



Response to Benoit and Thackeray (2017): 'A cladistic analysis of *Graecopithecus*'

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KEYWORDS:

Hominini; Africa; Eurasia

HOW TO CITE:

Fuss J, Spassov N, Böhme M, Begun DR. Response to Benoit and Thackeray (2017): 'A cladistic analysis of *Graecopithecus*'. *S Afr J Sci.* 2018;114(5/6), Art. #a0267, 2 pages. <http://dx.doi.org/10.17159/sajs.2018/a0267>

PUBLISHED:

30 May 2018

Benoit and Thackeray¹ provide a cladistic analysis that aims to refute the hypotheses that *Graecopithecus* is a member of the hominin clade and that hominins could have originated in the Eastern Mediterranean. In our response, we point out that the authors' thesis relies on a selective use of data and a series of misrepresentations of our results and conclusions that reflect what we see as an a priori hostility to the very idea of a non-African origin of the hominin clade.

It is useful to recall that ever since the widespread acceptance among scientists of the reality of human evolution there has been debate, often contentious, about the place of origin of the first humans (hominins). While Darwin and Huxley advocated Africa, Darwin recognised the possibility that it might be Europe – a fact often overlooked today. Haeckel and Dubois believed it was Asia while Dawson profited from the racist ideology of the day to promote a forgery (*Eoanthropus*, a.k.a. Piltdown) as proof that it was Europe. Osborn even proposed Nebraska! Following the description by Dart of *Australopithecus*, and especially the subsequent discoveries by Broom, the overwhelming consensus has been that Africa is the continent of hominin origins. This has become so widely accepted as to rise to the level of dogma, with the result that any claim to the contrary is automatically disputed if not ridiculed. The media coverage to which Benoit and Thackeray refer in their comment concerning the hypothesis of a European origin of hominins – when in fact we propose an Eastern Mediterranean (which also includes Africa) origin – is a perfect example.

Fuss et al.² propose that *Graecopithecus* may be a hominin, given the small size of the root of the lower canine but especially the root morphology of the lower premolar in the Greek specimen and the upper premolar in the specimen from Bulgaria (not lower premolar, contra Benoit and Thackeray). We note that if it is a hominin, *Graecopithecus* would be the oldest known. Given what we know about mammalian faunas in the Eastern Mediterranean and Africa between 10 and 7 Ma, dispersals clearly occurred between the two areas and, as is the case for elephantids, giraffids and bovids, hominins could certainly have dispersed from Eurasia into Africa. However, we are clear that the evidence is not overwhelming and that homoplasy may account for the hominin characters of *Graecopithecus*.

With less than thorough consideration of the details of our argument, Benoit and Thackeray¹ repeat the classic position points favouring an African origin of the hominins. An African origin of Hominini is well documented by the huge number of fossils that represent an unambiguous lineage of hominins from *Australopithecus* to *Homo*, probably also including *Ardipithecus*, *Orrorin* and *Sahelanthropus*. In addition, as argued by Huxley and Darwin, our nearest living relatives, *Pan* and *Gorilla*, are both exclusive to Africa, so it is most parsimonious to suggest that hominins arose there as well.

Neither argument is relevant to our conclusions. First, our results concern fossils that are about 3 million years older than the oldest *Australopithecus* and probably at least 600 000 years older than the oldest putative African hominin (*Sahelanthropus*). The completeness of the fossil record of hominins in Africa is not relevant to their origins, much as the fossil record of platyrrhines, which is exclusively American, is not relevant to their origins in Africa.

Second, dismissing the hypothesis of the presence of a late Miocene hominin in Europe ignores the large body of data demonstrating the widespread presence of hominids of modern aspect in Europe well before any appear in Africa. Nearly every phylogenetic analysis of Miocene apes, whether cladistic or not, concludes that dryopithecids and related taxa, which are exclusive to Europe, are hominids. This includes the analysis in Benoit and Thackeray¹. The most comprehensive analyses have further concluded that they are hominines (African apes and humans) (e.g. Begun et al.^{3,4}; Young and MacLatchy⁵). The same logic used to refute the Eastern Mediterranean origins hypothesis actually serves to support it. Because the overwhelming majority of Miocene hominid fossil taxa known are from Eurasia, it is reasonable to suppose that one or more of the extant subfamilies evolved there as well.

Benoit and Thackeray¹ state: 'Even if *Graecopithecus* can be attributed to Hominini, the fact that it is older than *Sahelanthropus* does not make it the basal-most representative of this clade.' We agree. We are well aware of the fact that geological age does not reveal phylogenetic position, nor does it establish divergence times. The age of the oldest known fossil of a particular taxon can only be interpreted as the currently known first appearance datum, not the origin, whether in time, geography or phylogeny. Our point is simply that the hypothesis that *Graecopithecus* is the oldest known hominin cannot be dismissed out of hand with the convenient invocation of homoplasy. The large body of data used to support this hypothesis must be addressed. Indeed, it is currently not possible to resolve the question of the most basal hominin. Neither *Sahelanthropus* nor *Graecopithecus* are known well enough to provide an unambiguous answer. Nonetheless, at 7.2 Ma, *Graecopithecus freybergi* remains the oldest candidate for this clade.

Benoit and Thackeray¹ also state: 'If *Graecopithecus* happens to be more derived than *Sahelanthropus*, then the evolutionary tree of Hominini would remain rooted in Africa and *Graecopithecus* would only represent an offshoot that dispersed out of Africa very early in the evolutionary history of hominins.'

This critique might have some relevance if we had actually reached the conclusion that *Graecopithecus* was derived relative to *Sahelanthropus*. However, we never stated that *Graecopithecus* was derived relative to *Sahelanthropus* in either P4 or canine root morphology. In fact, we state that there is variability in P4 root morphology in hominins, but that root fusion never occurs in Miocene apes and very rarely in *Pan*. We also never state, contra Benoit and

Thackeray¹, that canine root reduction is more derived in *Graecopithecus* than *Sahelanthropus*. We do not comment on the significance of this difference simply because it is obvious that the differences in canine root size between *Graecopithecus* and *Sahelanthropus* are well within ranges of within-sex variation in most hominoids – both fossil and extant. Once again, we are simply reporting that the canine root is reduced, as in hominins and to the distinction of other hominoids. Falsely attributing provocative conclusions to our work does not advance this debate.

Benoit and Thackeray¹ state: 'On the other hand, *Graecopithecus* might be closely related to *Ouranopithecus*, with which it has been synonymised for a long time or to other Eurasian apes, as suggested by previous cladistic analyses. In these cases, the evolutionary root of humankind would definitely remain in Africa.'

We provide extensive documentation of the differences between *Graecopithecus* and *Ouranopithecus*, none of which is addressed in Benoit and Thackeray¹. We are not aware of any phylogenetic analysis that 'synonymises' these taxa, or either of them to other Eurasian apes. Only a sister clade relationship between *Ouranopithecus* and *Graecopithecus* would call our conclusions into question; however, we have presented ample evidence that this hypothesis of relationship is unlikely. We present evidence that *Graecopithecus* shares derived characters with hominins not found in *Ouranopithecus*. The most parsimonious interpretation of this distribution of characters is that *Ouranopithecus* predates the divergence of hominins and *Graecopithecus*. To assert that '*Graecopithecus* might be closely related to *Ouranopithecus*' without justification other than tradition, is not useful to this exchange.

About the cladistic analysis

Benoit and Thackeray¹ modified a character matrix published by Finarelli and Clyde⁶, in turn modified from Begun et al.⁴, to produce a cladistic analysis. Unfortunately, this character matrix is outdated in terms of both taxonomic units and character states, yielding a misleading and less parsimonious cladogram. More recent analyses (e.g. Begun et al.³; Young and MacLatchy⁵) yield very different cladograms from that in Benoit and Thackeray or Finarelli and Clyde but have the advantage of having been produced by researchers who compiled the character matrices from direct observation of the fossils, which is not the case for Finarelli and Clyde or Benoit and Thackeray. Finarelli and Clyde⁶ were interested in the relationship between phylogeny and temporal sequence, which also influences their results. A revision of the original Begun et al.⁴ data matrix, the most comprehensive published so far, is in preparation but is beyond the scope of this response.

It is unfortunate that when Benoit and Thackeray¹ state that 'none of the characters cited by Fuss et al. is strictly unique to Hominini, as thick enamel and megadonty' they omit the characters we actually say are unique to Hominini: reduction of premolar root complexity and canine root size. Nowhere in our publication do we say that thick enamel and megadonty are hominin synapomorphies. This mischaracterisation of our work only serves to polarise this debate.

It is clear that if *Graecopithecus* were found in Africa instead of Europe, its age and morphology would be taken as evidence that it is the earliest

known hominin. *Chororapithecus* is accepted by many as an early gorilla, despite a very fragmentary sample and the fact that much more complete fossils with gorilla-like attributes are known from Europe.⁷ But it is from Africa, where the earliest gorillas are supposed to be. The real problem is not morphology or preservation but a location that does not conform to the expectations of generations of palaeoanthropologists.

Our final quote from Benoit and Thackeray is most revealing of the confusion and artificial nature of this exchange: 'Our analysis supports the view that *Graecopithecus* is potentially an important taxon for the origin of Hominini, but this is not certain and deserves further investigation and more material.'

This is almost precisely the same conclusion we reached: 'Therefore, we submit that the dental root attributes of *Graecopithecus* suggest hominin affinities, such that its hominin status cannot be excluded. ... More fossils are needed but at this point it seems likely that the Eastern Mediterranean needs to be considered as just as likely a place of hominine diversification and hominin origins as tropical Africa.'

Far from being an 'assertion that *Graecopithecus* belongs to Hominini' (Benoit and Thackeray^{1(p.1)}), we clearly present our results as preliminary and in need of additional fossils for confirmation. In contrast, Benoit and Thackeray¹ make numerous assertions about our results that are either unsubstantiated or inaccurate. The better way forward is through a thoughtful assessment of data and results as they are actually presented. We are hopeful that future contributions to this debate will maintain this focus.

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