

Pierolapithecus catalaunicus, a New Middle Miocene Great Ape from Spain

Salvador Moyà-Solà,^{1*} Meike Köhler,¹ David M. Alba,^{1,2}
Isaac Casanovas-Vilar,¹ Jordi Galindo²

We describe a partial skeleton with facial cranium of *Pierolapithecus catalaunicus* gen. et sp. nov., a new Middle Miocene (12.5 to 13 million years ago) ape from Barranc de Can Vila 1 (Barcelona, Spain). It is the first known individual of this age that combines well-preserved cranial, dental, and postcranial material. The thorax, lumbar region, and wrist provide evidence of modern ape-like orthograde body design, and the facial morphology includes the basic derived great ape features. The new skeleton reveals that early great apes retained primitive monkeylike characters associated with a derived body structure that permits upright postures of the trunk. *Pierolapithecus*, hence, does not fit the theoretical model that predicts that all characters shared by extant great apes were present in their last common ancestor, but instead points to a large amount of homoplasy in ape evolution. The overall pattern suggests that *Pierolapithecus* is probably close to the last common ancestor of great apes and humans.

Anatomical and molecular data indicate that extant great apes (orangutans, bonobos, common chimpanzees, and gorillas) and humans form a monophyletic group of primates sharing a common ancestor (1). Present available evidence based on molecular information suggests that the divergence between great apes and gibbons occurred at the end of the Early Miocene or during the Middle Miocene, depending on the calibration point selected (1–3). In spite of important recent discoveries and interpretations of a number of Early and Middle Miocene taxa such as *Kenyapithecus* (4), *Morotopithecus* (5), *Equatorius* (6), and *Nacholapithecus* (7), the nature of the last common ancestor of extant great apes and humans is in doubt, and the relationships between most Miocene hominoids and extant forms are a matter of ongoing debate (1). Here we report the discovery of a Middle Miocene [12.5 to 13 million years ago (Ma)] partial hominoid skeleton at a new locality, Barranc de Can Vila 1 (BCV1) (Hostalets de Pierola, Barcelona, Spain). It is the first known hominoid individual of this stratigraphic age associating well-preserved cranial, dental, and postcranial material. It thus promises to contribute substantially to our understanding of the origin of extant great apes and humans.

Systematics. Order Primates Linnaeus, 1758. Suborder Anthroipoidea Mivart, 1864. Superfamily Hominoidea Gray, 1825. Family Hominidae Gray, 1825. *Pierolapithecus* gen. nov. **Type species:** *P. catalaunicus* gen. et sp. nov. **Etymology:** Refers to the village close to the site, Els Hostalets de Pierola. **Generic diagnosis:** As for the type species. *P. catalaunicus* gen. et sp. nov. **Holotype:** A partial skeleton of a single adult male individual composed of 83 bones or identifiable fragments [specimen number IPS-21350, housed in the Institut de Paleontologia M. Crusafont (Fig. 1)] with splanchnocranium; left and right maxillae, all cheek teeth, maxillae with both canines and right central incisor, nasals, both zygomatics, lacrimals, and a partial frontal bone; carpals, metacarpals, and several manual phalanges of both hands, tarsals, metatarsals and pedal phalanges, the distal epiphysis of the right patella, the left radius, several long bone diaphyses, two pelvic fragments, three vertebrae, two complete ribs, and 12 other large rib fragments (8). **Etymology:** *catalaunicus* refers to Catalunya (Catalonia). **Type locality:** BCV1 (Els Hostalets de Pierola, Barcelona, Spain). **Geological age and stratigraphic position:** The lowermost part of the MN 7/8 biostratigraphic unit (Middle Miocene, between 12.5 and 13 Ma) (9).

Species diagnosis. Face with the frontal processes of the maxillae, the nasals, and the orbits on the same plane. Flat nasals, projecting anteriorly beneath the level of the lower orbital rim. Low face with glabella situated posteriorly (10). Thin superciliary arches. Rhinion above

P4/ (10). High zygomatic root situated anteriorly at the level of M1/ (10). High nasoalveolar clivus. Posterior border of the incisive foramen located at the level of P3/. Short, wide, and deep palate. Wide nasal aperture, widest close to the base. Wide interorbital distance. Laterally expanded zygomatics. P3/ of similar size to P4/, with reduced cusp heteromorphy. Elongated molars, except for M3/. Upper molars and premolars without cingula. Peripheral position of lingual cusps in upper molars. Large M2/ and small M3/. Large, low-crowned, and compressed upper canine. Low-crowned and procumbent I1/. Strong rib curvature forming a wide and anteroposteriorly compressed thorax. Large and robust clavicle. Mid-lumbar vertebra lacks ventral keel; robust, wide, and short pedicles of the neural arch; spinous processes oriented slightly caudally; transverse processes insert at the junction between pedicle and body. Transverse process of the last lumbar vertebra arises from the pedicle and is oriented dorsally. Short metacarpals and phalanges. Unfused os centrale. Small triquetrum that does not articulate with ulnar styloid, with crevice for meniscus attachment and pisiform facet shifted distally.

Differential diagnosis. *Pierolapithecus* differs from all known Late Miocene Eurasian hominoids by having a less orthognathous face with a low and posteriorly situated glabella, by the position of the zygomatic root over M1/, by the relative proportions of the upper molars, and by the procumbent I1/. *Pierolapithecus* differs from *Griphopithecus* by the complete lack of cingula, by the long and narrow upper molars, and by the marginal position of lingual cusps on molars. *Pierolapithecus* differs from all known Early and Middle Miocene African hominoids by high zygomatic roots, a wide nasal aperture, a deep palate, flat nasals, the relative proportions of the teeth, and the lack of cingula; and from afropithecids by reduced cusp heteromorphy in the upper premolars.

Description and comparisons: The skull. Considering the stratigraphic age and the geographic location of the new finding, it is of great interest to compare *Pierolapithecus* with the genus *Dryopithecus*, present in the latest Middle and in the Late Miocene of Europe (11, 12). *Pierolapithecus* differs from all species currently included in the genus *Dryopithecus* by the relative size of the upper molars (M2/ > M1/ > M; not known for *D. fontani*), in particular the association of a large M2/ with a small M3/, by the larger, low-crowned, and laterally compressed canines, and the larger, low-crowned, spatulate, and more procumbent central incisor (Table 1). The facial anatomy is completely different

¹Institut de Paleontologia M. Crusafont, Escola Industrial 23, Sabadell, Barcelona 08201, Spain. ²Palaeotheria, S.C.P. Provençals 5, 2^a, 1^a, Barcelona 08019, Spain.

*To whom correspondence should be addressed. E-mail: moyass@diba.es

from that of *Dryopithecus*. In lateral view, the face of *Pierolapithecus* (Fig. 2) is low dorsoventrally, with the glabella situated

posteriorly at the level of M3/, contrasting with the more orthognathous face of *Dryopithecus*, in which the glabella is situated

higher and more anteriorly with respect to the level of the teeth rows (12, 13). *Pierolapithecus* has a relatively shorter and wider palate than *Dryopithecus*, and the zygomatic roots are situated more anteriorly (above M1/) than in *Dryopithecus* (above M2/).

In spite of the important differences in facial anatomy, both taxa share a set of derived features such as the frontal processes of the maxillae, the nasals, and the orbits on a same plane; flat nasals that project anteriorly beneath the level of the lower orbital rims, a high zygomatic root, a high nasoalveolar clivus, a deep palate, and a broad nasal aperture widest close to the base. This facial anatomy characterizes extant great apes and must be considered to be shared derived. In the fossil record, these characters are known only in *Pierolapithecus*, *Dryopithecus* (11, 12), *Sivapithecus* (14), *Ankarapithecus* (15), and *Ouranopithecus* (16), but are absent in the known Early and Middle Miocene forms and in gibbons. Thus, *Proconsul* (17), *Afropithecus* (18), and *Morotopithecus* (19) retain a longer muzzle with convex nasals projecting above the lower orbital rim, a primitive catarrhine condition (20). Also the known facial specimen of the Middle Miocene hominoid *Nacholapithecus* (7, 21) shows a primitive, *Proconsul*-like, narrow nasal aperture, low zygomatic roots, and a shallow palate.

Although the overall facial structure of *Pierolapithecus* is great ape-like, it still retains a primitive hominoid sagittal profile. The low face with a posteriorly situated glabella and the frontal squama forming an open angle with the orbital plane provide a primitive sagittal profile in which the nasals form an acute angle with the palate (Fig. 2). This contrasts with the more orthognathous profile observed in Late Miocene hominoids and in extant great apes and resembles that of primitive extant hominoids, the hylobatids, or primitive fossil taxa such as *Afropithecus*. This unexpected association of cranial great ape features with a primitive hominoid facial profile is of considerable importance, as it suggests that the facial anatomy of *Pierolapithecus* could make a good prototype for early great apes.

The postcranial skeleton. The partial skeleton of *Pierolapithecus* provides evidence of the morphology of the thorax, the vertebrae, and the carpal-antebrachial complex, key anatomical parts in any diagnostics of the habitual positional and locomotor behaviors that characterize extant hominoids, and thus sources of important phylogenetic information.

Thoracic shape. Differences in thoracic shape between apes and monkeys are significant, with monkeys having a narrow, deep thorax, whereas apes have a broad, shallow thorax, related to an increase in the range of movement of the upper limbs and a shift of the center of gravity in vertical climbing (22).

Fig. 1. Complete specimens and large bone fragments of the skeleton of *P. catalaunicus* gen. et sp. nov. (specimen IPS-21350). More fragmentary specimens such as smaller rib fragments, isolated joint facets of vertebrae, and other small specimens are not included.

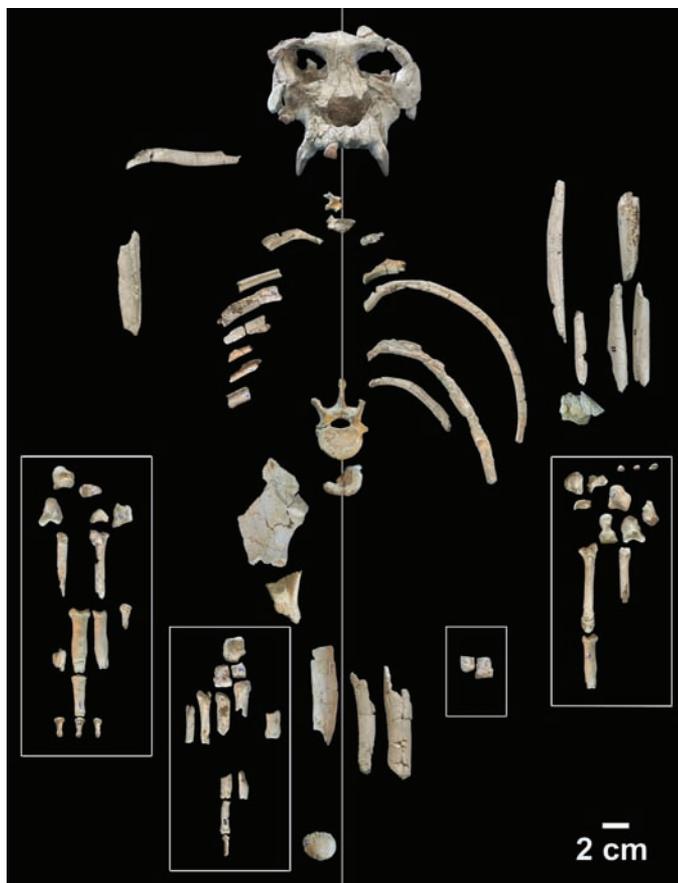
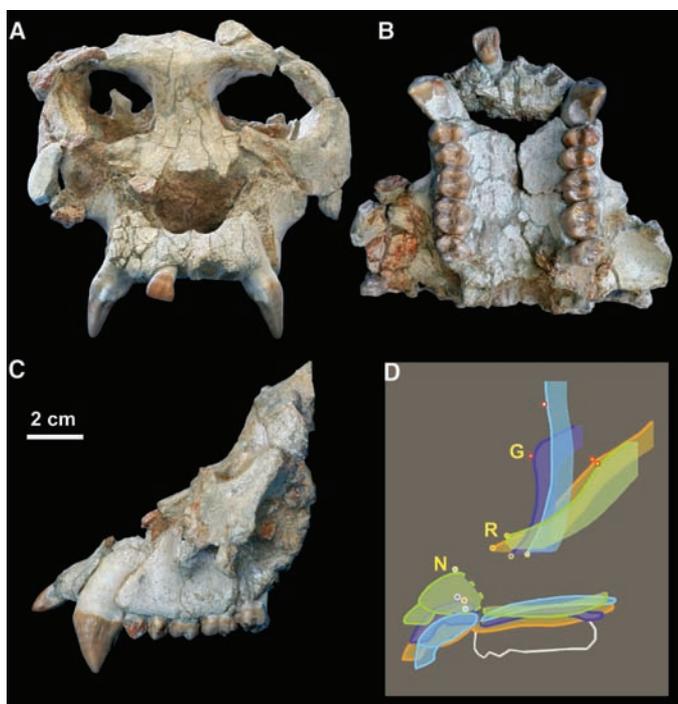


Fig. 2. The face of *Pierolapithecus catalaunicus* (specimen IPS-21350.1). (A) Frontal view (the palate is oriented horizontally). (B) Palatal view. (C) Lateral view. (D) Schematic sections of the skulls of *P. catalaunicus* (green), *Afropithecus turkanensis* (orange) from Kalodirr (Kenya) (KNM-WT 16999), *Ouranopithecus macedoniensis* (dark violet) (XIR-1) from Ravin de la Pluie (Greece), and *Sivapithecus indicus* (light blue) (GSP 15000) from the Siwaliks (Pakistan). The sections of the skulls are superimposed and oriented on the base of the cheek teeth drawn to the same length. The primitive profile of *Pierolapithecus* is more similar to *Afropithecus* than to the Eurasian Late Miocene hominoids (here exemplified by *Ouranopithecus* and *Sivapithecus*, two of the best-preserved skulls from the Eurasian Late Miocene), which are characterized by having more orthognathous faces. N, nasospinal; R, rhinion; G, glabella.



Associated with a broad and shallow thorax in extant hominoids is an increase in rib curvature and angulation. Rib fragments of *Proconsul heseloni* (specimen KNM-RU 2036) (23), in particular specimen N°CI, as well as the first rib of *Equatorius africanus* (6), suggest a narrow and deep monkeylike thorax for these taxa. The hitherto oldest fossil evidence of apelike thoracic morphology comes from Late Miocene genera [ribs of *Oreopithecus* (24, 25) and thoracic vertebrae of *Dryopithecus* (26)]. *Pierolapithecus* now yields the first evidence of a broad and shallow apelike thorax in the Middle Miocene. All complete ribs or rib fragments of *Pierolapithecus* [left rib VIII or IX (specimen IPS 21350-58), proximal right rib III or IV (IPS 21350-66), and proximal left rib XII (IPS 21350-67) (Fig. 3)] show a higher degree of curvature and an increased angulation (Fig. 3) in comparison to the corresponding ribs of monkeys, suggesting a more ventral position of the spinal column in the chest cavity. This constitutes direct evidence that the thorax of *Pierolapithecus* was broader mediolaterally than in monkeys and in known African Miocene hominoids and was close to the pattern of extant apes. This is consistent with a dorsal position of the scapulae on the rib cage inferred from the large size and the chimpanzee-like shape of the clavicle (Fig. 1).

The lumbar vertebrae morphology. The morphology of the lumbar vertebrae of extant apes differs considerably from that of monkeys, most noticeably in the shape of the vertebral body, the shape of the pedicle, and in the insertion and orientation of the transverse processes, characters related to a decrease in mobility in the lumbar region of apes (27). A nearly complete mid-lumbar vertebra (IPS 21350-64) (Fig. 3) of *Pierolapithecus* resembles the ape pattern in the robustness of the wide and short pedicles, the somewhat caudally oriented spinous process, the reduced wedging, and the lack of the distinct ventral keel and the associated concave shape of the ventrolateral sides found in monkeys and in primitive hominoids such as *Proconsul*. The transverse processes do not arise from the wider part of the vertebral body as in monkeys, *Proconsul* (27), and *Nacholapithecus* (7), or from the pedicle as in extant great apes, but instead they insert at an intermediate position at the junction between pedicle and body as in extant *Hylobates* and *Ateles*. The position of the transverse processes of the Early Miocene lumbar vertebra of *Morotopithecus* (27, 28) is described by some (29) as similar to the pattern of *Pongo*. However, when orienting the specimen with the dorsal surface of the vertebral body (the floor of the neural channel) perpendicular to the lens of the camera, it clearly fits the intermediate pattern of *Hylobates* (27) and *Ateles*. In *Pierolapithecus*, the transverse processes of

the mid-lumbar vertebrae insert somewhat lower than in *Morotopithecus* (Fig. 4). Among fossil apes, only a mid-lumbar vertebra of *Dryopithecus* unambiguously shows the pattern of *Pongo*, siamangs, and African apes, in which the transverse processes arise directly from the pedicle (Fig. 4). The last lumbar vertebra of *Pierolapithecus* (IPS 21350-65) is most interesting, as the transverse processes are confluent with the pedicle and oriented upwardly, approaching the modern pattern of extant apes (Fig. 3).

The wrist-antebrachial joint. The wrist-antebrachial character complex of ex-

tant hominoids is unique among primates and is characterized by a nonarticular ulnar styloid process associated with a semilunar meniscus (30, 31). Functionally, this increases the capacity of adduction (ulnar deviation) and supination at the wrist during climbing and suspension (30, 31). Early Miocene *Proconsul* (32) and Middle Miocene *Equatorius* (6) are described as having a long styloid process of the ulna in contact with the proximal carpal row as in monkeys, permitting weight transfer in quadrupedal locomotion through both the radius and the ulna. The 11 carpal bones found in Can Vila com-

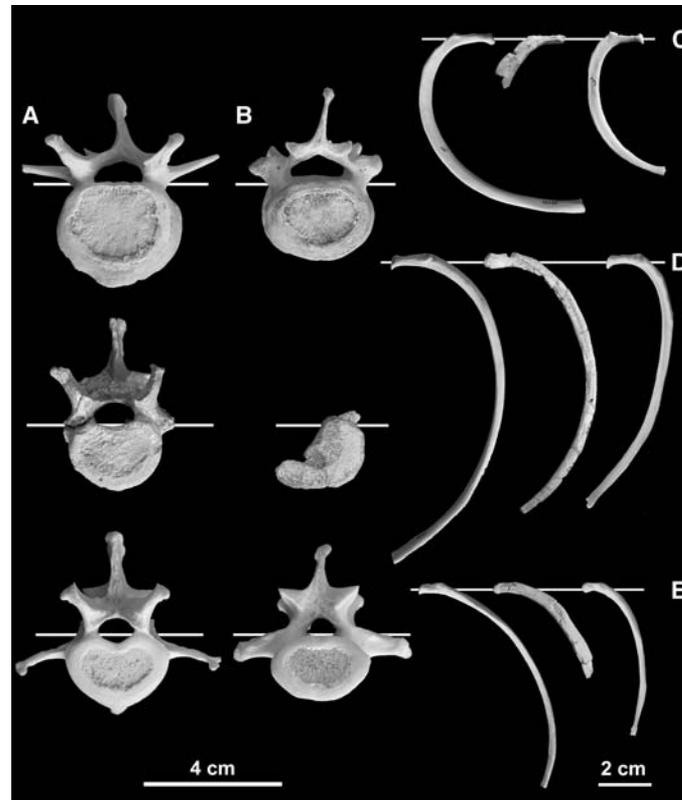


Fig. 3. Ribs and vertebrae of *P. catalaunicus* gen. et sp. nov. (A) Mid-lumbar vertebrae of *Pan* (top), *P. catalaunicus* (IPS-21350.64) (middle), and *Papio* (bottom). (B) Last lumbar vertebrae of *Pan* (top), *P. catalaunicus* (IPS-21350.65) (middle), and *Papio* (bottom); scale bar, 4 cm. (C) III-IV rib of *Pan* (left), *P. catalaunicus* (IPS-21350.59) (middle), and *Papio* (right). (D) VIII-IX rib of *Pan* (left), *P. catalaunicus* (IPS-21350.58) (middle), and *Papio* (right). (E) VIII-IX rib of *Pan* (left), *P. catalaunicus* (IPS-21350.67) (middle), and *Papio* (right). The ribs are oriented with the axis of the costal neck parallel to the horizontal white lines.

Table 1. Dental and selected cranial measurements of the face of *P. catalaunicus* (IPS-21350.1).

	Right maxilla		Left maxilla	
	Length (mm)	Breadth (mm)	Length (mm)	Breadth (mm)
M3/	7.65	10.8	8.4	11.7
M2/	11.25	11.9	10.8	12.2
M1/	10.23	11	10	11.3
P4/	7.10	11.8	7.3	11.7
P3/	7.45	11.7	7.64	11.8
C1/	15.6	11.4	16.2	10.9
I1/	7.6	9		
Length from P3/ to M3/		43.8		44
	<i>Cranial measurements (mm)</i>			
Maximal interorbital distance	20			
External biorbital breadth (estimated)	110			
Height of glabella from alveolar margin	65			
Breadth of the palate at the level of P3/	29.9			
Breadth of the palate at the level of M2/	27.4			
Height of the zygomatic root	19			
Height of the nasoalveolar clivus	13.7			

prise all carpal elements except for the pisiform. Capitate, hamate, lunate, and triquetrum from the left side articulate perfectly (Fig. 5). In comparison with the other carpals, the compact triquetrum is smaller than in monkeys, *Proconsul* (32), and *Hylobates*, but slightly larger than in great apes. It is elongated proximodistally and proximally it has a large, convex, nonarticular summit without any trace of a facet for the styloid process of the ulna. On the distolateral surface, the bone shows a depressed area with small pits and porosity for fibrous attachments homologous to the semi-lunar crevice of the chimpanzee triquetrum for the attachment of the fibrous capsule of the meniscus. The morphology of *Pierolapithecus* differs, however, from that of *Pan* by its wider and more extended crevice (Fig. 5). The facet for the pisiform is large and flat and is shifted distally in comparison with that of monkeys and *Proconsul* (31, 32). The pisiform facet of *Pierolapithecus* makes an angle of 90° with the lateral surface as typically found in apes, contrasting with the obtuse-angled orientation that occurs in monkeys and *Proconsul* (32). The loss of ulnocarpal contact that characterizes extant apes is not known from the fossil record. *Pierolapithecus* thus provides the first evidence that the apelike wrist pattern appeared early in the evolution of apes, dating at least as far back as 13 Ma.

Although *Pierolapithecus* shares the derived wrist-antebrachial morphology with ex-

tant hominoids, the hand shows a series of primitive hominoid characters. Some features of the proximal phalanges, such as the proximal articular facet tilted proximodorsally, extending slightly onto the dorsal surface of the shaft; the large and widely separated plantar tubercles that enclose a deep central depression; and a wide and flat proximal articular surface, indicate the use of the hand in palmigrady, a posture rarely adopted by extant apes. The *Pierolapithecus* phalanges (proximal and middle) are less curved and shorter than those of extant apes and Late Miocene *Dryopithecus* species [*D. laietanus* (26) and *D. brancoi* (33)] (Fig. 4). Taking into account that the body mass of the *Pierolapithecus* specimen is comparable with that of the *D. laietanus* CL1-18800 specimen from Can Llobateres (34), and that the hand length/body mass ratio of *Dryopithecus* CL1-18800 fits the pattern of long hands that is typical of extant apes adapted for suspensory behavior (35), the considerably shorter phalanges of *Pierolapithecus* rather suggest similarities with the short hand pattern of monkeys (Fig. 4).

Discussion and phylogenetic conclusions. The postcranial skeleton of *Pierolapithecus* preserves key morphological regions that provide evidence for an overall mechanically and functionally congruent modern body structure. Thus, the increased capacity of adduction and supination at the wrist, associated with a wide and anteroposteriorly

shallow thorax, the shift of the scapulae onto the back (inferred from the long and chimpanzee-like clavicle), and the stiff lumbar region suggest an emphasis on orthograde locomotor and positional behavior. This body structure is diagnostic for extant apes and humans, and little fossil evidence has been documented. The only relatively complete material suggesting this pattern belongs to *Oreopithecus* (24, 25) and, though less complete, to *Dryopithecus* (26), both of which are Late Miocene genera. Early and Middle Miocene taxa such as *Proconsul*, *Afropithecus*, *Equatorius*, or *Nacholapithecus*, however, still retain the primitive pronograde monkey-like pattern. Hitherto, the only hint of orthograde skeletal structure in the Early/Middle Miocene comes from a few remains of the axial skeleton of Early Miocene *Morotopithecus* (5, 36). However, the facial skeleton of this genus (19) exhibits an overall primitive hominoid pattern, suggesting *Morotopithecus* to be a sister taxon of all extant apes (6).

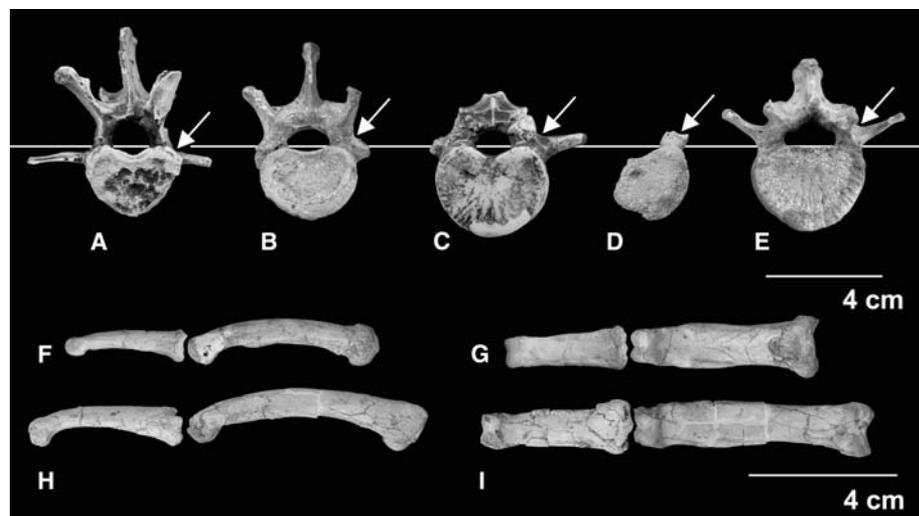


Fig. 4. Comparisons of mid-lumbar vertebrae and medial and proximal phalanges of the third digit. (A to E) Cranial view of mid-lumbar vertebrae. (A) Cast of *Proconsul nyanzae* (specimen KNM-MW 13142-J) from Mfangano Island (Kenya). (B) *P. catalaunicus* (IPS-21350.59). (C) Cast of *Morotopithecus bishopi* (UPM 67.28) from Moroto (Uganda). (D) *D. laietanus* (IPS-18000) from Can Llobateres (Spain). (E) *Pongo pygmaeus*. Specimens are oriented with the dorsal surface of the vertebral body (the floor of the neural channel) perpendicular to the lens of the camera. The arrows show the origin of the transverse processes. In *Proconsul* (A), the transverse processes arise from the wider part of the vertebral body as in monkeys but do not contact the pedicle. In both *Pierolapithecus* (B) and *Morotopithecus* (C), the transverse processes root partially on the uppermost part of the body and partially on the pedicle. Only in *Dryopithecus* (D) do the transverse processes arise from the pedicle as they do in the extant *Pongo* (E). The white horizontal line represents the dorsal limit of the cranial articular surfaces. (F to I) Middle and proximal phalanges of the third digit of *Pierolapithecus* compared with those of *D. laietanus* (IPS-18800). (F) and (H) Lateral view. (G) and (I) Palmar view.

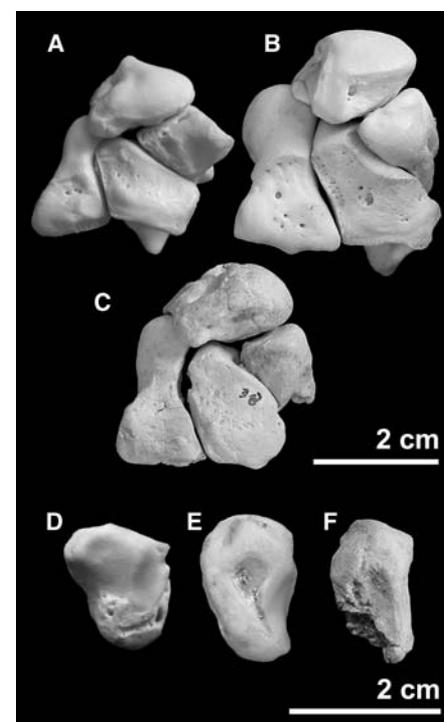


Fig. 5. Comparisons of the carpus of *P. catalaunicus* with that of *Papio* and *Pan*. A dorsal view of the articulated right capitate, hamate, lunate, and triquetrum complex of (A) *Papio* sp., (B) *Pan troglodytes*, and (C) *P. catalaunicus* is shown. Observe the relative large size of the triquetrum and the proximal orientation of the ulnar facet in *Papio*, in comparison with the smaller size and lateral orientation of the triquetrum in *Pan* and *Pierolapithecus*. (D to F) Lateral view of triquetrum in (D) *Papio* sp., (E) *P. troglodytes*, and (F) *P. catalaunicus*. Note the large articular facet for the ulnar styloid process in *Papio* and its absence in *Pan* and in *Pierolapithecus*, where the homologous surface is nonarticular and shows a crevice for the attachment of a meniscus.

Pierolapithecus, on the contrary, shows the basic derived facial pattern of extant great apes. This facial morphology, combined with the large set of modern ape-like postcranial features, strongly suggests that this taxon is an early member of the great ape and humans clade. The overall pattern suggests that *Pierolapithecus* is close to the last common ancestor of great apes and humans (Fig. 6). Recent molecular results coincide with our interpretation, suggesting that the split between hylobatids and great apes took place about 14.9 ± 2 Ma (2) or 14.6 ± 2.6 Ma (3).

Nevertheless, the overall postcranial morphology of *Pierolapithecus* is not completely extant ape-like. Although derived features of the chest, lumbar region, and wrist are clearly modern ape-like, *Pierolapithecus* also retains primitive monkeylike skeletal features (such as short phalanges with palmargrade morphological characters) not present in extant apes. This association of primitive and derived features bears important implications for the reconstruction of modern ape evolution. Thus, *Pierolapithecus* provides evidence that the basic orthograde adaptations are not unequivocally and functionally linked to all features commonly shared by extant apes and claimed to be synapomorphies present in the last common ancestor of the group (1, 37). The primitive morphology of the *Pierolapithecus* hand,

indicating little (if any) suspensory behavior, strongly suggests that the two basic components of extant ape locomotion—vertical climbing and suspension—appeared independently. Thus, modern ape-like below-branch suspensory locomotion is likely to have been acquired later and independently by the extant members of this clade. Hence, adaptations for below-branch suspensory behaviors might have evolved in parallel and repeatedly, leading to a large amount of homoplasy in ape evolution. This premise suggests that vertical climbing with a basic orthograde body design is the original modern ape adaptation, confirming the hypothesis previously suggested by other authors (31, 38).

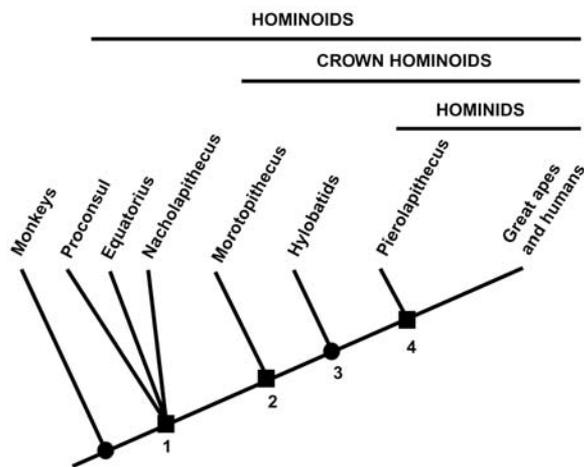
The incompleteness of the fossil material of Miocene hominoids, which yields little evidence of the axial skeleton (1), and the significant occurrence of homoplasy have combined to obscure the early evolution of great apes, leading to the formulation of different, even contradictory, phylogenetic and taxonomic hypotheses. Our finding provides evidence that the association of a basic orthograde postcranial pattern with a great ape-like facial morphology can be traced back to the Middle Miocene. Under the premise that this association identifies a member of the great ape and humans clade, early great apes are recognizable in the fossil record at least as early as the late Middle Miocene. This

new perspective sheds light on two important aspects of hominoid evolution. First, it shows that the known Middle Miocene African taxa are too primitive to be regarded as stem great apes, as has been suggested by some (39). Instead, the new information provided by *Pierolapithecus* lends strong support to recent phylogenetic hypotheses (40) that exclude the Early/Middle Miocene African taxa with pronograde postcranial pattern and primitive facial anatomy (*Afropithecus*, *Kenyapithecus*, *Equatorius*, and *Nacholapithecus*) from the great ape and humans clade, and classifies them as stem hominoids. Second, our finding provides evidence that early great apes are more primitive than inferred from neontological data (1, 37), because it associates primitive hominoid and derived great ape features. This mosaic of characteristics may explain why most of the known Late Miocene taxa apparently fail to show some of the shared derived features that characterize extant members of the great apes, a perception that has led to ongoing debates (1, 12, 26, 39–41) about the high-level phylogenetic relationships between Late Miocene fossil hominoids and extant taxa.

References and Notes

1. D. Pilbeam, *Mol. Phylogenet. Evol.* 5, 155 (1996).
2. S. Kumar, B. Hedges, *Nature* 392, 917 (1998).
3. R. L. Stauffer, A. Walker, O. A. Ryder, M. Lyons-Weiler, S. Hedges, *J. Hered.* 92, 469 (2001).
4. M. L. McCrossin, B. R. Benefit, in *Function, Phylogeny, and Fossils. Miocene Hominoid Evolution and Adaptations*, D. R. Begun, C. V. Ward, M. D. Rose, Eds. (Plenum, New York, 1997), pp. 225–267.
5. D. L. Gebo et al., *Science* 276, 401 (1997).
6. S. Ward, B. Brown, A. Hill, J. Kelley, W. Downs, *Science* 285, 1382 (1999).
7. H. Ishida, Y. Kunimatsu, T. Takano, Y. Nakano, M. Nakatsukasa, *J. Hum. Evol.* 48, 69 (2003).
8. Two lower molars discovered in 1941 (42) in the same area (between Can Vila and Can Mata) were described as a new species of the genus *Sivapithecus*, *S. occidentalis* (43). Later this species was synonymized with *Dryopithecus* (*Hispanopithecus*) *laietanus* (44), an attribution that has been generally accepted. Considering that the two molars are undistinguishable from those of *D. laietanus* and that neither the site (Can Vila) nor the stratigraphic horizon is identifiable, because the area is larger than 2 km² and the stratigraphic sequence is 500 m thick, spanning biozones MN 6 through MN 7/8 (Middle Miocene), the species name *occidentalis* cannot be applied to the new genus and must be considered a nomen dubium (45).
9. Fauna and age of BCV1. The fauna recovered in BCV1 comprises 17 mammalian species. The rich rodent fauna is dominated by cricetids (mainly *Eumyarion* and *Democricetodon*) and also includes several glirids, ground and flying squirrels. This faunal association and the relative abundance of its representatives suggests the existence of a wooded and relatively humid biotope, similar to other localities of the Late Aragonian such as Sant Quirze A. On the basis of the presence of *Democricetodon larteti*, this site is placed in MN 7/8. However, *Democricetodon larteti* from BCV1 is very similar in size and morphology to younger populations of species from the Calatayud-Teruel Basin. The age of these “advanced” populations of the Calatayud-Teruel area is close to 12.5 Ma (46, 47). Thus, on the basis of biostratigraphic data, BCV1 is correlated to the lowermost part of the MN 7/8 zone, between 12.5 and 13 Ma (48). The faunal list is as follows: *Democricetodon larteti*, *Democricetodon gaillardi*, *Eumyarion* aff. *leemani*, *Megacricetodon minor* *debruijii*,

Fig. 6. Cladogram depicting the phylogenetic relationships of Early and Middle Miocene hominoids, with special reference to *P. catalaunicus*. Only those taxa with evidence of the axial skeleton and/or wrist/ulnar joint complex are considered. Therefore, *Afropithecus* does not appear in the cladogram. 1: Absence of tail, medial torsion of the humeral head, low position of the maxillopremaxillary suture/nasal contact, wide anterior palate, and other features discussed in (39). 2: The lumbar vertebra of *Morotopithecus* shows clear affinities with extant apes. This is, however, the only evidence that situates this genus within the crown hominoids. 3: Strong rib curvature forming a wide and anteroposteriorly compressed thorax; long and robust clavicle, scapula situated on the back of the thorax; high intermembral index; ulnar shelf of radius excluding ulnar head from joint, mediolaterally broad radiolunate facet; reduced triquetrum with distal migration of pisiform, reduction of the contact between styloid process and triquetrum; lumbar vertebrae reduced in number, lacking ventral keel, with robust, wide, and short pedicles of the neural arch, caudally oriented spinous processes, and transverse processes that do not arise from the broader part of the vertebral body as in monkeys, nor from the pedicle as in extant great apes, but instead insert at an intermediate position at the junction between pedicle and body; wide ilium. 4: The orthograde body plan of *Pierolapithecus* situates this genus within the crown hominoids. The great ape facial anatomy makes it a sister group of great apes and humans. Short face, with the frontal processes of the maxillae, the nasals, and the orbits in the same plane, and flat nasals that project anteriorly beneath the level of the lower orbital rims; high zygomatic roots, a high nasoalveolar clivus, and a broad nasal aperture widest at the base. Triquetrum not articulating with the ulnar styloid. This clade includes all Late Miocene Eurasian hominoids. (Reported characters for this clade are only those that can be observed in *Pierolapithecus* with the available material.)



- Cricetodon* sp., *Microdyromys complicatus*, *Paragilirulus werenfelsi*, *Glirudinus undosus*, *Muscardinus sansanien-sis*, *Bransatoglis* sp., *Spermophilinus bredai*, *Albanensia albanensis*, *Soricidae* indet., *Erinaceidae* indet., *Deinotherium giganteum*, *Euprox furcatus*, *Dorcatherium* sp., *Listriodon splendens*, *Carnivora* indet.
10. These descriptions are made with the tooth row oriented horizontally.
 11. D. Begun, *Yrbk. Phys. Anthropol.* **37**, 11 (1994).
 12. S. Moyà Solà, M. Köhler, D.M. Alba, in *Hominoid Evolution and Climatic Change in Europe*; Vol. 2: *Phylogeny of the Neogene Hominoid Primates of Eurasia*, L. de Bonis, G. K. Koufos, P. Andrews, Eds. (Cambridge Univ. Press, Cambridge, 2001), pp. 192–215.
 13. L. Kordos, D. R. Begun, *J. Hum. Evol.* **41**, 689 (2002).
 14. D. Pilbeam, *Nature* **295**, 232 (1982).
 15. B. Alpagut et al., *Nature* **382**, 349 (1996).
 16. L. de Bonis, G. Bouvrain, D. Geraads, G. Koufos, *Nature* **345**, 712 (1990).
 17. W. E. Le Gros Clark, L. Leakey, *Fossil Mamm. Afr.* **1**, 1 (1951).
 18. R. E. Leakey, M. G. Leakey, *Nature* **324**, 143 (1986).
 19. M. Pickford, *Hum. Evol.* **17**, 1 (2002).
 20. M. G. Leakey, R. E. Leakey, J. T. Richtsmeier, E. L. Simons, A. C. Walker, *Folia Primatol.* **28**, 519 (1991).
 21. Y. Kunimatsu et al., *J. Hum. Evol.* **46**, 365 (2004).
 22. A. H. Schultz, *Primateology* **4**, 1 (1961).
 23. J. Napier, P. R. Davis, *Br. Mus. Nat. Hist. Fossil Mamm. Afr.* **16**, 1 (1959).
 24. A. H. Schultz, *Z. Morph. Anthropol.* **50**, 136 (1960).
 25. T. Harrison, *J. Hum. Evol.* **15**, 541 (1987).
 26. S. Moyà-Solà, M. Köhler, *Nature* **379**, 156 (1996).
 27. C. V. Ward, *Am. J. Phys. Anthropol.* **92**, 291 (1993).
 28. A. Walker, M. D. Rose, *Nature* **217**, 980 (1968).
 29. W. J. Sanders, B. E. Bodenbender, *J. Hum. Evol.* **26**, 203 (1993).
 30. O. J. Lewis, in *Primate Locomotion*, F. A. Jenkins, Ed. (Academic Press, New York, 1974), pp. 143–169.
 31. E. Sarmiento, *Int. J. Primatol.* **9**, 281 (1988).
 32. C. Beard, M. F. Teaford, M. Walker, *Folia Primatol.* **47**, 97 (1986).
 33. D. R. Begun, *J. Hum. Evol.* **24**, 737 (1993).
 34. Body mass (BM) estimates were based on the regressions (29) derived for the following measurements, taken on the mid-lumbar vertebra (level L VI): vertebral body width at the cranial end = 30.0 mm, vertebral body height at the cranial end = 21.7 mm, caudal surface area of the vertebral body = 5.7 cm² for nonhuman catarrhines, and vertebral body length at the ventral margin = 22.0 mm for nonhuman hominoids. BM estimates derived from these measurements (23, 32, 24 and 42 kg, respectively) give an average value for the body mass of the *Pierolapithecus* specimen of about 30 kg. Results from dental parameters suggest that the new taxon would be approximately of the same size as IPS18000 *D. laietanus* from Can Llobateres, because both provide the same postcanine tooth row length. BM estimation from M1/ area (averaging left and right measurements) on the basis of a regression equation for males and females separately (49, 50) yields a value of 32 kg for *Pierolapithecus*, which is somewhat larger than the 29 kg obtained for the IPS18800 *Dryopithecus* specimen. 34 kg was obtained for specimen IPS18000 on the basis of femoral head estimators (26), a parameter not available for the BCV1 skeleton. For this individual, we thus propose a BM between 30 and 35 kg, which is very similar to that of the *D. laietanus* male skeleton of Can Llobateres (Spain) (26).
 35. S. Moyà-Solà, M. Köhler, L. Rook, *Proc. Natl. Acad. Sci. U.S.A.* **96**, 313 (1999).
 36. N. M. Young, L. MacLatchy, *J. Hum. Evol.* **46**, 163 (2003).
 37. T. Harrison, *J. Hum. Evol.* **16**, 41 (1987).
 38. J. Fleagle, *Folia Primatol.* **26**, 245 (1976).
 39. P. Andrews, *Nature* **360**, 641 (1992).
 40. D. R. Begun, C. V. Ward, M. D. Rose, in *Function, Phylogeny, and Fossils. Miocene Hominoid Evolution and Adaptations*, D. R. Begun, C. V. Ward, M. D. Rose, Eds. (Plenum, New York, 1997), pp. 389–415.
 41. D. Pilbeam, in *Function, Phylogeny, and Fossils. Miocene Hominoid Evolution and Adaptations*, D. R. Begun, C. V. Ward, M. D. Rose, Eds. (Plenum, New York, 1997), pp. 13–28.
 42. J. F. Villalta, M. Crusafont, *Bol. Inst. Geol. Min. Esp.* **55**, 129 (1941).

43. J. F. Villalta, M. Crusafont, *Not. Com. Inst. Geol. Min. Esp.* **13**, 1 (1944).
44. M. Crusafont, J. Hürzeler, *C. R. Acad. Sci. Paris* **252**, 562 (1961).
45. A. Mones, *J. Vert. Paleontol.* **9**, 2, 232 (1989).
46. R. Daams, A. J. van der Meulen, M. A. Alvarez-Sierra, P. Peláez-Campomanes, W. Krijgsman, *Earth Planet. Sci. Lett.* **165**, 287 (1999).
47. A. J. van der Meulen, P. Peláez-Campomanes, R. Daams, *Coloquios Paleontol. V.E.1*, 385 (2003).
48. J. Agustí et al., *Earth Sci. Rev.* **52**, 247 (2001).
49. P. D. Gingerich, B. H. Smith, K. Rosenberg, *Am. J. Phys. Anthropol.* **58**, 81 (1982).
50. R. J. Smith, W. L. Jungers, *J. Hum. Evol.* **32**, 523 (1997).
51. We thank M. Brunet, F. K. Howell, B. Senut, M. Pickford, D. Pilbeam, L. Rook, T. D. White, and two anonymous referees for comments on the manuscript and for improving style and spelling. We thank P. Andrews for casts of Pasalar specimens. This study has been

supported by the Diputació de Barcelona, Departaments d'Universitats Recerca i Societat de l'Informació (grant 2003 FI 00083) and Cultura de la Generalitat de Catalunya, Cespa Gestió de Residuos, Ministerio de Ciencia y Tecnología (project no. BTE2001-1076), Fundació La Caixa and Fundació Conjunta Paleontològica de Teruel. The support of the Researching Hominid Origins Initiative (RHOL-HOMINID-NSF-BCS-0321893) is gratefully acknowledged. We also acknowledge the collaboration of the Ajuntament dels Hostalets de Pierola. We thank I. Pellejero and S. Val for the excellent restoration of the specimens and À. Blanco, L. Checa, C. Rotgers, and B. Poza for their enthusiasm and collaboration during excavation. We thank W. Kelson for improving the English. The first two authors dedicate this work to the memory of the late J. Pons, an enthusiastic paleontologist and good friend.

22 July 2004; accepted 18 October 2004

The 1.2-Megabase Genome Sequence of Mimivirus

Didier Raoult,^{1*} Stéphane Audic,² Catherine Robert,¹ Chantal Abergel,² Patricia Renesto,¹ Hiroyuki Ogata,² Bernard La Scola,¹ Marie Suzan,¹ Jean-Michel Claverie^{2*}

We recently reported the discovery and preliminary characterization of Mimivirus, the largest known virus, with a 400-nanometer particle size comparable to mycoplasma. Mimivirus is a double-stranded DNA virus growing in amoebae. We now present its 1,181,404-base pair genome sequence, consisting of 1262 putative open reading frames, 10% of which exhibit a similarity to proteins of known functions. In addition to exceptional genome size, Mimivirus exhibits many features that distinguish it from other nucleocytoplasmic large DNA viruses. The most unexpected is the presence of numerous genes encoding central protein-translation components, including four amino-acyl transfer RNA synthetases, peptide release factor 1, translation elongation factor EF-TU, and translation initiation factor 1. The genome also exhibits six tRNAs. Other notable features include the presence of both type I and type II topoisomerases, components of all DNA repair pathways, many polysaccharide synthesis enzymes, and one intein-containing gene. The size and complexity of the Mimivirus genome challenge the established frontier between viruses and parasitic cellular organisms. This new sequence data might help shed a new light on the origin of DNA viruses and their role in the early evolution of eukaryotes.

Mimivirus, the sole member of the newly proposed *Mimiviridae* family of nucleocytoplasmic large DNA viruses (NCLDVs) was recently isolated from amoebae growing in the water of a cooling tower of a hospital in Bradford, England, in the context of pneumonia outbreak (1). The study of Mimivirus grown in *Acanthamoeba polyphaga* revealed a mature particle with the characteristic morphology of an icosahedral capsid with a diameter of at least 400 nm. Such a virion size comparable to that of a mycoplasma cell

makes Mimivirus the largest virus identified so far. A phylogenetic study with preliminary sequence data from a handful of conserved viral genes tentatively classified Mimivirus in a new independent branch of NCLDVs (1). The sequencing of the genome of Mimivirus was undertaken to determine its complete gene content, to predict some of its physiology, to confirm its phylogenetic position among known viruses, and to gain insight on the origin of NCLDVs.

Overall Genome Structure

The Mimivirus genome (Fig. 1) was assembled (2) into a contiguous linear sequence of 1,181,404 base pairs (bp), significantly larger than our initial conservative estimate of 800 kbp (1). The size and linear structure of the genome were confirmed by restriction digests and pulsed-field gel electrophoresis. Two inverted repeats of about 900 nucleotides are

¹Unité des Rickettsies, Faculté de Médecine, CNRS UMR6020, Université de la Méditerranée, 13385 Marseille Cedex 05, France. ²Information Génomique et Structurale (IGS), CNRS UPR2589, Institut de Biologie Structurale et Microbiologie, 13402 Marseille Cedex 20, France.

*To whom correspondence should be addressed. E-mail: Jean-Michel.Claverie@igs.cnrs-mrs.fr (J.-M.C.); Didier.Raoult@medecine.univ-mrs.fr (D.R.)