

Second gorilla or third chimp?

David Dean and Eric Delson

WHAT is the origin of and the relationships within the primate lineage including gorillas, chimpanzees and humans? That nexus of questions is among the most compelling in anthropology, and David Begun¹ has brought two new hypotheses to bear on it.

Begun's analysis of recently recovered fossils of *Dryopithecus*, a European ape dating to 13–9 million years ago, leads him to suggest, first, that this group of species shares with the gorilla a complex of facial and dental features which are ancestral for the African-ape and human subfamily, Homininae. Even more intriguing is Begun's second suggestion, that features shared by chimpanzees and the extinct 'early human' *Australopithecus* link the chimp and the human sublineages within Homininae to the exclusion of the gorilla. This second hypothesis has long been championed by some molecular systematists^{2,3}, although others have disagreed⁴. If Begun's work is correct, it would constitute a major contribution to palaeoanthropology (see also ref. 5). But, stimulated by his proposals, we have examined them in light of other recently described fossils and come to somewhat different conclusions.

Although several species of *Dryopithecus* are now represented by partial craniofacial remains, the 8–10 million-year-old Greek ape *Graecopithecus* (also called *Ouranopithecus*^{6,7}) is known by most of a male face (Fig. 1a) and numerous jaws. These fossils show greater similarity to *Pan*, *Australopithecus* and especially *Gorilla* (Fig. 1b) than does *Dryopithecus*. In our opinion, *Graecopithecus* is a far stronger candidate for an early member of Homininae, if not of the gorilla subclade.

Shared features

Begun lists a variety of character states which link *Dryopithecus* to hominines, and he specifically indicates that *Graecopithecus* shares all that could be seen on the known fossils, but he refrains from further interpretation of the Greek face. He relates several of these shared features to klinorhynch (the downward bending of the face on the brain case⁸); we agree, and explicitly suggest that an increase in klinorhynch was related to the origin of Homininae. Three further characteristics of the upper dentition are shared by all hominines, including both European fossils: the incisor crowns are oriented vertically to take advantage of what was probably a horizontally oriented posterior temporalis muscle like that seen in the African apes and humans; the canines, especially their shear

facets, are in line with postcanine teeth rather than laterally rotated; and the lingual cusps on the molars tend to be posterior to their buccal neighbours — species with less klinorhynch or airorhynch (upwardly bent) faces tend to have transversely aligned cusps and squared-off molars.

Begun also does not take into account the point that *Graecopithecus* presents more extreme klinorhynch than does *Dryopithecus*. For example, the brow ridge of the new Greek face⁷ is continuous as in *Dryopithecus*, but it projects at glabella (in the midline) to a degree otherwise found only in later hominines. In addition, *Graecopithecus* resembles *Gorilla* more than other

hominines in its superolateral brow and lateral orbit margin shape; the sharply angular muzzle shape with supra-alveolar waisting; anterior nasal bone projection; and (less definitively due to damage) in the development of the frontal trigone, the area just behind the brow ridge bounded by the anterior temporal line.

Different interpretations

So why does Begun not include *Dryopithecus*, much less *Graecopithecus*, squarely in the Homininae (see Fig. 2a)? The reason is that he interprets a somewhat elongated premaxilla and larger maxillary sinus as possibly having characterized the hypothetical common ancestor of living great apes, excluding *Dryopithecus*. In our opinion, both features are probably size related, and Begun himself realizes that the naso-alveolar elongation in the airorhynch

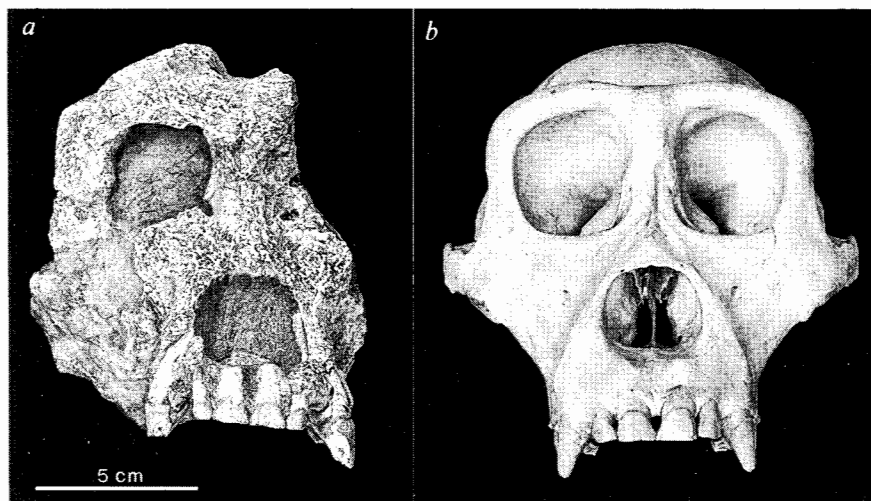


FIG. 1 Frontal view (alveolar plane horizontal) of, a, *Graecopithecus freybergi* (cast of male face from Xirochori⁷) and, b, female *Gorilla gorilla*. Similarities between the two species are discussed in the text. Photo Lorraine Meeker/Eric Delson.

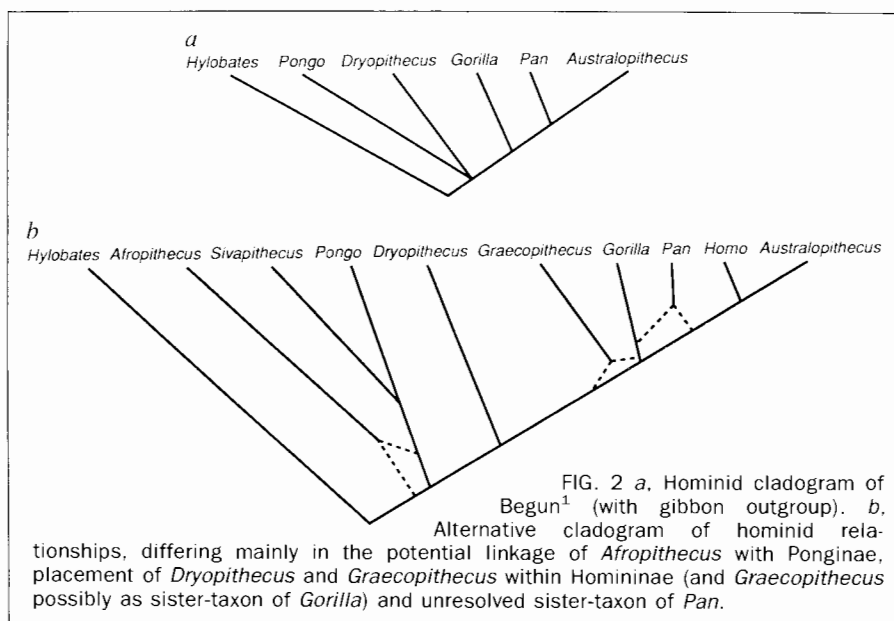


FIG. 2 a, Hominid cladogram of Begun¹ (with gibbon outgroup). b, Alternative cladogram of hominid relationships, differing mainly in the potential linkage of *Afropithecus* with Ponginae, placement of *Dryopithecus* and *Graecopithecus* within Homininae (and *Graecopithecus* possibly as sister-taxon of *Gorilla*) and unresolved sister-taxon of *Pan*.

orangutan clade (Ponginae) is convergent with that seen in the klinorhynch *Pan*.

Our cladogram (Fig. 2b) presents a rather different interpretation of hominid relationships. The Asian fossil ape *Sivapithecus* is airorhynch and clearly a pongine craniodentally, although it lacks several postcranial features that have long been interpreted to characterize all hominids⁹. Moreover, the 17-million-year-old face of Kenyan *Afropithecus*¹⁰ is also airorhynch, as demonstrated for example by its upturned orbits and premaxilla, procumbent incisors and molar cusps aligned transversely. If *Graecopithecus* is on the gorilla subclade, that lineage dates to at least 9 million years ago.

Begun¹ also proposes morphological support for a link between chimpanzees and the human subclade, which he claims share derived features of the frontal bone, subnasal region, upper molars and molar proportions not seen in *Gorilla*. This aspect of the work is less detailed and less convincing; if some of these states are ancestral or convergent, the case would be greatly weakened. For example, the subnasal elongation and concomitant increase in maxillary sinus size in *Pan* and *Australopithecus* may be convergent, as it is not associated in the latter with the extreme klinorhynch shared by *Pan* and *Gorilla*.

Moreover, Begun reasonably questions the evidence from tooth enamel thickness linking *Pan* and *Gorilla*, but also rejects the uniqueness of their shared knuckle-walking morphology. He argues that the latter is a single functional complex and thus effectively of lesser weight than the multiple dento-facial characters which oppose it. But the question of how to weight a complex of perhaps dozens of individual 'characters' is far from resolved: if we weight each component at half a 'full' character, the chimp-gorilla link 'wins'. We consider that the trichotomy remains unresolved.

Diamond¹¹ has referred to humans as "the third chimpanzee" in recognition of our close biomolecular similarity to the

two living species of *Pan*. Begun's article supports this view, but we are not entirely convinced that the closest genealogical relative of chimpanzees is the human clade rather than the morphologically similar gorilla. We await further specimens of the *Graecopithecus* cranium to assess variation, as well as deeper analysis to confirm that its similarities to *Gorilla* are derived within Homininae. At the least, however, the reinterpretation here of *Graecopithecus* suggests that it is a fourth lineage within the Homininae, if not a 'second gorilla'. □

David Dean is in the Department of Cell Biology, New York University Medical Center, New York, New York 10016, USA. Eric Delson is in the Department of Anthropology, Lehman College and the Graduate School, City University of New York, Bronx, New York 10468, USA.

1. Begun, D. R. *Science* **257**, 1929–1933 (1992).
2. Ruvolo, M., Disotell, T. R., Allard, M. W., Brown W. M. & Honeycutt, R. L. *Proc. natn. Acad. Sci. U.S.A.* **88**, 1570–1574 (1991).
3. Horai, S. et al. *J. molec. Evol.* **35**, 32–43 (1992).
4. Marks, J. *Am. J. phys. Anthropol.* **85**, 207–219 (1991).
5. Gibbons, A. *Science* **257**, 1864–1865 (1992).
6. Martin, L. & Andrews, P. *Courier Forschungs-Institut Senckenberg* **69**, 25–40 (1984).
7. De Bonis, L., Bouvraïn, G., Geraads, D. & Koufos, G. *Nature* **345**, 712–715 (1990).
8. Shea, B. in *Orang-utan Biology* (ed. Schwartz, J. H.) 233–245 (Oxford University Press, 1988).
9. Pilbeam, D. R., Rose, M. D., Barry, J. C. & Ibrahim Shah, S. M. *Nature* **348**, 237–239 (1990).
10. Leakey, R. E., Leakey, M. G. & Walker, A. C. *Am. J. phys. Anthropol.* **76**, 289–307 (1988).
11. Diamond, J. *The Rise and Fall of the Third Chimpanzee* (Random House, New York, Hutchinson/Radius, London, 1991).