

On *Bahinia pondaungensis*, an Alleged Early Anthropoid

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ABSTRACT

In order to assess the orientation of the orbit of *Bahinia*, a middle Eocene fossil from Myanmar that has been interpreted as an anthropoid, laser surface scanning was used to develop three-dimensional models of the one facial specimen of *Bahinia* for comparison with *Notharctus* and *Rooneyia*, examples of a relatively early strepsirhine and haplorhine, respectively. Paired 3D montages were produced by graphically resizing *Bahinia* to the same molar lengths as the reference fossils and aligning them according to the contour and position of the inferior orbital margin. The composites indicate that while the orbit of *Bahinia* appears to be relatively small, as previously reported, its placement more closely resembles the laterally facing orbit of *Notharctus* than the anteriorly facing orbit of *Rooneyia*, which resembles anthropoids. In the size and shape of the snout, depth of the maxilla, and orientation of the tooththrow in the face, *Bahinia* shares a distinctive resemblance with *Notharctus*, not with *Rooneyia*. Since the dental and gnathic features presented as evidence that *Bahinia* is an anthropoid also are often found among adapiforms, in which case they are generally understood to be convergent similarities to some anthropoid characters, we conclude that a more cogent argument can be made that *Bahinia* is a strepsirhine, with a large face and small, laterally facing orbits. *Bahinia* thus contributes little to the argument that the Chinese eosimiids are anthropoids.

INTRODUCTION

Jaeger et al. (1999) described *Bahinia pondaungensis* from three associated specimens—a moderately large left and right maxilla and a lower jaw—recovered from the middle Eocene Pondaung Formation of Myanmar. They viewed the species as an early anthropoid, citing features relating to mandibular morphology, upper incisor orientation, obliquity of lower premolars, trigonid cusp structure, and hypocone development. Several studies have since accepted this interpretation (e.g., Beard 2002; Chaimanee et al. 2000; Kay et al. 2004; Marivaux et al. 2005; Takai et al. 2005) without reservation and none of the features invoked by Jaeger et al. (1999) have been reassessed or challenged in detail, with the exception of the character analysis by Gunnell and Miller (2001). This defining list of traits overlaps considerably the battery of features long used to support the adapid-anthropoid hypothesis and now regarded as likely convergences (e.g., Rosenberger et al. 1985). Kay et al. (2004) also added to the basic argument of Jaeger et al. (1999) by suggesting that the orbit of *Bahinia*, as inferred from the radius of curvature of its inferior margin, was relatively small as in typical anthropoids.

The thrust of this work has led to the inclusion of *Bahinia* in the Family Eosimiidae, and this has had two seemingly contradictory effects: 1) adding credibility to the hypothesis that eosimiids are anthropoids; and, 2) expanding the morphological concept of eosimiids to embrace highly disparate tooth and mandibular morphologies, i.e., creat-

ing the impression of eosimiids as a morphologically diverse group (see Beard 2002). However, as perhaps the literature's sole doubters, Miller et al. (2005) noted that the case for *Bahinia* being an anthropoid is tied to the status of *Eosimias*, whose anthropoid affinities they tend to question. And, in the parsimony analysis of Seiffert et al. (2005), *Bahinia* fell immediately outside a clade comprised of definitive anthropoids plus amphipithecids, while *Eosimias* and the allied *Phenacopithecus* (plus the controversial *Alt-atlasius*) were linked as another lineage further outside that group.

The right maxilla of *Bahinia* preserves the morphology of the snout and an integral segment of the orbit (Kay et al. 2004: Figure 8). The specimen is full of cracks and has probably suffered some distortion via bilateral compression and displacement of fragments high up between the orbit and nasal aperture. Nevertheless, it appears to preserve a faithful approximation of the shape of the lateral aspect of the face, especially in the maxillary region between tooththrow and orbit. The segment of the inferior orbital margin that Kay et al. (2004) used as a basis for judging orbit size remains fairly intact. We have focused on that anatomical remnant as a basis for asking a question that may have important bearing on the affinities of the genus: What was the orientation of the orbits in the face? As is well known, anthropoids have orbits that are both relatively small and markedly convergent and frontated (see Cartmill 1980; Ross 1995) rather than laterally facing.

MATERIALS AND METHODS

In the absence of a reference midline or standard horizontal on the fossil from which the angles describing the orbital plane can be easily measured as intersections (e.g., Ross 1995), we developed an alternative comparative graphical approach to the problem. We compared the shapes of comparable parts of the faces and maxillae in the genera *Bahinia*, *Notharctus*, and *Rooneyia* by using fixed-point overlays of 3D models based on laser surface scans of sharp epoxy casts. *Notharctus* and *Rooneyia* were selected as models for several reasons. All three are relatively small-eyed. Their Eocene ages makes for a pointed comparison with the middle Eocene *Bahinia* and it also means that their morphology is more likely to reflect the primitive states of early euprimate clades than any modern forms. From a systematics perspective, each of the analogs also represents a major euprimate division. *Notharctus* was used as an example of

the strepsirhine condition, where the orbits tend to be laterally directed, while *Rooneyia* was used as an exemplar of a small-eyed haplorhine. Ross (1995) also has shown that *Rooneyia* is essentially indistinguishable from anthropoids in orbital orientation, so it serves as a good surrogate for an anthropoid. Following Rosenberger (2006; see also Hogg et al. 2005), *Rooneyia* has even more relevance for anthropoid origins than being merely a morphological model because there are other derived features of the frontal bone and orbital region which suggest that this genus may represent the sister-group of anthropoids, Protoanthropoidea, rather than an omomyid (as it is often classified) of more remote affinities.

We developed 3D digital models of the specimens and compared them visually by generating fixed-point overlays on-screen using the inferior orbital margins as a common reference surface. The models were constructed by render-

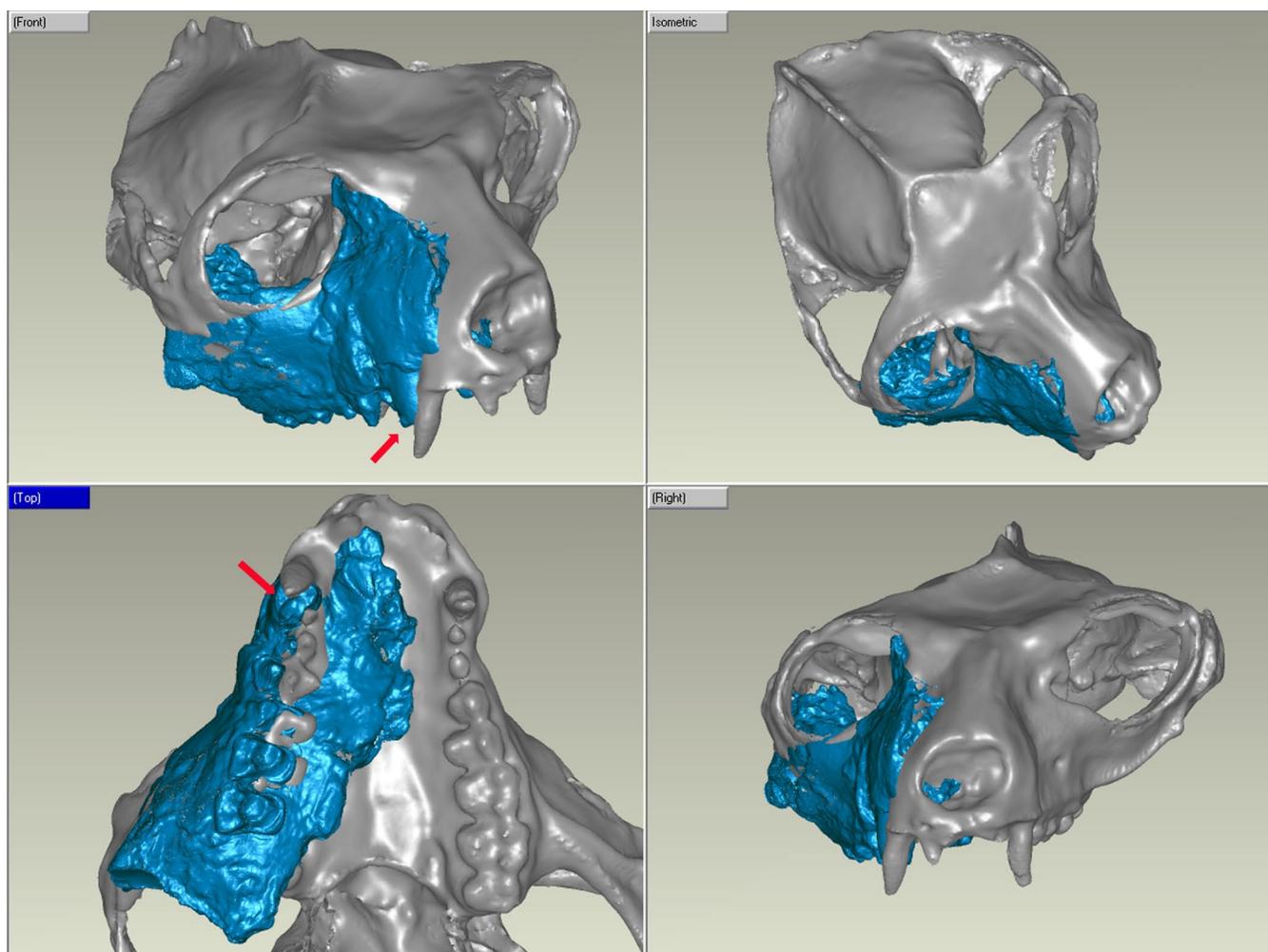


Figure 1. A composite of two 3D models based on laser surface scans of *Notharctus* and *Bahinia*. Red arrows mark the position of the *Notharctus* canine. All the images are of the same composite, shown here in four different views (clockwise from top left—three quarters, superior, anterior, and palatal). The *Notharctus* skull is not distorted on the right side. Molars of the two fossils were scaled to approximately the same mesiodistal length and the composite was produced by fixed-point alignment of the inferior margins of the orbits in the specimens. The size and shape of *Bahinia* conforms well with *Notharctus* in the snout, the lateral aspect of the face below the orbit, and the tooththrow. The canine falls short of the *Notharctus* canine due to different premolar proportions, but the right tooththrows are aligned fairly well. Overall, the complimentary match between the shapes of these specimens indicates that their orbits are arranged similarly.

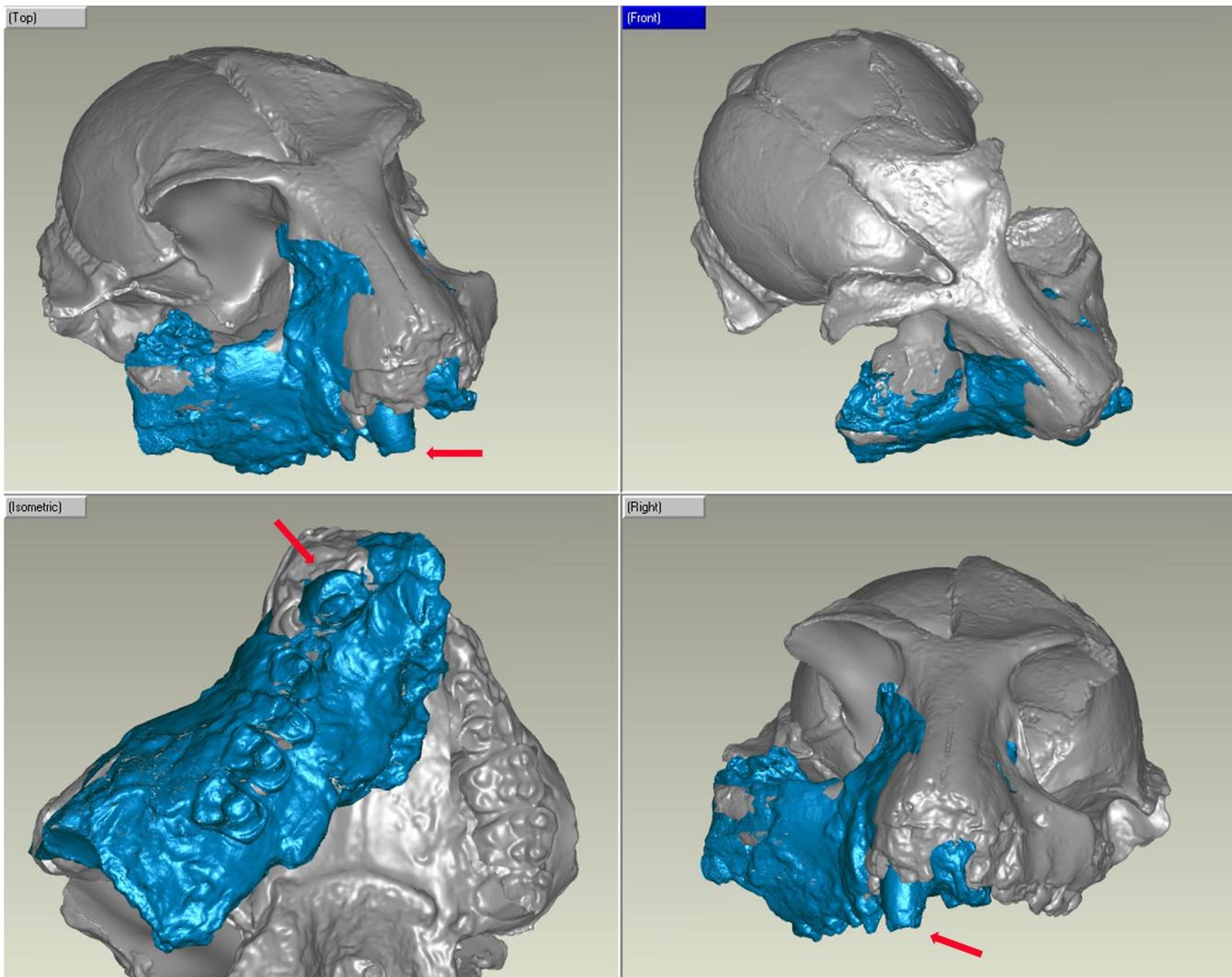


Figure 2. A composite of two 3D models of *Rooneyia* and *Bahinia* using the same criteria and convention as in Figure 1. The gross mismatch of the lower faces and palates relates to the greater suborbital depth and flaring posterior maxilla in *Bahinia*. Notice the asymmetry of tooththrows and palates, emphasized in part by the strongly medial position of the canine in *Bahinia*. This reflects contrasting orientations of the orbits, which were used to align the models. *Bahinia* does not have anteriorly facing orbits like *Rooneyia* or anthropoids.

ing a solid surface from the coordinate points collected by a high-resolution laser scanner as it mapped the morphology of the specimens. The thickness of each model's rendered surface is negligible, less than 1mm. To accommodate differences in the absolute sizes of the species, we resized the digital models of *Bahinia* to the same molar lengths of *Notharctus* and *Rooneyia*, respectively, in each set of comparisons, thus scaling the entire solid model isomorphically in length, breadth, and height dimensions. This technique is similar to the long standing method of illustrating specimens as 2D flat images brought to a standard anatomical length or breadth, with the original aspect ratio of each maintained and aligning them symmetrically on a page.

ANALYSIS

Figures 1 and 2 compare *Bahinia* with *Notharctus* and *Rooneyia* in a set of 3D composite models, shown from different angles. These composites were developed by joining

pairs of 3D models along the matching arcs of their inferior orbital margins. Because the margin is an arc that crosses the three orthogonal standard anatomical planes, matching them in three-space has the effect of also "forcing" the alignment of other anatomical features, such as the tooththrows. Mismatches between anatomical structures would thus be an indication that specimens have different shapes. The generally close correspondence of the *Bahinia* facial specimen with the snout shapes of *Notharctus* and *Rooneyia* adds confidence to the supposition that the *Bahinia* specimen is not blatantly distorted in places where it counts most for this study, in the suborbital region. Furthermore, close inspection of the direct congruity between the contours of the inferior orbital margin of *Bahinia* and the other fossils in these graphic comparisons corroborates the interpretation of Kay et al. (2004) that the orbit of *Bahinia* was not enlarged. However, our observations also suggest that the orbits of *Bahinia* were laterally oriented rather than ante-

riorly facing, and that the preorbital facial morphology of *Bahinia* more closely approximates a strepsirhine.

While it is evident that the inferior marginal segments of the orbits in both pairings conform, the montages also illustrate that the lower faces align quite differently in each set. This is seen most conspicuously in palatal view. In the *Bahinia-Notarctus* set (Figure 1), the models blend into one another, “competing” for space, particularly in the premolar region. Thus on P^{3,4}, the blue (*Bahinia*) and gray (*Notarctus*) regions representing occlusal surfaces crop out alternately at buccal and lingual aspects of the crowns. This means that there is only a small differential at the interface where their essentially congruent surfaces meet—in places, the bone or teeth of *Bahinia* lie slightly atop *Notarctus* whereas the opposite is true only a few millimeters away, where the surface anatomy of *Notarctus* becomes visible. It also is clear that the maxillae and tooththrows of *Bahinia* and *Notarctus* are oriented roughly in parallel to one another. Fusing them together when fixed by the orbit produces a realistic palate morphology. The major difference between the species appears to relate to the length of the tooththrow, for the canine of *Bahinia* falls short of the canine position of *Notarctus*.

In contrast, the maxillae and the tooththrows in the *Bahinia-Rooneyia* composite are misaligned (Figure 2). The blending pattern seen previously is essentially absent—nowhere do the surfaces of the models “compete” for space because the separation between them is too large, and, almost everywhere the surface of the *Bahinia* model is exposed. In palatal view, the right tooththrow of *Bahinia* cuts obliquely across the postcanines of *Rooneyia*, effectively displacing the *Bahinia* canine far medially and close to the midline of *Rooneyia*. Thus the right-side tooththrows are obliquely offset and the fused models present a highly mismatched set of dental arcades.

This lack of congruence between the surfaces of the models in palatal view is an effect of the more laterally oriented orbital aperture in *Bahinia* relative to its face and dental arcade. In other words, *Bahinia* does not have anteriorly facing, convergent orbits like *Rooneyia*. Because they are more laterally facing in *Bahinia* than in *Rooneyia*, the angularity of the tooththrow appears to be exaggerated in the overlays—too medial toward the front and too lateral toward the rear. It also appears from these comparisons that the anteorbital proportions of the face differ, with *Bahinia* resembling the large-faced *Notarctus* much more than the relatively smaller-faced *Rooneyia*. Thus in dorsal and anterior views, the more rostral parts of the face in *Bahinia* plunge into the nasal cavity in *Rooneyia*, whereas in the *Bahinia-Notarctus* montage (Figure 1) the snouts tend to match up better. Differences are also evident suborbitally and palatally, where the maxilla of *Bahinia* fits much better against the face of *Notarctus* than against *Rooneyia*, where the maxilla is relatively shallow.

CONCLUSIONS

These observations cast doubt upon an already vulnerable phylogenetic interpretation of *Bahinia* (see Gunnell and

Miller 2001; Miller et al. 2005). As Jaeger et al. (1999) noted, several of the dental and mandibular characteristics cited as anthropoid synapomorphies or phenetic resemblances to anthropoids in their original description of the species are found among adapids as well (see Rosenberger et al. 1985; Gebo 2002), in combination. Some traits also have been documented in the amphipithecids *Amphipithecus* and *Pondaungia*, which is consistent with our view that the latter genera are strepsirhines. Specific features found widespread among adapiforms and in *Bahinia* include a well developed mandibular symphysis, deep horizontal ramus, vertically implanted upper incisors, weakly developed molar hypocones (in some forms), and three-premolar dental formula. These traits have been used repeatedly in efforts to substantiate an adapid-anthropoid link, to little avail. It is nearly inescapable that adapids are cladistically strepsirhine rather than haplorhine, thus neither anthropoid nor in the ancestry of anthropoids (Rosenberger and Szalay 1980; Rosenberger et al. 1985; Beard et al. 1988; Gebo 2002; but see Miller et al. 2005 for a different interpretation).

We conclude that the evidence for *Bahinia* being an anthropoid is weak. Morphologically, nothing seems to preclude it from being an adapiform. There are no evident homologies that are shared derived haplorhine characteristics; the case for haplorhine status rests on the argument that it is an anthropoid. *Bahinia* may be another mark of success of the Asian radiation of Eocene strepsirhines, about which we still know very little. It also remains possible that *Bahinia* represents a heretofore unrecognized branch of euprimate. It seems unlikely, however, that it is a plesiadapiform *sensu lato*.

Removing *Bahinia* from the Eosimiidae adds more coherence to the dental and mandibular morphology of this two-genus family, but it also reduces the range of characters that can be used to argue that eosimiids are actually anthropoid. Assuming, as has been done, that *Bahinia* is monophyletically related to eosimiids and that both are, in turn, cladistically linked with anthropoids raises an odd possibility. *Eosimias*-like (i.e., omomyid- or plesiadapiform-like) traits of this family might be highlighted as homologies in making the case that eosimiids are anthropoid while *Bahinia*-like (i.e., adapid-like) traits could be invoked as homologies for the same purpose. It seems more parsimonious to regard this situation not as a paradox but as an indication that the affinities of *Bahinia* are elsewhere, not among the anthropoids.

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