

Comment on “*Pierolapithecus catalaunicus*, a New Middle Miocene Great Ape from Spain”

The recent report of *Pierolapithecus catalaunicus* by Moyà-Solà *et al.* (1) provides important new information on great ape origins. We congratulate the authors on their spectacular discovery and excellent analysis and propose some alternative phylogenetic and functional interpretations based on the data they present.

Moyà-Solà *et al.* conclude that *Pierolapithecus* is a new genus that represents the sister taxon to the great ape and human clade. From their descriptions and photographs, we were able to code 96 characters for *Pierolapithecus* into our database of living and fossil hominoid morphology (2, 3). Our published data matrix was modified for this analysis by dropping poorly known taxa and adding missing characters based on more recent discoveries. The results are consistent with the consensus phylogeny in (2) for previously known taxa but suggest that *Pierolapithecus* is most parsimoniously interpreted as a stem hominine (basal member of the African ape and human clade) rather than a stem hominid (great ape and human clade) (Fig. 1). The average consistency index (CI) for the nine characters supporting *Pierolapithecus* as a basal hominine (Table 1) is 0.89. Support for the hypothesis that *Pierolapithecus* is a stem hominid (1) requires six additional steps, and the seven characters supporting this hypothesis have a lower average consistency index of 0.74.

Although it is most parsimonious to consider *Pierolapithecus* a hominine, an additional argument in favor of this hypothesis is the effect on the support for a crown hominid clade. Most hypotheses, including those in previous analyses cited here (1–3), include both *Dryopithecus* and *Sivapithecus* in a crown hominid clade. However, when *Pierolapithecus* is interpreted as a stem hominid, as in (1), support for the crown hominid clade that includes *Dryopithecus* and *Sivapithecus* falls from 11 characters (average CI = 0.86) to only 2 characters (average CI = 0.75) (Table 1). In other words, the most prudent hypothesis interpreting *Pierolapithecus* as a hominine is also more consistent with most previous analyses of relations among fossil and extant hominids. We also found some support for the hypothesis that *Pierolapithecus* is the sister taxon to *Dryopithecus*, but the average CI is only 0.66 for the three characters placing *Pierolapithecus* on the *Dryopithecus* clade.

We interpret these results as strong evidence that *Pierolapithecus* is a basal hominine, although its position as a member of the *Dryopithecus* clade is only weakly supported. As a hominine, the morphology of *Pierolapithecus* reinforces the hypothesis that a number of postcranial similarities of orangutans and African apes may be homoplasies (4).

Moyà-Solà *et al.* (1) conclude that *Pierolapithecus* was less suspensory than are extant apes and that suspensory adaptations in late Miocene and living apes are largely homoplasious. This interpretation is based on the shorter fingers and more dorsally oriented metacarpophalangeal joints of *Pierolapithecus* compared with *Dryopithecus* and extant great apes, and less dorsally placed vertebral transverse processes. Although these morphologies differ from those seen in extant apes, they do not preclude suspensory behavior. The fundamentally reorganized hominoid-like torso and wrist seen in *Pierolapithecus* is associated with

both climbing and suspension in extant hominoids (5, 6). Although admittedly not identical to those of extant apes, the *Pierolapithecus* vertebrae and ribs resemble those of hylobatids, and so do not suggest limited suspensory behavior (5). The proximal and intermediate phalanges of *Pierolapithecus* are curved and bear strong attachments for the flexor tendon sheaths, also consistent with climbing and suspension. The incomplete preservation of the hand phalanges makes it difficult to be certain from which digital ray the specimens in figure 4 come (1). If they are not from ray 3, the comparison to ray 3 of *Dryopithecus*, the longest and most curved, may be misleading and could at least partly account for the shorter length and lower curvature.

We agree that the postcrania overall suggest that *Pierolapithecus* had a unique positional repertoire. We think, however, that the evidence suggests that this repertoire included climbing and suspension and a limited amount of palmigrady. Changes seen in later hominoids may represent further specialization for forelimb-dominated below-branch arboreality

Table 1. Characters supporting the position of *Pierolapithecus* in Fig. 1.

<i>Pierolapithecus</i> as the sister clade to <i>Dryopithecus</i>	
	low radial lunate/scaphoid angle
	narrow I ¹
	rounded supraorbital region
<i>Pierolapithecus</i> as a hominine (These are characters at the hominine node that includes <i>Pierolapithecus</i> , although most of them are not actually known to us for <i>Pierolapithecus</i> .)	
	concavoconvex centrale facet on capitate
	biconvex alveolar premaxilla
	broad nasal aperture base
	horizontal frontal squama
	broad temporal fossa
	long neurocranium
	fused articular and tympanic temporal
	lacrimal fossa visible
	small articular tubercle
Crown hominids (with <i>Pierolapithecus</i> as a hominine) (These are characters at the hominid node that includes <i>Pierolapithecus</i> as a hominine, although most of them are not actually known to us for <i>Pierolapithecus</i> .)	
	capitate head intermediate breadth
	no I ² cingulum
	P ₃ mesiodistal beak present
	high P ₄ talonid
	large maxillary sinus
	high maxillary sinus floor
	long neurocranium
	maxillary sinus anterior to the canine alveolus
	deep alveolar process
	high zygomatic root
	labiolingually large lower incisors

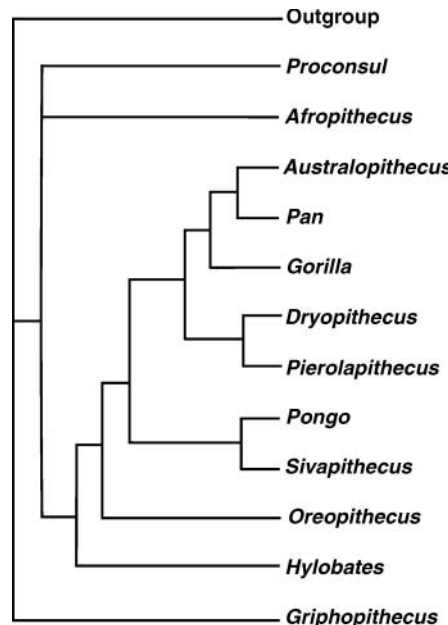


Fig. 1. Cladogram representing the single most parsimonious phylogenetic hypothesis retrieved by adding 96 characters known for *Pierolapithecus* to a morphological data matrix modified from (2). Support for *Pierolapithecus* as a hominine is strong, but support for its being a sister clade to *Dryopithecus* is less so. We conclude that *Pierolapithecus* is near the base of the hominine clade.

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coupled with large body size and abandonment of palmigrady. We commend Moyà-Solà *et al.* on this astonishing discovery and look forward to further analysis of this important fossil.

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7. We are grateful to an anonymous reviewer for comments that improved this contribution. This research was funded by the University of Toronto, the University of Missouri, the L. S. B. Leakey Foundation, and the Natural Sciences and Engineering Research Council of Canada.

1 December 2004; accepted 15 March 2005
10.1126/science.1108139