

Paranasal sinus anatomy of *Aegyptopithecus*: Implications for hominoid origins

James B. Rossie*[†], Elwyn L. Simons[‡], Suellen C. Gauld[§], and D. Tab Rasmussen[¶]

*Department of Anthropology, Yale University, New Haven, CT 06520; [‡]Department of Biological Anthropology and Anatomy and Primate Center, Duke University, Durham, NC 27705; [§]Department of Earth Sciences, Santa Monica College, Santa Monica, CA 90405; and [¶]Department of Anthropology, Washington University, St. Louis, MO 63130

Contributed by Elwyn L. Simons, May 1, 2002

The East African Early Miocene apes, or proconsulids, have often been considered to be among the earliest members of the Hominoidea, as defined by the divergence of the Cercopithecoidea, but this hypothesis is only weakly supported by available fossil evidence. The ethmofrontal sinus is one of a few morphological features that may link proconsulids with later hominoids. Here we present direct evidence of an ethmofrontal sinus in an early Oligocene stem catarrhine, *Aegyptopithecus zeuxis*. The presence of this sinus in *Aegyptopithecus* suggests that its presence in proconsulids is most likely to be a retained primitive condition. The morphological evidence bearing on proconsulids' purported hominoid affinities is further weakened by this conclusion, and alternative phylogenetic possibilities, such as the placement of proconsulids as stem catarrhines are considered more likely.

Although the East African Early Miocene proconsulids are usually included in the Hominoidea (1, 2), it has become increasingly evident in recent years that many may, in fact, be stem catarrhines (3–5). As the best known member of this radiation, the genus *Proconsul* has been the primary focus of these discussions. *Proconsul* lacks numerous features of the postcranium that are associated with habitual orthograde and suspensory behaviors and that unite the extant hominoids to the exclusion of most early and middle Miocene apes (3–8). The distal humeral morphology of *Proconsul heseloni* has been considered hominoid-like (9), but it and the complimentary joint morphology of the ulna and radius more closely resemble platyrrhines than hominoids (10). Although this evidence indicates that *Proconsul* is not a crown hominoid (Fig. 1), limited evidence [the absence of such crown catarrhine synapomorphies as enlarged surface area of lumbar centra (5) and callosity-bearing ischial tuberosities (8)] suggests that *Proconsul* may actually be a stem catarrhine that shares no special relationship with either hominoids or cercopithecoids (3, 4). An alternative interpretation of these latter features as convergences between cercopithecoids and hominoids would be justified only if convincing hominoid synapomorphies could be found in *Proconsul*. The ethmofrontal sinus seen in *Proconsul* (1) and the contemporaneous catarrhines, *Afropithecus* (11), *Morotopithecus* (12), and *Turkanapithecus* (13), may represent such a feature (2), and as such its potential as a hominoid synapomorphy deserves further scrutiny.

The ethmoid sinuses of humans and African apes are a group of epithelially lined cavities that pneumatize the ethmoid lateral mass while maintaining communication with the nasal cavity via small ostia in the middle meatus (14, 15). At around 5 years of age in humans, one or more of these sinuses per side usually extend into the frontal bone creating a “frontal sinus,” although this feature is variable in size and sometimes absent (14–17). Hence, by the standard criterion of sinus identity (18, 19), the “frontal” sinus is actually one of the ethmoid sinuses (18). For this reason we will refer to the entire complex as the ethmofrontal sinus.

The presence of an ethmofrontal sinus has long been considered a synapomorphy of the living African apes and humans (19).

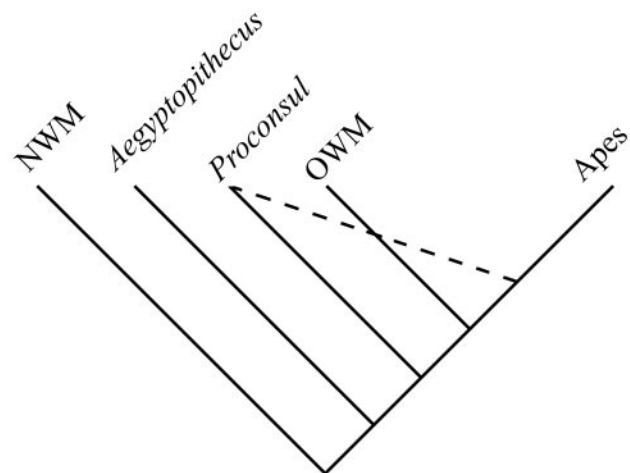


Fig. 1. Cladogram depicting the alternative phylogenetic positions of *Proconsul*; as a stem hominoid (dashed line), or a stem catarrhine (solid line). NWM = New World monkeys, OWM = Old World monkeys, Apes = great apes and gibbons.

This notion was based primarily on its absence in the other extant hominoids (*Pongo* and *Hylobates*) and cercopithecoids. However, similarities in nasal and paranasal anatomy between platyrrhines and hominoids suggest that cercopithecoids are specialized within Anthroidea in their ancestral loss of all paranasal sinuses and the reduction of the posterior and lateral portions of the nasal capsule (20–22). Hence, neontological comparisons imply that the ancestral catarrhine condition more closely resembled platyrrhines and hominoids than cercopithecoids (21). Moreover, the discovery of frontal sinuses in Miocene catarrhines such as *Proconsul*, *Turkanapithecus*, and *Afropithecus* has led many researchers to demote this feature to either a hypothetical synapomorphy of great apes (2) or of hominoids (23, 24). Until now, unequivocal fossil evidence for the primitive catarrhine condition has been unknown, leaving the polarity of this trait unresolved. As an undoubted stem catarrhine (25), *Aegyptopithecus* provides direct evidence bearing on this issue. We report here the results of computed tomography (CT) scanning of three faces of *Aegyptopithecus zeuxis* recovered from Fayum fossil quarry M in the Jebel Qatrani Formation, Fayum Province, Egypt, which is estimated to be 33.14 to 33.32 million years old (26).

Methods

Duke University Primate Center (DPC) 2803 was helically scanned at 1 mm collimation and reconstructed in 0.5-mm slice intervals on the CTi scanner at the Duke University Medical Center. These raw data were converted to 8-bit TIFF format for analysis using SCION IMAGE software (version 4.0.2; Scion,

Abbreviations: DPC, Duke University Primate Center; CT, computed tomography.

[†]To whom reprint requests should be addressed. E-mail: james.rossie@yale.edu.

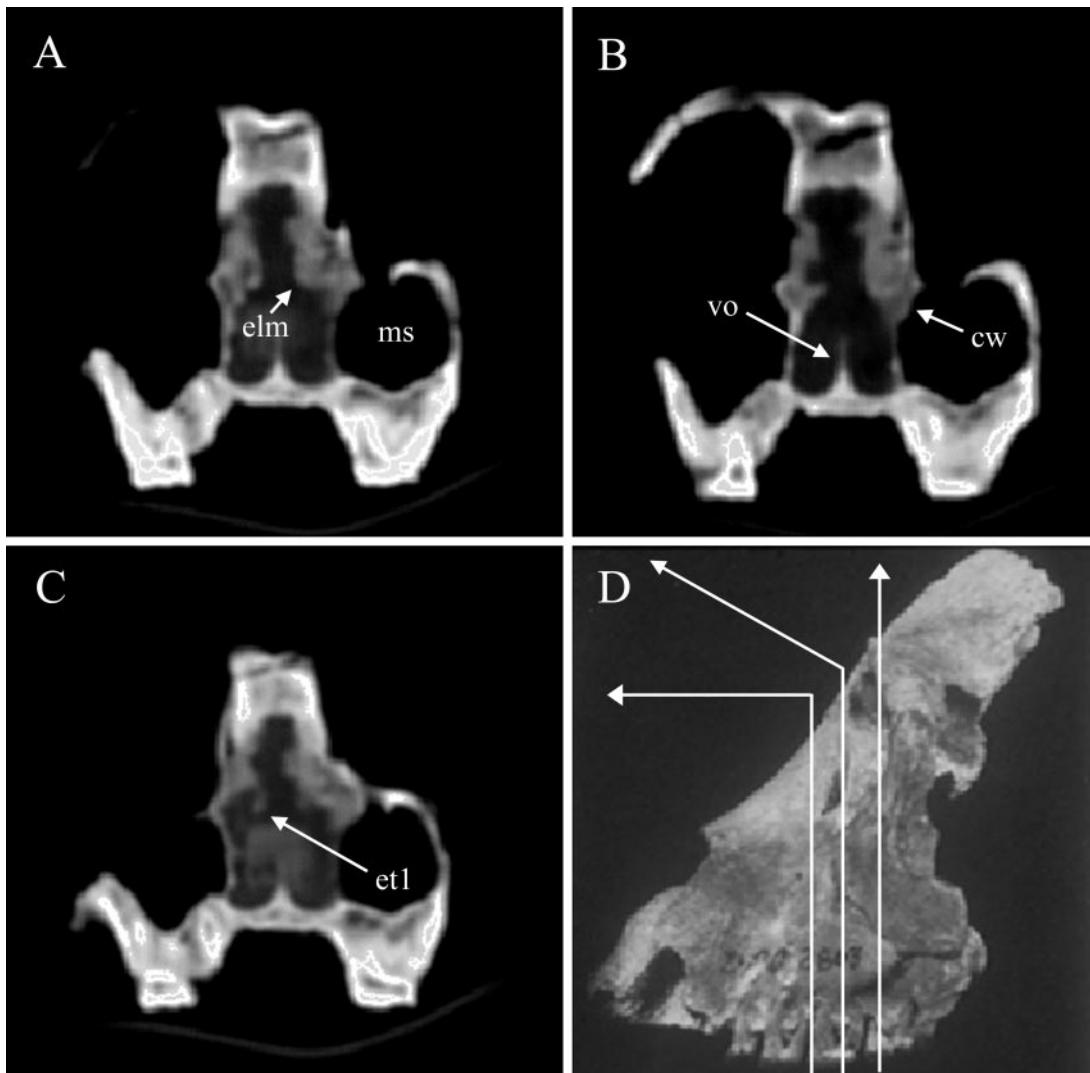


Fig. 2. Coronal slices (A, B, and C) through the region of the ethmoid sinuses of DPC 2803 (D). White lines in D indicate the positions of the slices. elm, ethmoid lateral mass; ms, maxillary sinus; cw, common wall shared by maxillary sinus and ethmoid lateral mass; vo, vomer; et1, first ethmoturbinal taking origin from the inferomedial portion of the ethmoid lateral mass as in extant African apes and humans.

Frederick, MD). We used this software to reconstruct the internal anatomy of the face in sagittal, coronal, and transverse planes. Where pneumatization appeared to be present, density plots across the region in question were used to confirm a background density. The other two specimens were scanned with a GE 9800 x-ray CT scanner at the Department of Radiological Sciences, School of Medicine, University of California, Los Angeles. Coronal and sagittal studies were performed using a 512×512 image reconstruction matrix with a 12.8-cm field of view. Between 40 and 70 slices were obtained by using 1.5-mm slice thickness and 1.0-mm center to center spacing.

Results

The best preserved ethmoid region is found in DPC 2803 (Fig. 2). The nasal cavity of this specimen posterior to the level of P³ is filled with a fine matrix, which has facilitated the preservation of many fragile regions of anatomy including much of the vomer (Fig. 2B) and the lamellae of both nasoturbinals and maxilloturbinals. In coronal sections through the level of the M² and M³, the ethmoid consists of a pneumatized mass of bone that conforms in every aspect of shape and position to the ethmoid labyrinth of living African apes and humans. The mass on the left

side of the specimen is relatively complete, whereas in the mass on the right side, the air cells are exposed by breakage. The ethmoid sinuses appear to be few in number and small compared with the few large air cells usually seen in *Pan* and *Gorilla* (27). This aspect of ethmoid pneumatization is apparently prone to variation, as human ethmoid sinuses can be composed of up to 13 small cells per side (14, 15). Because it differs from these taxa in the size and number of sinuses, we will refer to this structure as the ethmoid lateral mass following Cave and Haines (19).

In the other two specimens, DPC 8794 and DPC 5401, only the superior, interorbital portions of the ethmoid lateral mass are present. However, the supraorbital regions of the frontal bone are well preserved, especially in DPC 8794. Although there are no open sinus cavities in the supraorbital regions of either skull, both skulls show the presence of bilateral chambering in the interorbital region underlying glabella. Close to the midline, the diploe in these chambers, which are especially prominent in DPC 8794, becomes uneven in density and takes on a loculated appearance. In DPC 5401, a female, these chambers appear to be filled with a relatively light and uniform density of spongiform bone, whereas in the male skull, DPC 8794, they appear to be fully pneumatized air cells. These small extensions of the ethmoid sinuses

into the interorbital region of the frontal bone represent a developmentally homologous precursor to the more cavernous frontal sinus found in the African great apes and most humans.

Comparisons

The similarity in interorbital morphology between *Aegyptopithecus*, *Afropithecus*, and African apes has been noted previously (25). These taxa share a wide interorbital region and medial orbital margin that is often slightly convex. Internally, the wide interorbital region in African apes and humans is occupied by the ethmoid lateral mass containing the ethmoid sinuses, while the nasal cavity is restricted to a narrow corridor (19, 28). Superiorly, the lateral mass meets the frontal bone on either side of the cribriform plate. It is this topographical relationship that allows a variable number of ethmoid sinuses to invade the frontal bone. Inferiorly, the ethmoid labyrinth shares a common border with the dorsomedial wall of the large maxillary sinus (19, 28). Hence, there is no common wall shared by the orbits and the nasal cavity. This arrangement of the ethmoid lateral mass relative to surrounding structures is exactly matched in *Aegyptopithecus* (Fig. 2).

In *Pongo*, *Hyllobates*, and colobines, the anterior portion of the ethmoid lateral mass consists of an unpneumatized plate of bone forming a common wall between the medial wall of the orbit and the nasal cavity (19, 27–29). Cercopithecines differ in that their ethmoid is so reduced that it does not contribute to the medial orbital wall (28, 30). The absence of paranasal sinuses in these taxa appears to be related to the morphological simplification of their chondrocranial nasal capsules (22), although the subject requires further research.

Afropithecus, *Turkanapithecus*, *Oreopithecus*, *Ankarapithecus*, *Dryopithecus*, *Otavipithecus*, and *P. heseloni* are known to have frontal sinuses, but few details of their interorbital anatomy are known (1, 11, 13, 23, 31–33). However, *Morotopithecus* (UMP 62-11) does preserve some informative internal interorbital morphology, and the resemblance to *Aegyptopithecus* is striking. As described by Pilbeam (12), “a multilocular frontoethmoidal sinus was present at the level of the frontomaxillary suture and below and posterior to this. It extended medial to the lacrimal and ethmoid bones. The bone surrounding the sinus was

probably a little thicker, and the sinuses themselves less extensive, than in living African pongids.”

Conclusion

On the basis of the present data, it is most parsimonious to conclude that an African ape-like system of ethmoid frontal sinuses is the primitive condition for crown catarrhines. This conclusion receives further support from the recent report of a sinus in the frontal bone of another stem catarrhine, the pliopithecid *Anapithecus* (34). Conversely, the loss of this sinus complex in the orangutan and the Eurasian Miocene ape *Sivapithecus* is best interpreted as a synapomorphy (27). That the losses of the ethmoid frontal sinus in the gibbon and orangutan lineages were independent events is demonstrated by their retention in the stem great ape *Oreopithecus* (32) and in *Ankarapithecus*, which is either a stem great ape (31) or a stem member of the *Sivapithecus* and *Pongo* clade (35, 36).

The presence of an ethmoid frontal sinus can no longer be cited as supporting a relationship between any fossil catarrhine and the Hominoidea. Consequently, the argument that proconsulids are stem hominoids is further weakened, leaving the Early Miocene *Morotopithecus* as the earliest convincing member of the Hominoidea (6). The importance of proconsulids to our understanding of hominoid origins is in no way diminished by this finding. The recognition that cercopithecoids and hominoids are likely to have shared a common ancestor with *Proconsul*-like pronograde quadrupedal adaptations allows us to more fully understand the adaptive impetus for the divergence of the two modern clades. The broader significance of the present study lies in demonstrating the importance of paleontological data for resolving character polarity in cases, such as hominoid evolution, in which the living outgroups may be too derived to be appropriate (37).

We thank P. S. Chatrath for his invaluable help with fieldwork and preparation of the specimens, Dr. G. A. Johnson for permission to scan the specimens, Dr. C. Gatenby for converting the data to TIFF format, E. R. Seiffert for transport of fossils, and Dr. J. G. Rossie, Jr., for software support. We thank Dr. D. Valentino (University of California, Los Angeles) for help with the scanning. Early stages of this work benefited greatly from comments by S. C. Ward, E. R. Seiffert, E. J. Sargis, R. R. Lawler, A. Hill, and R. J. Sherwood. We also thank D. R. Pilbeam and S. C. Ward for providing helpful comments on an earlier version of this manuscript.

1. Le Gros Clark, W. & Leakey, L. S. B. (1951) in *Fossil Mammals of Africa* (British Museum of Natural History London), Vol. 1, pp. 1–117.
2. Walker, A. C. (1997) in *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, eds. Begun, D. R., Ward, C. V. & Rose, M. D. (Plenum, New York), pp. 209–224.
3. Harrison, T. (1987) *J. Hum. Evol.* **16**, 41–80.
4. Harrison, T. & Yumin, G. (1999) *J. Hum. Evol.* **37**, 225–277.
5. Harrison, T. & Sanders, W. J. (1999) *Am. J. Phys. Anthropol.* **108**, Suppl. 28, 146.
6. Gebo, D. L., MacLatchy, L., Kityo, R., Deino, A., Kingston, J. & Pilbeam, D. R. (1997) *Science* **276**, 401–404.
7. Rose, M. D. (1993) in *Postcranial Adaptation in Nonhuman Primates*, ed. Gebo, D. L. (Northern Illinois Univ. Press, DeKalb), pp. 252–272.
8. Ward, C. V., Walker, A. C., Teaford, M. & Odhiambo, I. (1993) *Am. J. Phys. Anthropol.* **90**, 77–111.
9. Andrews, P. (1992) *Nature (London)* **360**, 641–646.
10. Rose, M. D. (1994) *J. Hum. Evol.* **26**, 387–411.
11. Leakey, R. E. F., Leakey, M. G. & Walker, A. C. (1988) *Am. J. Phys. Anthropol.* **76**, 289–307.
12. Pilbeam, D. R. (1969) *Bull. Peabody Museum Nat. Hist.* **31**, 1–185.
13. Leakey, R. E. F., Leakey, M. G. & Walker, A. C. (1988) *Am. J. Phys. Anthropol.* **76**, 277–288.
14. Negus, V. (1958) *The Comparative Anatomy and Physiology of the Nose and Paranasal Sinuses* (Livingstone, London).
15. Moss-Salentijn, L. (1991) in *Surgery of the Paranasal Sinuses*, eds. Blitzer, A., Lawson, W. & Friedman, W. (Saunders, Philadelphia), pp. 1–24.
16. Shea, B. T. (1977) *Am. J. Phys. Anthropol.* **47**, 289–300.
17. Koertvelyessy, T. (1972) *Am. J. Phys. Anthropol.* **37**, 161–173.
18. Paulli, S. (1900) *Gegenbaurs Morphol. Jahrb.* **28**, 483–564.
19. Cave, A. J. E. & Haines, R. W. (1940) *J. Anat.* **74**, 493–523.
20. Rae, T. C. & Koppe, T. (2001) *Am. J. Phys. Anthropol.* Suppl. **32**, 122.
21. Ward, S. C. (1997) *J. Morphol.* **232**, 338.
22. Maier, W. (2000) in *Old World Monkeys*, eds. Whitehead, P. F. & Jolly, C. J. (Cambridge Univ. Press, Cambridge, U.K.), pp. 99–132.
23. Begun, D. R. (1992) *Science* **257**, 1929–1933.
24. Moyà-Solà, S. & Köhler, M. (1995) *J. Hum. Evol.* **29**, 101–139.
25. Simons, E. L. (1987) *J. Hum. Evol.* **16**, 273–289.
26. Kappelman, J. (1992) *J. Hum. Evol.* **22**, 495–503.
27. Ward, S. C. & Brown, B. (1986) in *Systematics, Evolution, and Anatomy, Comparative Primate Biology*, eds. Swindler, D. R. & Erwin, J. (Alan R. Liss, New York), Vol. 1, pp. 413–452.
28. Koppe, T. & Ohkawa, Y. (1999) in *The Paranasal Sinuses of Higher Primates*, eds. Koppe, T., Nagai, H. & Alt, K. W. (Quintessence, Berlin), pp. 77–120.
29. Weinert, H. (1926) *Z. Morph. Anthropol.* **25**, 243–357 and 365–418.
30. Delson, E. & Andrews, P. J. (1975) in *Phylogeny of the Primates: A Multidisciplinary Approach*, eds. Luckett, W. & Szalay, F. (Plenum, New York), pp. 405–446.
31. Alpagut, B., Andrews, P., Fortelius, M., Kappelman, J., Temizsoy, I., Celebi, H. & Lindsay, W. (1996) *Nature (London)* **382**, 349–351.
32. Harrison, T. & Rook, L. (1997) in *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, eds. Begun, D. R., Ward, C. V. & Rose, M. D. (Plenum, New York), pp. 327–362.
33. Pickford, M., Moyà-Solà, S. & Köhler, M. (1997) *C. R. Acad. Sci. Ser. IIA* **325**, 459–466.
34. Kordos, L. & Begun, D. R. (2000) *Am. J. Phys. Anthropol.* Suppl. **30**, 199.
35. Begun, D. R. & Güleç, E. (1998) *Am. J. Phys. Anthropol.* **105**, 279–314.
36. Köhler, M., Moyà-Solà, S. & Alba, D., M. (2001) in *Phylogeny of the Neogene Hominoid Primates of Eurasia*, eds. De Bonis, L., Koufos, G., D. & Andrews, P. (Cambridge Univ. Press, Cambridge, U.K.), Vol. 2, pp. 192–212.
37. Novacek, M. J. (1992) *Syst. Biol.* **41**, 58–73.