf. The crushed skull of *Nannopithex* may have a more developed expansion than *Necrolemur*, where it is modest but better developed than the extent seen in *Rooneyia*. Others, such as *Tetonius, Microchoerus* and *Necrolemur*, of varying body sizes, show varying degrees of laterally expanded orbital shelves but none appear to be anteriorly expanded, and none appear to have grossly everted zygomatic roots. The lack of anterior expansion may mean that these taxa did not evolve the elongate, tube-shape eyeballs of *Tarsius* (Castenholtz, 1984), but retain a more primitive, spherical eye, albeit an impressively large one. It may also simply signal a smaller relative eye size.

With a raised orbital floor and small orbits, the maxillary morphology of anthropoids is fundamentally different. *Rooneyia*, however, has a modest paralveolar expansion. We attribute this to the combination of a broad and shallow face, and a relatively wide anterior braincase and (inferentially) a wide zygomatic arch, which makes for a laterally positioned anterior zygomatic root. Since this is associated with unenlarged orbits and is closest to the non-haplorhine condition, we believe that the relatively small paralveolar shelf of *Rooneyia* represents the ancestral state for haplorhines.

14.3.2.3 Osseous Interorbital Septum

The enormity of tarsier eyes requires a medial shift in the position of the medial orbital walls, thus producing an extensive fusion of these surfaces (Le Gros Clark, 1934) into an osseous interorbital septum (see Starck, 1975). The septum occupies a large segment of the anteroposterior dimension of the orbit from its posterior apex to the anterior-inferior margin. As a consequence, the nasal fossa is restricted to the front of the snout and, as Starck (1975) and others have shown, the olfactory nerves are thus routed to the nasal fossa via a long olfactory tube above the septum. High resolution CT scans may determine how extensive interorbital septa are in the fossil tarsiids, and if they have an olfactory tube like this, but the morphology of several, e.g., *Tetonius, Necrolemur, Microchoerus* and *Pseudoloris* (Cartmill and Kay, 1978; Ross, 1994), for example, is similar enough to be highly suggestive of an osseous septum, or at least orbits closely approximated over an long antero-posterior span. Breaks in several specimens of the last three genera show that fusion definitely occurred according to Ross (1994, Figure 14.14), but it is important to determine not only the presence of fusion, which may be common at the orbital apex, but also the anterior extent of it. One *Pseudoloris* specimen (see Teilhard de Chardin, 1921) shows quite dramatically a combination of features that appears to be indisputably tarsier-like in this regard: a remnant of extensively fused orbital walls can be seen demarcating an anteriorly isolated nasal fossa. Thus it appears to be a rather solid conclusion that the eyeballs of *Pseudoloris* were exceptionally large, as Simons (e.g., 2003) has emphasized. In *Rooneyia* (Rosenberger, 2006; Figure 14.5), as with anthropoids and most strepsirhines, the medial orbital walls remain separated (only sometimes contacting posteriorly at the apex in smaller species), suggesting the more widespread and primitive condition with the olfactory nerves entering the nasal fossa through a typically positioned cribriform plate, posteriorly, at the interface with the anterior cranial fossa.

14.3.2.4 Choanae

Ross (1994) and Szalay (2000) have related the small, peaked choanae in *Tarsius* to hypertrophic eyes. Connected with this is the correspondingly narrow distance between the pyramidal processes. These features are fixed by the mediolateral position of the orbital walls. Because the walls have been drawn to fuse in the midline of the skull, the posterior nasal aperture is narrow and small, and the pterygoid plates which extend behind them are also drawn to the middle. This is a derived condition among euprimates and it does not occur in strepsirhines, *Rooneyia* or anthropoids (Rosenberger, 1985; Beard and MacPhee, 1994; Ross, 1994). All of the tarsiids that preserve either the pyramidal processes or the choanae resemble *Tarsius* (Figure 14.10), i.e., *Necrolemur, Microchoerus, Nannopithex, Tetonius* and *Shoshonius*. This is also indirect evidence that they all have an osseous interorbital septum, at least apically, within the orbit. *Teilhardina* appears not to have this pattern.

14.3.2.5 Everted Dorsal Margin

By comparison with the other features discussed here, the often subtle lipping (not so in *Tarsius*, where it is dramatic) of the superior margin of the orbit seems less trenchant. However, the comparative evidence suggests that it is correlated consistently with eyeball hypertrophy. For example, other extant primates that show at least a slight eversion of the superior margin are *Loris* and *Aotus*. With the eyeballs of *Tarsius* jutting beyond the perimeter of the orbital fossa (Castenholtz, 1984), it seems reasonable to infer that the strongly everted superior margins are a direct correlate, as discussed above. Similar margins appear in *Necrolemur, Microchoerus, Hemiacodon*, and *Shoshonius*. In the smaller-eyed *Rooneyia* and most strepsirhines, the lip is not everted, suggesting that the tarsiid condition is derived.

To summarize, these features all appear to be associated with large eyes in tarsiids, suggesting a functional pattern that is part of the orbital hypertrophy syndrome, a derived euprimate adaptation that is most highly modified in *Tarsius*. Several of these features are graphically compared in chart form (Figure 14.11), derived from the images shown in Figure 14.10. In contrast, *Rooneyia* differs in nearly every detail, and is more primitive than any of the tarsiiforms (see Rosenberger, 1985). The morphology of *Teilhardina* is still not fully described but it appears not to manifest many of these features. Thus, *Teilhardina* may serve as a good model for the ancestral, small-eyed, haplorhine condition.

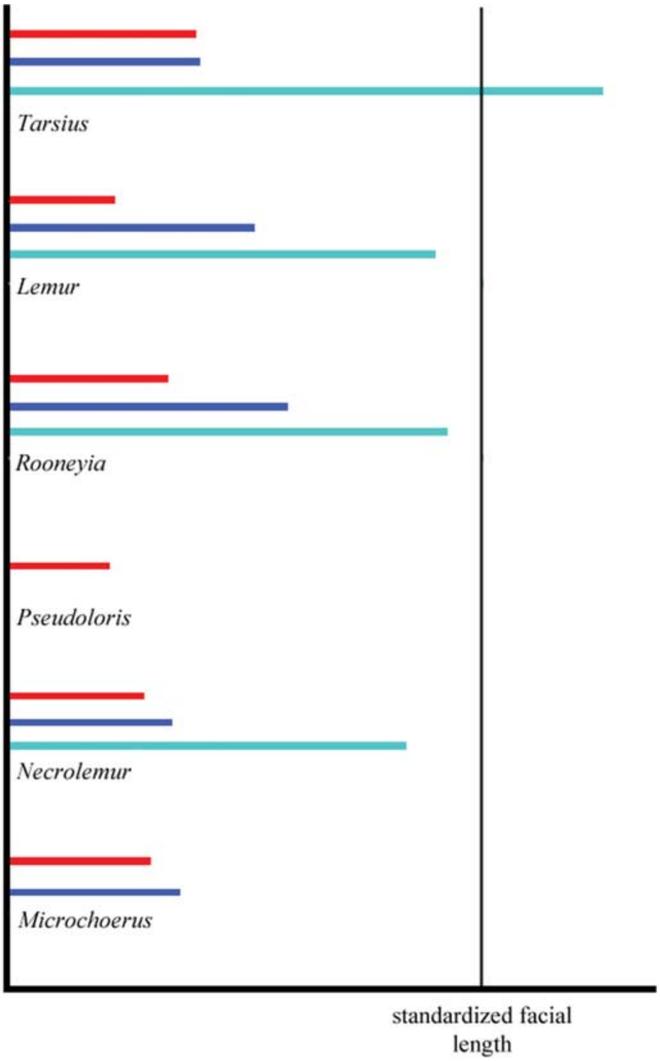

FIGURE 14.11. Graphic representation of features marked in Figure 14.10 to show their proportions. The position of the vertical line along the horizontal axis of the chart represents a standardized facial length, generated by scaling all the skulls to the same palatal length (see Figure 14.10). The horizontal bars represent the ratios, measured against this standard palatal length, of paralveolar extension of the maxilla (red), choanal breadth (blue), and postorbital breadth (teal). The relatively wide choanae of *Lemur* and *Rooneyia* are apparent, in contrast to the large-eyed tarsiids. *Tarsius, Necrolemur*, and *Nannopithex* have strikingly similar proportions of choanal breadth and paralveolar breadth.

14.4 Discussion

14.4.1 Systematics Of *Rooneyia viejaensis*

To our knowledge, *Rooneyia* is the only non-anthropoid primate, with the exception of *Tarsius*, that has been mentioned for its potential as being structurally "on the way" to evolving postorbital closure. We have made it central to our morphological discussion, but its systematics must also be "right" if our hypothesis is to have extended credibility. As reviewed above, Szalay's (1976) interpretation of *Rooneyia* as an omomyid has been the most influential (see Szalay and Delson, 1979; Fleagle, 1999; Gunnell and Rose, 2002), and his overall view of haplorhine evolution was also important in establishing what he called omomyids as a likely ancestral stock for Anthropoidea (Rosenberger and Szalay, 1980). Taken literally, that notion is itself a complex proposition, for it implies that Szalay's omomyids are paraphyletic. In the decades since his landmark monograph, workers have come to be more convinced that this is indeed the case (e.g., Rosenberger, 1985; Beard et al., 1991; Beard and MacPhee, 1994; Dagosto et al. 1999; Ross et al., 1998). So, if Omomyidae *sensu* Szalay is not monophyletic, is *Rooneyia* one of the taxa whose inclusion forced the family's paraphyly – and obscured the close phylogenetic links between many "omomyids" and tarsiers?

The most recent treatments bearing on the systematics of *Rooneyia* are pertinent here. Gunnell and Rose, for example, classify *Rooneyia* within a subfamily (Omomyinae) of the Omomyidae but state (2002:70), "The taxonomic position of *Rooneyia* is in question…and further evidence is required to elucidate its phylogenetic relationships." Still, they do not go so far as to remove the genus from the family in their classification, as was done with several other questionable forms (*Ekgmowechashala, Altanius, Kohatius, Afrotarsius, Altiatlasius*; see Delson et al., 2000) – these they label "Problematic Taxa."

A series of parsimony (PAUP*) studies (e.g., Ross, 1994; Kay et al., 1997; Ross et al., 1998; Kay and Kirk, 2000; Kay et al., 2004) more directly challenged the *status quo*, stunningly removing *Rooneyia* from both of the accepted major ordinal-level taxonomic groups of primates on account of its tendency to link cladistically with disparate taxa (see above) depending on how the input character/taxon matrices were constructed and coded. Thus, as a new taxonomic alternative, *Rooneyia* has been separated from both Semiorder Strepsirhini and Semiorder Haplorhini and placed in Semiorder *incertae sedis* (e.g., Kay et al., 2004). In a different judgment, *Rooneyia* was installed even more remotely, into a taxonomic gehenna – "Plesion indet." (Kay and Kirk, 2000).

While a detailed examination of the characters, character coding and missing-data cells used in the large character/taxon data matrices at the heart of these projects (e.g., Ross, 1994; Kay et al., 1997; Ross et al., 1998; Kay and Kirk, 2000; Kay et al., 2004) may shed light on why so many divergent solutions to the *Rooneyia* problem were found, several larger points are worth mentioning here. In one sense, the mere fact that the cladistic position of *Rooneyia* was highly unstable means only that specific cladistic hypotheses could not be corroborated using these particular methods and conditions. It does not mean that the relationships of *Rooneyia* are imponderable, unknowable or to be found among some heretofore unrecognized group of primates. From another perspective, all of these proposed solutions are conjectural. Other than in Ross's (1994) robust character analysis, which dealt with a relatively small list of the full data set used in this series of studies, little effort was given to refute the evidence and analyses provided in other studies except in a *post hoc* fashion, after the cladograms were automatically constructed. Thus, even if Omomyidae *sensu* Szalay is paraphyletic, the phylogenetic ambiguity promoted in this string of papers is not a compelling rationale for abandoning the still unfalsified interpretation of *Rooneyia* as a haplorhine: there is a difference between saying "Wrong." and saying "We can't tell." But what kind of haplorhine is it? Our concurring analysis of the morphology of the orbital region also suggests that the affinities of *Rooneyia* are outside of Szalay's omomyids. We have proposed that *Rooneyia* is more closely related to Anthropoidea than any other euprimate genus for which we have cranial evidence (Rosenberger, 2006). But, importantly, the refinement we offer of the hypothesis Szalay began to conceptualize decades ago (Szalay, 1976; Rosenberger and Szalay 1980) is that the ancestral stock or nearest relatives of Anthropoidea that he anticipated would be found among the "omomyids" in fact appears to be one that he included in the family – *Rooneyia*.

The orbital morphology discussed above presents several correlated derived characters that *Rooneyia* appears to share exclusively with anthropoids. These may be reduced to anatomical shapes, proportions and spatial relationships of the frontal bone, and they relate to how the orbit is constructed on nearly all its sides – the aperture (high convergence plus frontation), the roof (large size and anteriorly extended frontal), its posterior (large, dorsoventral and laterally extensive lateral frontal process or flange), and, conjecturally, its lateral segment (potentially somewhat enlarged ascending process of zygomatic). Postero-inferiorly, the orbital floor is still open; there is a large inferior orbital fissure. The orbital fossa is still not fully drawn in beneath the forebrain, which is still almond-shaped but noticeably less so than in strepsirhines, and the space is probably not sealed by anything more than an incipiently large zygomatic. But, as Wilson (1966) and Szalay (1976) noted, the orbital morphology of *Rooneyia* fulfills what was then seen as the primary structural requirement of an antecedent to anthropoid postorbital closure. Dorsally, perhaps half of the height of the opening was closed by the transversely aligned frontal flange. How to "get there from here?" Rosenberger (2006) suggested that further widening of the forebrain in anthropoids may have induced a rotation of the "postorbital flange" into a parasagittal plane, thus making it possible to (1) widen the frontal-zygomatic suture complex and (2) reshape the zygomatic into the spoon-like enclosure that is universal in anthropoids.

We have rendered the characters this way in part to emphasize that they are likely to be interconnected. However, it is legitimate to question our character analysis, specifically the homologies of the unit characters making up this suite. For example, why interpret the high levels of orbital convergence plus frontation as homologous in *Rooneyia* and anthropoids? Or, why isn't the lateral frontal process making the postorbital flange of *Rooneyia* regarded as the homologue of the postorbital alisphenoid-septum of *Tarsius*? Our reasoning regarding the orbital aperture is partly philosophical and partly based on related hypotheses. Apart from a *few* of the ambiguous results of the PAUP* studies, there are simply no alternative cladistic hypotheses offered in the literature to compete with the notion of *Rooneyia* as haplorhine. *Rooneyia* shares many primitive euprimate features with strepsirhines and haplorhines (Rosenberger, 1985; Beard and MacPhee, 1994), along with others that show it to be a haplorhine (Szalay, 1976) and a protoanthropoid (Rosenberger, 2006). Therefore, since there is no reason to suspect that any particular resemblance to anthropoids is a likely product of analogy, and the orientation of its orbits, for example, fits the universal expectation of a pre-anthropoid pattern, why not assume it is homologous as a working hypothesis until that hypothesis fails?

The debate about the homologies of the anthropoid and tarsier septa has been carried out with no mention of *Rooneyia*, but for Szalay's (1976) comment. Concerning the possibility that the frontal flange of *Rooneyia* is homologous with the tarsier septum, it appears that the evidence is strongly against it. *Rooneyia* is relatively small-eyed; *Tarsius* eyes are hypertrophic. As discussed above, fossil tarsiids with eyes that may approach a tarsier's in size (*Shoshonius*), or are relatively smaller (*Necrolemur*), do not have a flange of any kind, suggesting that the *Tarsius* pattern is neomorphic. Thus, this particular similarity of *Tarsius* and *Rooneyia* appears to be a classic case of convergence.

14.4.2 Origins Of Postorbital Closure

Based on the forgoing, to limit semantic confusion we suggest a redefinition of the character states relating to the separation of orbital and temporal fossae in euprimates. A frontal-alisphenoid septum evolved in *Tarsius, sui generis*. A postorbital flange of the frontal evolved in the common ancestor of *Rooneyia* and the anthropoids. Postorbital closure, distinguished and defined by a large contribution of the zygomatic, evolved in anthropoids, in connection with enlargement and rotation of the flange. While we regard both the interference and structural support hypotheses as having merit as adaptive explanations, and sometimes difficult to distinguish, the specific selective conditions that may have influenced the morphology of tarsiers and anthropoids were probably quite different. Common to both, and what is likely to have set the stage for this example of functional parallelism, is that haplorhines since their inception had an orbital fossa that was recessed posterior-medially into the face and positioned at the craniofacial junction, unlike the more primitive strepsirhines. This may have added a new range of developmental influences which came into play as tarsiid eyeballs evolved their large size and as anthropoid eyes and faces shifted further beneath an enlarging anterior cranial fossa.

14.5 Epilogue

Fleagle and Kay asked, "Where did the anthropoid condition come from?" (1994:693). At a time when primatologists were looking at "prosimian grade" primates for the answer, Szalay (1976) saw that the haplorhine concept was more powerful and turned our attention to tarsiiforms for ideas about the anthropoid's ancestral stock. He recognized that *Rooneyia viejaensis* offered a structural example of pre-anthropoid morphology, with an incipient postorbital septum. We have extended his analysis and found that the orbital morphology of *Rooneyia*, now conceived more broadly, indeed suggests that *Rooneyia* is more closely related to Anthropoidea than any other early euprimate, meaning that postorbital closure could have evolved from the group we have called Protoanthropoidea.

And "…the tarsier condition, for that matter?" – Fleagle and Kay (1994:693). To paraphrase Cartmill (1994:563): Are we now compelled to conclude that the septa of tarsiers and anthropoids are not homologous, because a convincing analysis of haplorhine phylogeny has given us convincing reasons for thinking that the last common ancestor of tarsiers and anthropoids lacked a postorbital septum? Our answer is: Yes. Unlike Szalay (1976), who believed that the enlarged frontal-alisphenoid flange of tarsiers was equivalent to *Rooneyia's* frontal postorbital flange, we suggest that an impressive suite of cranial features among fossil tarsiiforms argue otherwise. For several fossil tarsiiforms these demonstrate an exclusive monophyletic relationship shared with tarsiers, while also showing that the morphology of their last common ancestor was too derived – in a tarsier direction – to have been ancestral to anthropoids as well. The postcranial evidence, basically from the same collection of species, shows the same thing. This means that there is a powerful case for modern tarsiers evolving from an array of faunivorous, small, nocturnal, leaping quadrupeds, Eocene tarsiiforms which already had members that presaged the ultra-large eyed, hyper-leaping mode of life that is the *Tarsius bona fides*.

Did the two postorbital partitions of anthropoids and tarsiers evolve for the same reason, as Szalay (1976) and Cartmill (1980) suggested, for "…protecting the eyeballs and associated structures from the contraction of the temporalis (Szalay, 1976:349)"? From the perspective of a character analysis, which has been our vantage point, this matter can only be addressed indirectly. But it tends to indicate there is little common ground in the local and peripheral morphologies or transformational histories of the two patterns, making it unlikely that they share the same underlying causality. While postorbital closure in anthropoids is largely effected by framing the eyeball laterally with an enlarged zygomatic and backing it medially by the braincase, tarsiers are different. They have radically expanded the frontal into a plate-like shield, with a small splint of alisphenoid tethered to it. Large-eyed fossil tarsiids anticipate this pattern in developing a brim-like frontal differing only in degree from the morphology of *Tarsius*. What the fossil tarsiids lack are the maxillary process and the alisphenoid splint, both of which would seem to provide additional support for the eyeball. In other words, the ancestors of tarsiers were already developing a scaffold to cup giant eyeballs before the alisphenoid-septum was selected, either for its support or insulation value. There is no evidence that the small-eyed anthropoids passed through such a stage. Rosenberger and Pagano (in press) suggested that fusion of the frontal bone was influential as a preadaptation in basal anthropoids by producing a new biomechanical regime that shunts masticatory strains laterally towards the frontal-zygomatic sutures as opposed to being dissipated by a mobile, open interfrontal (metopic) suture.

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