Frontal Fusion: Collapse of Another Anthropoid Synapomorphy

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ABSTRACT

We test the hypothesis that the fused interfrontal suture of anthropoids is a uniquely distinguishing feature and a derived characteristic indicative of their monophyletic origin. Our survey of nonanthropoid primates and several archontan families indicates frontal fusion is widespread. It is most variable (fused, open or partially fused) inter- and intra-specifically among strepsirhines. The frontal bone is more commonly fused in living lemuroids and indrioids than among lorisoids. It appears to be fused regularly among Eocene adapids. Among nonanthropoid haplorhines, the interfrontal is fused in *Tarsius*, even in neonates and invariably in adults, probably also in all fossil tarsiiforms preserving the frontal bone, and in the late Eocene protoanthropoid *Rooneyia*. The plesiadapiform pattern remains uncertain, but fusion is ubiquitous among living tree shrews, colugos and bats. Distributional evidence implies that interfrontal fusion was present in the last common ancestor (LCA) of haplorhine primates and possibly in the LCA of euprimates as well. Anthropoids, therefore, cannot be defined cladistically by interfrontal fusion, not out of concern for homoplasy but because it is probably a primitive feature inherited from other taxa related to anthropoids. Fusion of the large anthropoid frontal bone, which was extended anteriorly to roof the orbits and expanded laterally in connection with a wide forebrain in the LCA of anthropoids and protoanthropoids, may have been preadaptive to the evolution of the postorbital septum. The zygomatico-frontal suture of the septum may provide an alternative mechanism for dissipating the calvarial strains of mastication formerly taken up by an open interfrontal suture. Anat Rec, 291:308–317, 2008. © 2008 Wiley-Liss, Inc.

Key words: interfrontal suture; frontal bone; skulls; postorbital septum; anthropoids; primate phylogeny; tarsiers

It is widely believed that closure of the interfrontal suture in primates, that is, the development of a fused frontal bone (closure of the metopic suture of humans), is a shared derived homology unique to anthropoids. This view appears regularly in detailed studies of anthropoid cranial morphology and origins (e.g., Rosenberger, 1985; Rosenberger and Shea, 2000; Miller et al., 2005), technical syntheses on primate evolution (e.g., Simons, 1972: Martin, 1990), more general summaries of the order's history and anatomy (e.g., Conroy, 1990; Fleagle, 1999; Ankel-Simons, 2000), and recent

assessments of Eocene fossils thought to pertain to Anthropoidea (e.g., Gunnell et al., 2002; Takai and Shigehara, 2004; Beard et al., 2005). However, there is reason to think that frontal fusion may not be an anthropoid synapomorphy at all. As with the mandibular symphysis, which was long considered a shared derived feature of anthropoids based on comparisons of living platyrrhines and catarrhines (e.g., Rosenberger, 1986) but now appears to be contravened by the report of an open symphysis in some Fayum anthropoids (e.g., Simons, 1990), the fossil evidence—this time of nonanthropoids—suggests that a fused frontal bone evolved early in the history of primates, suggesting it may be a primitive retention in the anthropoid morphotype.

In this report, we contribute new information pertinent to this question by surveying the status of the interfrontal suture in a large sample of modern strepsirhines, tarsiers, fossil tarsiiforms and other early euprimates, as well as colugos, bats, and tree shrews. In several cases, our personal observations correct ambiguities or errors that have appeared in the literature regarding the condition of the interfrontal suture in critical fossils. We caution, however, in view of the variability we discovered among modern lemuriforms and lorisiforms, and the diversity of Eocene strepsirhine taxa, many of which are not known from skulls, that questions remain about the distribution and evolution of interfrontal closure in nonhaplorhine euprimates. We also did not personally examine plesiadapiform fossils, another diverse group crucial to the matter.

While the idea of frontal fusion as an anthropoid hallmark can be traced to workers in the early 20th century, it is likely that a major study by Montagu (1937) helped cement the notion. In a comprehensive cross-sectional survey of over 5,000 modern primate specimens, Ashley Montagu documented the near universality of early ontogenetic fusion of the interfrontal suture in anthropoids. Although Montagu's survey was handicapped by some notable taxonomic shortcomings in his appraisal of strepsirhines and callitrichines, for example, the large sample sizes of platyrrhines and especially catarrhines, and the range of specimens observed, from prenatals to infants to advanced adults, makes a convincing case that all modern anthropoids do have a fused interfrontal suture. It should be noted for clarity that open interfrontal sutures, even in very young individuals, were found to be rare but not entirely inconsequential. Montagu reported relatively high percentages of partially open sutures in the sample of *Pongo pygmaeus* (21.8%, N = 87) and *Macaca fascicularis* (25%, N = 16), and completely open sutures were recorded for *Cercocebus chrysogaster* (8.6%, N = 35) and *Cercopithecus aethiops* (10.3%, N = 29). Since then, however, some 70 years of additional observation made by numerous morphologists have not led to any questions about Montagu's fundamental results regarding anthropoids.

In contrast, Montagu (1937) found fused frontals to be uncommon among adult strepsirhine primates, which he called "prosimians." Thus, we surmise that the long held assumption that interfrontal fusion is an anthropoid synapomorphy grew out of the once ordinary phylogenetic dichotomy of prosimians vs. anthropoids. In Montagu's view, and presumably for others as well, this taxonomic distinction would have been logically consistent with the gradistic supposition of a prosimian-to-anthropoid, unfused-to-fused, transformation series. However,

this oversimplifies the facts behind the story, for one outstanding "prosimian," *Tarsius*, was not prosimianlike in pattern. Montagu's assessment was uncharacteristically muted concerning tarsiers. He stated that the interfrontal was fused in all the individuals he examined, but he also hedged his conclusion by stressing that his sample size, seven individuals and only one juvenile, meant his observation were not conclusive. He further tempered his comments by noting that Remane (1923, cited in Montagu, 1937) found the one infant *Tarsius* that he examined to have had a patent suture.

Other experienced anatomists of the era were quite certain of the tarsier condition. Woolard (1925, p 1077), in his classic anatomical study of the tarsier, simply said, "The frontal bone is single." Hill (1955) agreed: "...the frontal is single in the adult, there being no interfrontal suture." Duckworth (1915) had previously made a finer point by saying that, in *Tarsius*, the frontal fused earlier in life than in other nonanthropoids. Modern morphologists, surprisingly, have rarely remarked on the status of the interfrontal in tarsiers. Its fused condition has not been disputed, nor has this character state been invoked as evidence for the tarsier–anthropoid hypothesis—as one would imagine it should have been—during the preparsimony decades when the support for this idea was based on extensive trait-by-trait character analyses of the skull (e.g., Cartmill and Kay, 1978; Cartmill, 1980, 1994; MacPhee and Cartmill, 1986). Nor was this point promulgated during the formative period when the Haplorhini hypothesis was being wrought by Pocock (1918), who already believed that the expanded postorbital bar of *Tarsius* was a cranial homology shared with anthropoids and a strong measure of their close relationship.

That the fused interfrontal has achieved almost iconic status as an anthropoid synapomorphy is evidenced by rarity of any discussion of its evolution in a paleontological context. Although those working on early higher primate crania from the Fayum, or questionable Paleogene primate crania from the Far East, consistently point out (or note when scoring characters) that the suture is fused in all of the anthropoid species for which the frontal is known (e.g., Simons, 1959, et seq.; Beard, 2002), few have related this observation to nonanthropoid stocks implicated in anthropoid origins. One exception is the excellent character analysis of Ross (1994). Another exception is the review of Simons (1972). He drew attention to several Eocene European tarsiiform fossils, including *Necrolemur* and some of its allies, where the frontals were known and proved to be merged, but he did not discuss the possible systematic implications. Ross (1994) also noted that the interfrontal is fused in *Necrolemur* and wondered if that genus could be more closely related to the hypothesized tarsier–anthropoid clade (see Ross and Kay, 2004, for a review) he and his colleagues endorsed than the results of his parsimony analysis seemed to indicate. In a more extensive PAUP analysis, Ross and colleagues (Ross et al., 1998) went further, suggesting that the fused frontal was not a reliable anthropoid synapomorphy, ostensibly due to its propensity to evolve in parallel in one or two (see below) tarsiiform genera.

MATERIALS AND METHODS

We have surveyed the collections of living nonanthropoid primates and several other pertinent orders at the

TABLE 1. Living nonanthropoid primates and several other pertinent orders surveyed

Primates	Sample size	Mean fusion score	State of fusion	Primates	Sample size	Mean fusion score	State of fusion
Tarsiidae				*Lemur catta*	6	1.33	Fused
T. bancanus	1	2	Obliterated	Varecia variegata	14	1.93	Obliterated
T. borneanus	1	2	Obliterated	Hapalemur griseus	5	1.4	Fused
T. pumilus	1	2	Obliterated				
*T. spectrum	35	2	Obliterated	**Lepilemuridae**			
T. syrichta	6	1.91	Obliterated	Lepilemur mustelinus	8	0.69	Unfused
Lorisidae				**Dermoptera**			
*Loris tardigradus	2	0.25	Unfused	Cynocephalidae			
Arctocebus calabarensis	2	0.5	Unfused	Cynocephalus variegatus	9	2	Obliterated
*Perodicticus potto	31	1.08	Fused	Cynocephalus volans	9	2	Obliterated
Nycticebus coucang	35	1.24	Fused				
Galagidae				**Scandentia**			
Galago alleni	3	0.17	Unfused	Tupaiidae			
Galago demodovii	9	0.28	Unfused	Tupaia glis	12	1.83	Obliterated
*Galago senegalensis	10	0.2	Unfused	Tupaia javanica	9	1.89	Obliterated
Otolemur crassicaudatus	11	0.18	Unfused	Tupaia minor	12	1.92	Obliterated
Cheirogaleidae				**Chiroptera**			
Microcebus murinus	33	0.53	Unfused	Phyllostomatidae			
				Erophylla sezekorni	10	1.7	Obliterated
Daubentoniidae				Glossophaga soricina	10	2	Obliterated
Daubentonia madagascariensis	1	0	Unfused	Lonchophylla sp.	10	2	Obliterated
				Phyllostomus discolor	10	1.95	Obliterated
Indriidae				**Vespertilionidae**			
*Indri indri	8	1.5	Obliterated	Eptesicus argentinus	10	1.95	Obliterated
Propithecus coquereli	3	0.17	Unfused	Kerivoula hardwickii	10	1.5	Obliterated
*Propithecus deckenii	4	1.13	Fused	Miniopterus australis	10	1.5	Obliterated
Propithecus verreauxi	6	0.83	Unfused	Murina sp.	8	1.88	Obliterated
Lemuridae				**Pteropodidae**			
Eulemur rubriventer	2	2	Obliterated	Cynopterus sphinx	10	2	Obliterated
Eulemur mongoz	1	2	Obliterated	Epomophorus sp.	10	2	Obliterated
Eulemur macaco	4	2	Obliterated	Macroglossus sp.	10	1.95	Obliterated
Eulemur fulvus	10	1.85	Obliterated	Pteropus sp.	13	2	Obliterated
Eulemur coronatus	3	2	Obliterated	Rousettus sp.	10	1.9	Obliterated
Lemur sp.	4	1.75	Obliterated	Styloctenium wallacei	10	2	Obliterated

*Species observed in both this study and Ashley Montagu (1937).

TABLE 2. Status of the metopic suture in nonanthropoid fossil haplorhines[a]

Genus	Status	Sources	Sample figures
Hemiacodon[3]	Likely fused	This report	Szalay (1976:322)
Microchoerus[3]	Fused	Simons (1972)	Whitehead et al. (2005:267)
Necrolemur[1]	Fused	Simons (1972)	Simons (1972:164)
Shoshonius[3]	Likely fused	This report	Beard et al., (1991:65)
Teilhardina[3]	Fused	This report	Ni, pers. com.
Tetonius[1,3]	Likely fused	This report	Fig. 4 Cope, 1884, Fig. XXIV
Rooneyia[2]	Fused	This report	Fig. 3 Wilson, 1966

[a]Superscript numbers indicate how the taxa were coded in the reports of Ross et al. (1998, 2004) using their protocol, as follows: fused[1]; Unfused[2]; not determinable[3].

American Museum of Natural History (AMNH), Department of Mammalogy (Table 1). No effort was made to tally or further quantify the occurrence of interfrontal fusion among anthropoids in view of the quality and fullness of Montagu's (1937) work, which remains robust. For the other primates, we have greatly augmented the sampling of taxa and individuals, acknowledging that Montagu's study must have involved many of these same AMNH specimens. Our sample of tarsiers, for example, is much larger—we examined 48 tarsier individuals and Montagu inspected only 7—and our coverage of strepsirhines is much more thorough. We have also personally examined all the tarsiers in the Natural History Museum, London, and a variety of specimens in other collections, and crania of all Eocene haplorhines for which the anatomy is known (Table 2), except for *Hemiacodon gracilis* and *Teilhardina asiatica*. Several adapids, including *Smilodectes*, *Notharctus*, *Adapis*, and *Leptadapis*, have also been personally studied.

Because fusion is a dynamic process that occurs over time, in evaluating its condition among the living forms, we used a 0–1–2 scoring system: 0 represents a fully
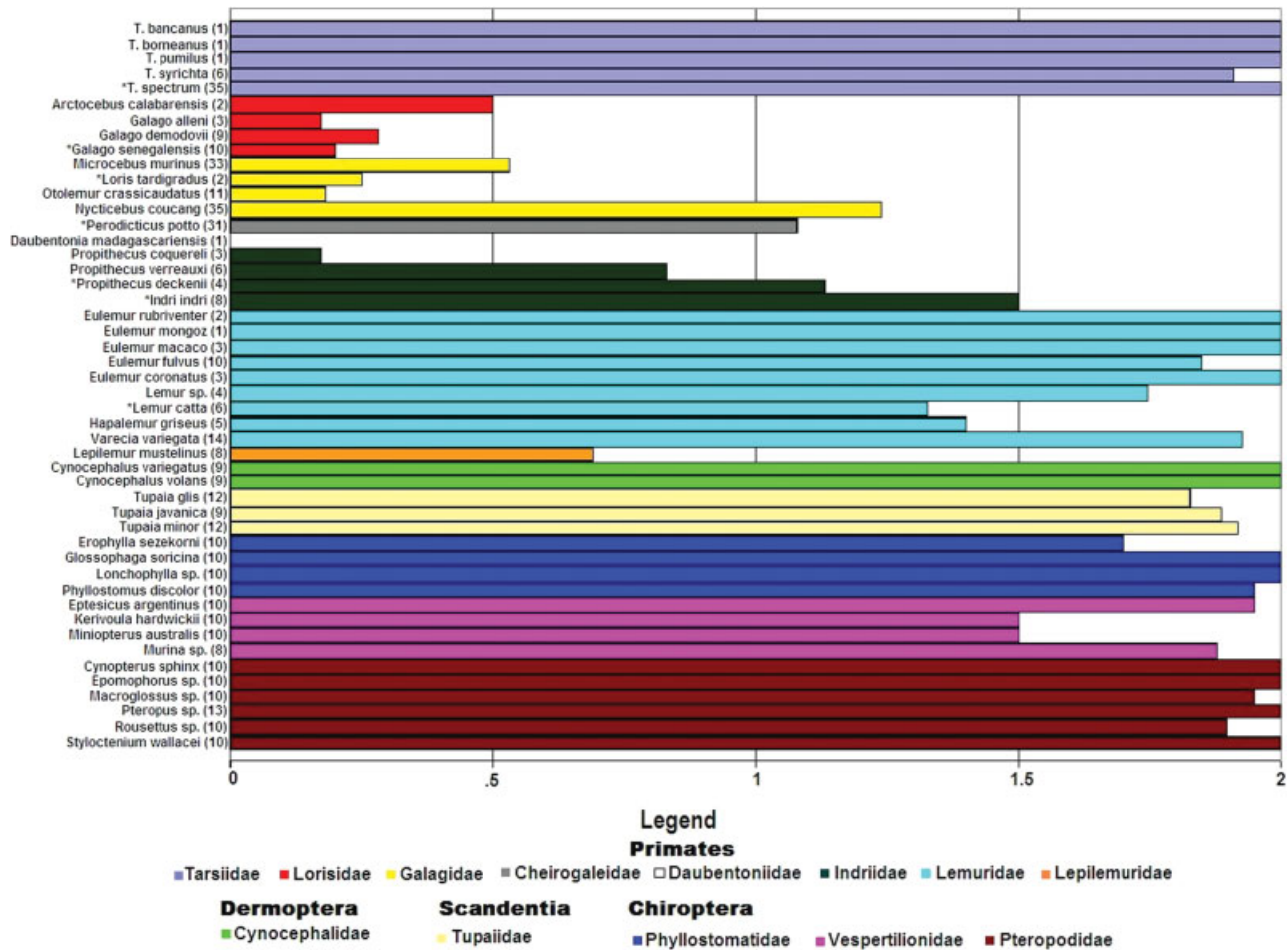
Fig. 1. Histogram showing the distribution of sample means of the status of interfrontal suture fusion among modern adults surveyed in this study. Samples sizes for species are given in parentheses.

open interfrontal; 1 reflects a range of morphologies, from any coalescence of the frontals to an all but invisible suture line; 2 denotes full obliteration to the naked eye. This system is roughly comparable to Ashley Montagu's (1937) method. We report the scores for species as averages tallied across all the adults in our samples. To simplify our discussion, we hereafter often refer to scores 1 and 2 as "fused." We applied the same ranking criteria to the spheno-occipital synchondrosis, which we used as an indicator of a specimen's ontogenetic age. However, only a score of 2 was considered adult. Fossils, about which observations were collected over several years, were simply judged to be fused or unfused at the interfrontal. Their relative ages were assessed by the state of dental eruption and tooth wear.

Regarding classification (see Delson et al., 2000), which is currently quite in flux, we include Plesiadapiformes in the Primates (e.g., Szalay and Delson, 1979; Silcox et al., 2005), but emphasize that the implications of our character analysis would be the same if we had not, and had only considered them as archontans. Among haplorhines, we call the late Eocene *Rooneyia* a protoanthropoid, holding that it is probably the sister taxon to Anthropoidea (Rosenberger, 2006). Because it is becoming progressively more clear that Omomyidae

sensu Szalay (1976) is paraphyletic and now less productive as a taxonomic concept (e.g., Rosenberger, 1985; Dagosto et al., 1999; Kay et al., 2004; Rosenberger et al. in press), we simply refer to the Eocene forms that were maintained under that rubric as Tarsiiformes, which taxon also includes modern *Tarsius*. For the strepsirhines, the Eocene forms are called Adapiformes and the moderns are referred to as Lemuriformes, broken down into Lemuroidea, Indrioidea, and Lorisoidea.

RESULTS

Our larger sample of adult tarsiers and strepsirhines does not corroborate Ashley Montagu's (1937) generalizations. The data on strepsirhines present a more complicated picture of inter- and intra-taxon variability (Table 1; Fig. 1). A fused state occurs with high frequency or universality in a considerable number of genera. An utterly unfused state in a genus is rare (in our sample only occurring in the one specimen of *Daubentonia* at our disposal); most show at least a low incidence of frontal fusion. At a higher taxonomic level, while lemuroids are rather consistent, lorisoids are quite variable. Lemurids and most indriids show a fused interfrontal, and both groups have a relatively high incidence of obli-
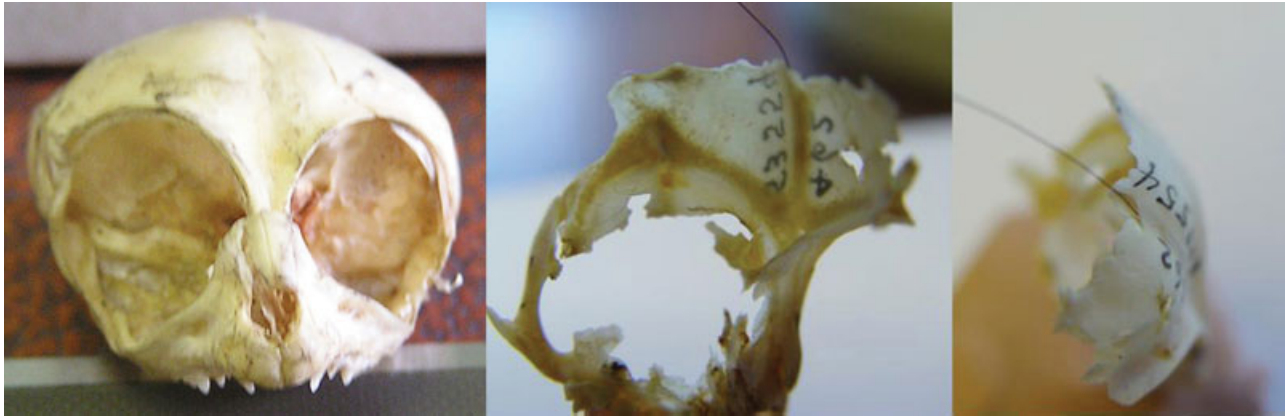
Fig. 2.   Left to right: Neonatal *Tarsius* sp. (BMNH 13219), maximum cranial length approximately 26 mm, showing early fusion of the interfrontal suture. Partial frontal bone of an adult tarsier (orbit is evident) with bristle inserted into sagittal canal, shown in an endocranial view looking anteriorly (middle panel) and an exocranial, lateral view (right panel).

terated sutures. Even in the lemuroid *Lepilemur*, the majority of individuals are ranked closer to the fused state than the unfused state by our definition. Among lorisoids, a more stark contrast occurs between fused and unfused taxa. In the lorisids *Nycticebus* and *Perodicticus*, the frontals are synostosed but they tend not to fuse in *Loris* and *Arctocebus*. The interfrontal is generally open in galagids. With fusion scores of approximately .5, the lorisid *Arctocebus* and the cheirogaleid *Microcebus* may be considered partially (or intermediately) fused.

Tarsiers have a consistently fused frontal bone, irrespective of Montagu's (1937) hesitation about this fact. Our ample interspecific sample of *Tarsius* (Table 1; Fig. 1) demonstrates that the interfrontal suture is typically fused even in young individuals. Several juveniles and two neonates showed this clearly (Fig. 2). At the same time, as Remane (1923, cited in Montagu, 1937) noted, a single very young individual has been observed (in a private collection) with a fully patent suture.

The morphology associated with the interfrontal suture in *Tarsius* appears to be distinctive. A sagittal canal runs within the frontal bone in this area, under a midline ridge that is a consistent feature on the external surface of the tarsier cranium. In the collections at AMNH, the canal was examined intracranially in nine broken specimens (AMNH 153288, 153552, 153287, 245094, 153289, 196478, 150448, 153286, 153555). This allowed us to probe the passage, which frequently contained remains of a blood vessel (Fig. 2). It is likely that the vessel is a frontal diploic vein. Posteriorly, the presence of the canal was confirmed as far back as bregma. Anteriorly, it was traced as far forward as the cribriform plate. At that point, the morphology varied. In some individuals, the canal split into two narrow channels; in some it appeared to continue into the olfactory tube, which leads to the nasal fossa. Bloch and Silcox (2006; Fig. 22) illustrate a midline lumen in a coronal section of a high-resolution CT scan of a *Tarsius syrichta* specimen that cuts through the sagittal canal. We are not aware of any previous discussion or illustration of this feature in the literature. The Bloch and Silcox image also reveals two symmetrically placed lateral lumina, which represent similar vascular canals observed in
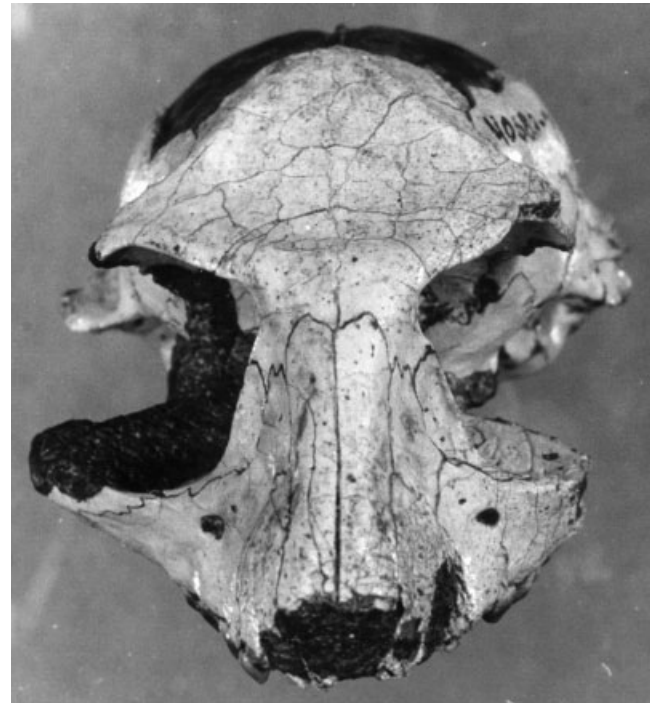

Fig. 3.   Anterior three-quarters view of *Rooneyia viejaenesis* (TMM 40688-7) before the right side of the frontal bone was removed to study the endocast. Although cracked, the frontal bone is clearly fused in the midline of this young adult specimen. The interfrontal suture is essentially obliterated, except for a small segment near the nasofrontal suture, which may also be an artifact. Courtesy of the Texas Memorial Museum, University of Texas at Austin.

numerous tarsier skulls running subvertically at the junction between frontal and alisphenoid. These likely house the anterior temporal diploic veins.

Regarding nonanthropoid haplorhine fossils, the frontal bone is adequately known for the purposes at hand in at least seven genera (Table 2). Our assessment is that the interfrontal suture is likely to have been fused or obliterated in all, although a few cases present ques-
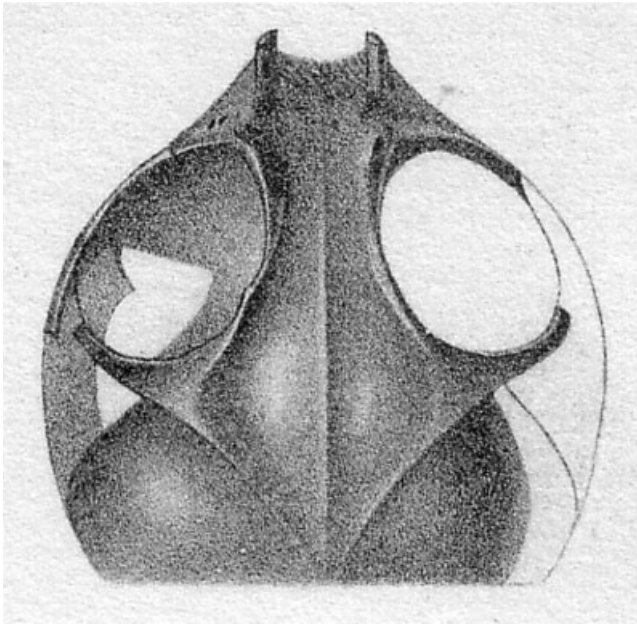
Fig. 4. Cope's 1884 illustration of *Tetonius homunculus* (AMNH 4194) before the left side of the frontal bone was removed. The line drawn along the midline probably represents a crack or slight defect of the outer table, rather than an unfused interfrontal suture, based on morphological similarities of this image and the actual specimen with more complete specimens of *Shoshonius*, whose anatomy is extremely similar in all regards.

tions. Because all of the fossil individuals observed are adults according to dental eruption criteria, we could not determine empirically if fusion occurs as early in life among these fossil haplorhines as it does in modern tarsiers or anthropoids.

Tetonius and *Rooneyia* deserve special mention here, for in their present conditions—after extensive preparation done to reveal the frontal lobes of natural endocasts —these fossils are difficult to assess, and each is represented by only one specimen. In both cases, only one side of the frontal bone remains intact. In each, the exposed medial edge is a long border, slightly irregular in surface texture, and situated almost precisely along the midline. This finding has led to confusion and misinterpretation. For example, Ross and colleagues (Ross et al., 1998; Kay et al., 2004), in different studies, coded the state of frontal fusion in *Tetonius* as indeterminate and fused, respectively. For *Rooneyia*, Ross et al. (1998) stated the interfrontal was unfused. However, the earliest published illustrations and photographs of these crania provide additional insight, and a correction.

When Wilson (1966) first described *Rooneyia* the frontal bones were utterly fused and the interfrontal was essentially obliterated (Fig. 3). There was only a small crack at the anterior pole in the interorbital process that might be taken as evidence for a trace of the interfrontal. This feature may also be an artifact, part of the splash of surface cracks relating to fossilization. It is also worth noting that this cranium is a young adult showing only small amounts of molar wear, indicating that fusion was not attained by means of ageing and remodeling, that it happened early in adulthood if not long prior.

Fig. 5. Dorsal views of the crania of *Adapis parisiensis* (top) and *Necrolemur antiquus* (bottom) brought to same skull length. The fully fused frontals of *Necrolemur* are evident. In *Adapis*, a segment of the interfrontal suture is visible at the frontonasal juncture. It is continuous with a short hairline crack running through the synostosed frontals behind this sutural remnant. In our scoring system, *Adapis* is a 1 (fused) and *Necrolemur* is a 2 (fused and obliterated). Photographs courtesy of the Museum National d'histoire Naturelle, Paris.

In *Tetonius*, the first published illustration, in Cope (1884; Fig. 4), shows that the right and left frontal bones were at that time essentially complete. By 1922 (see Gregory, 1922, p 197), the appearance of this specimen in a photograph was radically different, looking much as it does today. In Cope's shaded rendering, there is a long, thin line in the position of the interfrontal suture. It is impossible to tell if this represents a crest, a ridge, or a crack between the frontal bones. The local anatomy of the *Tetonius* frontal closely resembles the four new, relatively well-preserved crania attributed to *Shoshonius* (Beard et al., 1991; Beard and MacPhee, 1994). One of them presents a thin crisp line between the frontals but all are cracked in one way or another. These linear hairline cracks are probably artifacts, fractures that split the fused frontals at their junction. An alternative view might be that fusion was variably developed within *Shoshonius* as it is in some strepsirhines, such as galagos (Table 1). Either way, there is no evidence that the frontals were *unfused* in *Shoshonius*, thus differing from the closely related and morphologically similar *Tarsius*. Overall, this suggests the interfrontal suture was origi-

nally fused in *Tetonius* as well and that the strong sagittal line of Cope's illustration was imbued artistically.

The morphology of another pair of fossil nonanthropoids listed in Table 2 appears to be relatively straightforward. Several good specimens are known for *Necrolemur* (Fig. 5) and *Microchoerus*, and in all the interfrontal suture is either fused (sometimes showing a small unfused remnant) or fully obliterated. Simons (1972; p 162) also noted that in *Necrolemur* the frontal fused before maturity was reached, comparing it to *Tarsius*. Two fossil tarsiiforms are a little more difficult to assess. Figures of the relatively complete and undistorted frontal bone attributed to *Hemiacodon* (Gazin, 1958) appear to show a fused frontal (see the stereophotograph in Szalay, 1976; Fig. 104), somewhat cracked but fully knit, perhaps resembling *Shoshonius*. The skull of *Teilhardina asiatica* is badly crushed and has been reconstructed using CT scan imaging (Ni et al., 2004). However, Ni reports (personal communication) that its interfrontal is also fused. Like these tarsiiforms, all the Eocene fossil strepsirhines examined, *Notharctus*, *Smilodectes*, *Adapis*, and *Leptadapis*, exhibit examples of frontal fusion or partial fusion. In some cases, as in an *Adapis parisiensis* (Fig. 5), the interfrontal is clearly obliterated posteriorly but there is a zig-zag trace suggesting patency at the anterior pole.

Outside of the euprimates, the evidence for plesiadapiforms is difficult to assess, partly because it has not been carefully addressed. (We made no observations on these fossils personally.) For example, an excellent photograph of *Plesiadapis tricuspidens* in Szalay and Deslon (1979; Fig. 32) indicates the preorbital portion of the frontal is split in the midline. But the line is distorted and may be a hairline crack, like others on the face, looking similar to the interpremaxillary and nasomaxillary sutures on this specimen that are patent. One image of the high-resolution CT reconstructions of the plesiadpiform *Carpolestes simpsoni* (Bloch and Silcox, 2006, Fig. 1) suggests that the frontal may be fused but another of the same specimen (Bloch and Silcox, 2006, Fig. 3) shows that it is split and also damaged. High-resolution reconstructions of *Ignacius graybullianus* (Silcox, 2003; Fig. 1) show that the frontal bones are widely separated anteriorly, apparently due to damage.

Of the other living mammals examined (Table 1), our robust dermopteran series includes good samples of the only two known living species (one or two genera, according to different classifications), but only a small cross-section of tupaiid and chiropteran genera are included. Frontal fusion and obliteration appear to be the norm in the three species of *Tupaia* and the four different families of bats. LeGros Clark's (1926) observations on the tuapid *Ptilocercus* indicate that the interfrontal is fused in that genus as well. Thus fusion is present in both subfamilies of tupaiids, suggesting it is an ancestral condition in scandentians. The high incidence of fusion in all these nonprimate genera demonstrates that frontal fusion may be more common among them, to us the archontan relatives of primates, than in our total sample of modern strepsirhines.

DISCUSSION

Although there is a long history that regards anthropoids as unique in presenting a closed rather than open interfrontal suture, there is no prosimian–anthropoid, anthropoid–nonanthropoid, or even a strepsirhine–haplorhine dichotomy in this feature. Fused frontal bones are widespread among primates living and extinct, refuting the hypothesis that the anthropoid morphology is unique and lessening the likelihood that it evolved independently as a derived condition in higher primates. Although the evidence for plesiadapiforms is moot, and the adapiforms are not adequately understood, because interfrontal fusion appears to be the norm among all haplorhines and widespread among early fossil strepsirhines, many lemuroids, living dermopterans, tupaiids, and a variety of bats, it seems more likely that the continuum found among lorisoids, from fused to unfused, represents a departure from the more general primate condition, for reasons still to be addressed. Until the functional significance of interfrontal suture fusion is better understood, the evidence suggests it is unwise to presume that all of these cases share a common evolutionary polarity, that the condition evolved from unfused to fused states, which would suggest multiple cases of parallelism under different phylogenetic scenarios.

Frontal synostosis is a continuous character, not a discrete one. This means that an alternative reading of the distributional evidence might also regard variability in fusion among modern strepsirhines in a narrower way, as an indication of an intrinsic morphogenetic capacity to fuse the interfrontal in ancestral primates rather than a judgment about the species-specific state in primates generally. Even so, the point remains that only the strepsirhines appear to go either way—fused or unfused—while all other euprimates appear to develop the fused pattern inexorably. The implication for anthropoids remains the same: they are not unique in fusing the frontal.

The evidence presented does not allow a confident assessment of the ontogenetic trajectory of this condition, whether or not fusion is normally an early-finishing process among all the nonanthropoids as Montagu (1937) showed it to be in platyrrhines and catarrhines. However, full fusion does occur early in ontogeny in *Tarsius* also, unlike the majority of strepsirhines, and there is no reason to presume a different developmental pattern among any of the other haplorhines. We also cannot address definitively the possibility that tarsiiforms (or others) evolved interfrontal fusion independently relative to anthropoids. This is a point that deserves consideration because *Tarsius* is the only genus in which an unusual anatomical structure that would appear to be developmentally associated with fusion, the sagittal canal, is known to occur. We have not been able to evaluate this feature in the fossils. Still, unless evidence to the contrary is developed, the distributional information means it is more parsimonious to accept the null hypothesis that fusion in all haplorhines is homologous. One can easily conjure up explanations for tarsiers evolving autapomorphic venous drainage channels as a correlate to massive eyeball hypertrophy.

Contrary to the expectations we harbored at the outset of this study, modern strepsirhines are the only primates for which frontal fusion is intraspecifically variable while being widespread taxonomically across all superfamilies. The fact that fusion also occurs among the small sample of non–tooth-combed Eocene adapiforms examined raises the possibility that the last com-

mon ancestor of tooth-combed lorisoids, indrioids, and lemuroids presented a patent or a variably fused interfrontal suture at the population level, as a shared derived condition. We have no explanation for such a transformation at present. We suspect that several factors, perhaps interacting in complex ways, can influence fusion of the interfrontal, including overall developmental timing, neural growth, masticatory biomechanics, and craniofacial organization. It is worth noting that Eocene and modern strepsirhines are also known for variations in the morphology of the mandibular symphysis (see Ravosa, 1996), which may be mobile, or fused partially or solidly, and that it is likely that the first tooth-combed primates had an unfused mandibular symphysis. Fusion of the mandibular symphysis is not uncommon in adapids, either.

As indicated above, our observations and results differ from other recent surveys that have included the interfrontal suture in cladistic studies. These include studies in which homology decisions were made both before and after completion of algorithmic parsimony analyses (Ross, 1994; Ross et al., 1998; Kay et al., 2004), and they invoke multiple parallelisms or convergences as the explanation for the allegedly rare occurrence of frontal fusion in primates outside of Anthropoidea, especially among tarsiiforms. We, in contrast, found fusion to be commonplace among euprimates, with the closed state being remarkably stable among disparate groups, while the unfused condition is more labile phylogenetically and taxonomically.

Regarding the affinities of anthropoids, the group whose origin has been pinned to the interfrontal and is most likely to be impacted by undoing the assumption that fusion should be heavily weighted as an exclusive derived homology, the cladograms produced in these PAUP studies (Ross, 1994; Ross et al., 1998; Kay et al., 2004; see also Seiffert et al., 2004) conflict severely with other phylogenetic assessments that have been conducted without algorithms (e.g., Rosenberger, 1985, 2006; Rosenberger et al., in press) or with PAUP* but using a more restricted set of taxa and a more homogeneous collection of traits (e.g., Beard and MacPhee, 1994; Dagosto et al., 1999). We refer to the support attributed in the first set of studies to the tarsier–anthropoid hypothesis, which posits a sister-group relationship between *Tarsius* and anthropoids to the exclusion of all others. We have argued that it is not *Tarsius* but *Rooneyia* that is the most likely sister group of anthropoids (Rosenberger, 2006; Rosenberger et al., in press). The degree to which coding discrepancies pertaining to the distribution of a fused interfrontal in tarsiiforms (Table 2) have added crucial discordance to the parsimony studies, which also tend to disbar *Rooneyia* from the Haplorhini, is difficult to assess.

These findings should encourage further study into the functional significance of interfrontal fusion in primates. There are various ways the data can be evaluated to develop a more detail hypothesis of the taxonomic distribution of the fused and unfused states, but that is beyond the scope of this report and would be a more profitable exercise if coupled with a model that explains *why* both of these patterns might be selected among primates and other mammals. Herring and colleagues (e.g., Herring and Teng, 2000) present a starting point, a compelling biomechanical analysis of the role of the interfrontal suture in mastication based on in vivo studies of miniature pigs. They show that the interfrontal, like other cranial sutures, transmits far greater strain during mastication than calvarial bone, and is especially responsive to contractions of the masseter and temporalis muscles. Working on opposite sides of the skull during mastication, these muscles produce a force couple that tends to pull apart the interfrontal suture anteriorly and squeeze the frontal bones together at the suture posteriorly. The same basic biomechanical regimen and masticatory cycle of muscle activity probably applies to primates, irrespective of the many differences in cranial shape and proportion that likely dictate differences in some of the engineering details.

This finding suggests an interesting functional explanation relating to the origins of the anthropoid skull and one of its cardinal novelties, the evolution of a complete postorbital plate that encircles the orbits laterally. The septum evolved from a postorbital bar by enlargement of the zygomatic and the lateral process of the frontal bone, that is, the development of a long fronto-zygomatic suture (e.g., Rosenberger et al., in press). It is a feature that is still unsatisfactorily explained functionally (see Ross and Hylander, 1996; Ravosa et al., 2007). We suggest a connection with the evolution of interfrontal fusion, which preceded the origins of the septum if our analysis is correct. When fusion of the interfrontal suture occurs, as in anthropoids, stress and strain generated by the masseter–temporalis muscular couple cannot be taken up kinetically in the midline as in the miniature pigs (Herring and Teng, 2000). It must be distributed to the perimeter of the solidly fused frontal bone, including the fronto-zygomatic sutures. As anterior breadth of the neurocranium increased in the stock leading to anthropoids, along with expansion of the forebrain, the moment of the force couple must have increased proportionately. This finding means that, under conditions where frontal fusion is advantageous, it will also be advantageous to provide an alternative outlet for dissipating the internal strain of the frontal bone that is experienced during feeding. The long frontal–zygomatic suture is well positioned to do this. The anthropoid postorbital septum may have evolved in part to transmit the stress and strain of chewing that is incurred by loading a fused frontal bone that is unusually enlarged to accommodate deep set eyes and a wide forebrain.

Conclusions

Distributional evidence refutes the hypotheses that a fused interfrontal suture in living anthropoids is a defining feature of this group based on the assumption that it is a rarity. To the contrary: seven genera of fossil haplorhines for which evidence is available, including two or three represented by good samples of individuals, all show a fused or obliterated interfrontal suture, as do tarsiers, the majority of living strepsirhines, several fossil adapiforms, and numerous genera representing three orders of more distantly related living mammals, colugos, tree shrews, and bats (archontans *sensu lato*). This means that closure of the interfrontal suture (possibly at an early stage of growth) is far more ancient cladistically that the origins of anthropoids. It is highly likely

to have been present among ancestral haplorhines. If additional study shows that the incidence of frontal fusion among the diverse adapiforms is also widespread, this would suggest that the last common ancestor of modern tooth-combed strepsirhines may have inhibited the developmental mechanism or program that produces fusion, only to have it evolve again in later radiations, most often in lemuroids. The functional–adaptive reasons behind a fused or unfused interfrontal suture remain obscure. However, biomechanical evidence from masticatory studies in miniature pigs, where the interfrontal is unfused, indicates that high levels of strain are transmitted at the suture during feeding, forcing the frontal bones to spread apart anteriorly. This suggests that, under similar loading condition in anthropoid primates, where the interfrontal suture is fused and the frontal bone is especially enlarged to accommodate deep set eyes and an enlarged wide forebrain, strain may be shunted to the postorbital plate, where it could be taken up by the frontal–zygomatic suture. Frontal fusion may be a preadaptation to the evolution of the anthropoid postorbital septum.

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