

Response to Comment on "Pierolapithecus catalaunicus, a New Middle Miocene Great Ape from Spain"

Uncertainties regarding phylogenetic affinities among fossil hominoids are still considerable and result from both the pervasive nature of homoplasy and the fragmentary nature of available fossil remains (1). The intrinsic difficulties of the material, as well as methodological problems, may distort the results of phylogenetic analyses. Thus, parsimony-based cladistic analyses may fail to reveal the true phylogenetic relationships as shown, for instance, through a cladistic test of the firmly established phylogeny of extant hominoids (2). One of the main problems with the assumed objective cladistic methodology is that it depends on the author's previous character selection, which is subjective by its very nature. Another problem emerges from the use of large sets of discrete, atomized characters without functional and structural considerations. This is especially problematic when the characters are coded from general descriptions and photographs instead of from the original material, as in the case of the analysis by Begun and Ward (3). Therefore, we consider a cladistic analysis as precipitate as long as the cranial and postcranial remains of *Pierolapithecus* are not described in detail.

Apart from these general considerations, the database of Begun and Ward (3) shows serious flaws. Among the nine characters claimed to support the position of *Pierolapithecus* as a hominine [figure 1 in (3)], four are not observable in our specimen (broad temporal fossa, long neurocranium, fused articular and tympanic temporal, and small articular tubercle); one (lacrima fossa visible) is also present in members of the *Pongo* clade [*Lufengpithecus* (4), *Ankarapithecus* (5)] and thus not derived hominine; one is actually a hominid synapomorphy (broad nasal aperture base) (6); and two are definitively not present in *Pierolapithecus* (horizontal frontal squama and concavoconvex centrale facet on capitata) (1). Hence, a discussion on consistency indices is futile, and the hypothesis of a hominine status of *Pierolapithecus* remains unsustainable.

Begun and Ward (3) conclude that the morphology of *Pierolapithecus* does not suggest limited suspensory behavior because (i) the morphology of torso and wrist is associated with both climbing and suspension in extant hominoids and (ii) the uncertain attribution of the phalanges to manual ray 3 might have led

to an underestimation of hand length. The ability to occasionally perform a particular type of locomotion, however, does not necessarily imply an adaptation [an adjustment that fits an organism to exploit a given adaptive zone, assisting its possessor in its existing niche (7)]. The current use that extant organisms make of their morphology should not be mistaken for its evolutionary origin. This is, however, what the authors do when they blend the two classes of characters that are actually present in extant apes but that do not have the same importance for the ability to perform suspensory behaviors. Although relative hand length is an essential trait that clearly separates apes specialized for below-branch arboreality from those that are more generalized (Fig. 1), no such features are found in vertebrae, ribs, or wrist that would distinguish suspensory apes from more generalized ones. Here, Begun and Ward misinterpret our conclusions (1), which are not based on vertebral morphology but on hand length only. Moreover, their argument that in extant hominoids, modern torso and wrist structure is associated with both climbing and suspension is inaccurate, because neither *Gorilla* nor *Homo* practice any type of suspension despite their modern torso and wrist morphology. Their limited

suspensory behavior is however, congruent with their short hands (1). Hand-length estimation for *Pierolapithecus* is based on two phalanges belonging to either the third or the fourth manual ray (in apes the third and fourth phalanges are similar in length; the second and fifth phalanges recovered are much smaller) and the length of the second metacarpal (which is always longer than the third one). Hence, the current material appears to be adequate to estimate hand length with confidence.

The short hands of *Pierolapithecus* (Fig. 1) strongly suggest that suspension did not constitute a major part of its locomotor repertoire despite the orthograde body plan. Orthograde, hence, was originally an adaptation to climbing. If this is correct, the suspensory adaptations of living hominoids must be largely convergent, which would imply a considerable amount of homoplasy in this group. Based on the character combination of *Pierolapithecus*, this hypothesis may help to establish a solid foundation on which to build a reliable phylogeny for Miocene hominoids.

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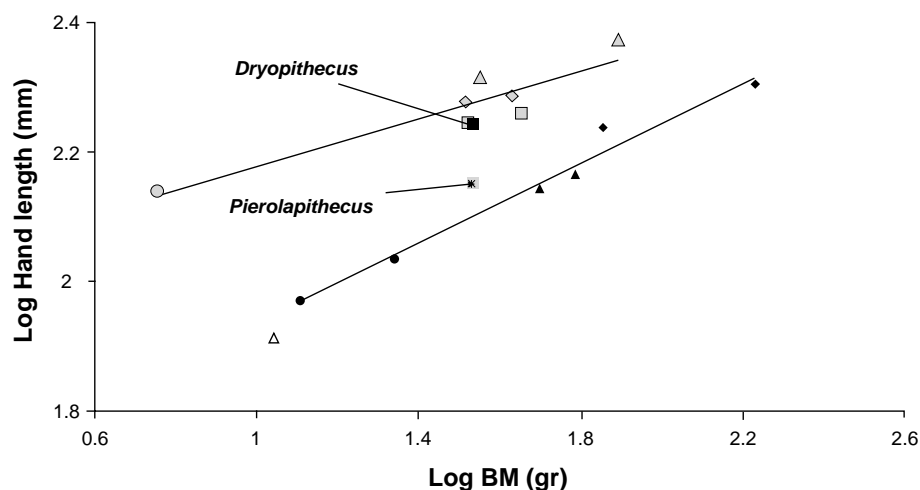


Fig. 1. Bivariate plot of hand length (third metacarpal, proximal, and medial phalanges, log 10, mm) and body mass (log 10, g) of extant apes separated by sex except for *Hylobates* (gray circles, *Hylobates* spp.; gray squares, *Pan paniscus*; gray rhombs, *P. troglodytes*; gray triangles, *P. pygmaeus*; black circles, *Papio* spp.; black triangles, *Homo sapiens*; black rhombs, *G. gorilla*; white triangle, *Proconsul heseloni*). The hand length of *D. laietanus* CLI-18800 individual (8) fits the suspensory extant ape regression, whereas *P. catalaunicus* is close to the nonsuspensory primates. Body mass estimation of *P. catalaunicus* and *D. laietanus* from (1) and (8).

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References and Notes

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9. This study has been supported by Departament d'Universitats, Recerca i Societat de l'Informació (grant 2003 FI 00083), Cessa Gestión de Residuos, Fundació La Caixa, and Fundación Conjunto Paleontológico de Teruel. The support of the Researching Hominid Origins Initiative (RHOI-HOMINID-NSF-BCS-0321893) is gratefully acknowledged.

29 December 2004; accepted 15 March 2005
10.1126/science.1108433