Title: Miocene small-bodied ape from Eurasia sheds light on hominoid evolution

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**Abstract**:

Miocene small-bodied anthropoid primates from Africa and Eurasia are generally considered to precede the divergence between extant catarrhines, i.e., hominoids (apes and humans) and Old World monkeys, being more primitive than the stem ape *Proconsul*. Here we describe *Pliobates cataloniae* gen. et sp. nov., a small-bodied (4-5 kg) primate from the Iberian Miocene (11.6 million years ago [Ma]) that displays a mosaic of primitive characteristics coupled with multiple cranial and postcranial shared-derived features of extant hominoids. Our cladistic analyses reveal *Pliobates* as a stem hominoid more derived than previously-known small catarrhines and *Proconsul*. This forces us to re-evaluate the role played by small-bodied catarrhines in ape evolution and provides key insight into the last common ancestor of hylobatids (gibbons) and hominids (great apes and humans).

**One Sentence Summary:** We describe a new small-bodied Miocene ape that shares multiple derived features with extant hominoids.

**Main Text:**

Apes and humans (hominoids) diverged from Old World monkeys (cercopithecoids) by the Oligocene (≥25 Ma) (*1, 2*) and subsequently diversified in both Africa and Eurasia during Miocene (23-5 Ma) (*3*). They are currently represented by crown hominoids (*4*), i.e., the small-bodied hylobatids (gibbons and siamangs) and the larger-bodied hominids (great apes and humans), which diverged by the Early Miocene ca. 17 Ma (*1*). Reconstructing the ancestral morphotype from which extant apes and humans evolved is a challenging task (*5-7*), given the mosaic nature of evolution (*8*), the confounding effects of independently-evolved features (homoplasy) (*5, 9*), the conflicting evidence provided by Miocene great apes (*6, 9*), and the incomplete and fragmentary nature of the hominoid fossil record [notably, the virtual lack of fossil gibbons until at least the latest Miocene (*10, 11*)]. Thus, although extant hominoids share numerous derived features, particularly in the trunk and forelimb, it is uncertain to what extent these characteristics were inherited from their last common ancestor, whose morphotype is still under discussion (*5, 6, 11, 12*).

Earliest hypotheses postulated a small-bodied gibbon-like ancestor (*13*), and for many years fossil catarrhines (anthropoid primates from Africa and Eurasia) of small body size were customarily considered broadly ancestral to gibbons (*14, 15*). Nowadays, hylobatids are generally considered a specialized and probably dwarfed lineage, evolved from a larger and more great ape-like last common ancestor with hominids (*6, 16*). This is because known small-bodied extinct catarrhines, such as the African dendropithecids (including at least *Dendropithecus*, *Simiolus* and *Micropithecus*)and the Eurasian pliopithecoids (*Pliopithecus*, *Epipliopithecus* and allied genera), lack most of the synapomorphies (shared-derived features) of crown catarrhines (*17-21*). Even dendropithecids, more derived than pliopithecoids and currently interpreted by some authors as stem hominoids (preceding the hylobatid-hominid divergence) (*3, 8, 22*), are considered as more basal than the stem ape *Proconsul* (*8, 21-23*). Here we describe a new Miocene small-bodied ape from Spain that, in some respects, primitively resembles previously-known small-bodied catarrhines such as dendropithecids, but which strikingly differs from them and from *Proconsul* by displaying multiple crown-hominoid derived features. This mosaic provides key insight into ape evolution by forcing us to re-evaluate the role played by small-bodied catarrhines in the emergence of crown hominoids.

**Systematic paleontology**

Order Primates Linnaeus, 1758. Suborder Haplorrhini Pocock, 1918. Infraorder Anthropoidea Mivart, 1864. Parvorder Catarrhini É. Geoffroy Saint-Hilaire, 1812. Superfamily Hominoidea Gray, 1821. Family Pliobatidae fam. nov.; type genus: *Pliobates* gen. nov., whose diagnosis is as for its type and only included species (*16*):

**Pliobates cataloniae *gen. et sp. nov.***

Holotype: IPS58443, partial skeleton with associated skull (Figs. 1-4; figs. S1-S2; movie S1), housed at the Institut Català de Paleontologia Miquel Crusafont (Sabadell, Spain). This skeleton is composed of 70 bones and bone fragments (table S1) found in close spatial association, and attributed to a single adult female individual (based on the small canine alveolus), with an estimated body mass of 4-5 kg (text S1; tables S2-S5). It includes large portions of the cranium with postcanine maxillary teeth (see measurements in Table 1), a mandibular fragment, a partial left forelimb (nearly complete humerus, radius, partial ulna, carpals and bones of the manual rays), more fragmentary elements of the right forelimb, and bones from the hind limb.

Type locality:ACM/C8-A4 (els Hostalets de Pierola, Catalonia, Spain), in the Abocador de Can Mata (ACM) stratigraphic series (Vallès-Penedès Basin, NE Iberian Peninsula).

Age, stratigraphic position and distribution: Only known from the type locality, which has an estimated age of 11.6 Ma (Middle/Late Miocene boundary) and is thus somewhat younger than all the ACM hominoid and pliopithecoid-bearing localities (*9, 25-28*), with those that have previously yielded pliopithecid remains being dated to 11.7–11.9 Ma [updated from refs. (*27, 28*)].

Etymology: Genus name from the Latin *plio-* (in turn, from the Greek, meaning ‘greater in extent’) and from the Greek *bates* (meaning ‘the one that walks or haunts’). The name is a contraction of genus names *Pliopithecus* (‘more ape’) and *Hylobates* (‘the one that walks in the woods or in the trees’), in allusion to the small body size and the mosaic of primitive (stem catarrhine-like) and derived (crown hominoid) features displayed by the new taxon. Species epithet is the genitive of the female substantive ‘Catalonia’, the Latin name of Catalunya (the country in which the type locality is situated).

***Diagnosis***

Small-bodied catarrhine primate (4-5 kg of estimated female body mass). Dental formula 2.1.2.3. Female upper canines moderately compressed. Upper cheek teeth low-crowned and with subpyramidal, moderately peripheral and inflated cusps. Upper premolars relatively broad and ovoid, P4 smaller than P3, both with heteromorphic cusps, a markedly convex lingual contour and a distinct lingual cingulum (more developed in the P4), a distinct transverse crest separating the restricted mesial fovea from the extensive trigon basin, and the postparacrista forming an abrupt angle with the distal marginal ridge. Upper molars only moderately broader than long, with markedly convex lingual profiles; buccal cusps quite peripheral and buccal cingula discontinuous; lingual cingula relatively well-developed, shelf-like and C-shaped, but not surrounding the hypocone (which is distinct and more peripheral than the protocone); mesial fovea restricted, with an obliquely directed preprotocrista, and trigon basin extensive, being separated by a continuous crista obliqua from the slightly smaller distal fovea, which displays no hypocone-metacone crest. M2 slightly larger than the M1, and M3 shorter and trapezoidal (due to the oblique buccal margin, with a centrally situated metacone and a rudimentary hypocone).

Face small but with a distinct snout, the anterior portion of the nasals being almost parallel to the palate. Maxillary sinus large and frontal sinus present but small. Nasal aperture narrow. Nasoalveolar clivus short, with an open palatine fenestra. Anteriorly slightly narrow palate with somewhat convergent upper tooth rows. Zygomatic root moderately high. Orbits subcircular, large and frontated, with telescopic orbital rims located over the P4. Estimated cranial capacity (69-75 cm3) indicating a monkey-like degree of encephalization. External auditory meatus tubular but short and not completely ossified, with a V-shaped end and its anterior portion fused with the postglenoid process. Carotid foramen perforating the bulla posterodistally, and carotid canal horizontally and anteriorly oriented. Spinosum and postglenoid foramina absent. Jugular foramen large and ventrally visible.

Humerus without entepicondylar foramen and capitular tail, with a well-developed capitulum, and a narrow and deep zona conoidea. Radial head rounded and not very tilted, with a markedly bevelled surface for articulation with the humeral zona conoidea, the articular surface for the ulnar radial notch extending along a large portion of the radial head, and a laterally-facing bicipital tuberosity. Distal radioulnar joint fully diarthrodial, with an expanded and two-faceted semilunar articulation on the ulnar head, and a partially developed ulnar fovea. Ulnar styloid process with reduced girth and not articulating with the short pisiform. Triquetrum small and with a reduced articular surface for the ulnar styloid process. Hamate relatively long proximodistally, with a steep triquetrum facet, a relatively large head and a distally-projecting hamulus. Capitate with a relatively small and oblong head, and a divided facet for the second metacarpal on its radial side.

***Differential diagnosis***

The new taxon differs from pliopithecoids and dendropithecids in the lack of humeral capitular tail, the hominoid-like proximal radial morphology, the expanded ulnar head with a two-faceted semilunar articulation, and the partially-developed ulnar fovea. It further differs from these taxa and proconsulids in the more hominoid-like carpal morphology (including the lack of a pisiform facet for the styloid process, a capitate facet for the second metacarpal divided by a deep ligamentary notch, and a distally-projecting hamulus in the hamate), and particularly from pliopithecoids in the overall larger muzzle and more horizontal nasals anteriorly, some details of the upper molars, and (at least compared to *Epipliopithecus*)the lack of entepicondylar foramen in the humerus. It also differs from all the above-mentioned taxa in the fusion between the ectotympanic and the postglenoid process, and from them as well as hominids in the horizontal and anteriorly-oriented carotid canal. Finally, it differs from crown hominoids (hylobatids and hominids) in the incompletely ossified ectotympanic, and the more primitive dentition and forelimb morphology (particularly in the humeroulnar articulation).

**Description and comparisons**

Although the lack of lower dentition precludes comparisons with some taxa, the upper cheek teeth of *Pliobates* (Table 1) generally resemble those of other small-bodied Miocene catarrhines in both occlusal morphology and proportions (figs. S3-S4). In contrast, they display a more primitive morphology than extant hominoids, including the similarly-sized hylobatids. The latter possess more elongated cheek teeth with more peripheralized cusps, less-developed cingula and a much more extensive central fovea. Compared to Miocene small-bodied catarrhines from Eurasia and Africa (fig. S3), the upper molars of *Pliobates* more closely resemble in several features those of the dendropithecid *Micropithecus* (*21, 29-31*), including the markedly convex lingual profiles and moderately-developed buccal cingula (albeit to a lesser extent than in *Micropithecus*), the C-shaped lingual cingulum mostly restricted to the protocone (not surrounding the hypocone), the well-developed and lingually-situated hypocone, and the relatively narrow M1 and M2. Nevertheless, *Pliobates* differs in several features from *Micropithecus*, which displays more reduced buccal cingula, a hypocone-metacone crest, and a relatively longer and less trapezoidal M3. The dentition of *Pliobates* more clearly differs from *Epipliopithecus* and other pliopithecoids (fig. S3), including *Barberapithecus* [also recorded at the Vallès-Penedès Basin (*32*)] and *Pliopithecus* [previously recorded at ACM (*25*)] in several features, including the more convex lingual profile, the more peripheral buccal cusps and the less developed cingula of the molars, as well as the narrower M1 and M2 and the M3 occlusal morphology and proportions (fig. S4). Dental microwear analysesindicate a mainly frugivorous diet for *Pliobates*, compatible with a high consumption of ripe fruit and a low sclerocarpic component (text S3; fig. S5; tables S6-S8).

Based on a 3D virtual reconstruction (Fig. 2; text S3; fig. S2; movie S1), the cranium of *Pliobates* differs from the primitive catarrhine condition (*22, 33, 34*) by being short, wide and high. However, the tubular ectotympanic is short and incompletely ossified, i.e., less developed than in *Saadanius* and extant crown catarrhines (*20-22*). The maxillary sinus is extensive, as in stem catarrhines and hominoids (*22, 35*)*,* and there is also a small frontal sinus, as in stem hominoids but unlike in stem catarrhines, cercopithecoids, hylobatids and pongines (*22,34, 35*). The face is short and displays anteriorly-situated orbits, as in hylobatids, colobines and some extinct small-bodied catarrhines such as *Epipliopithecus*, *Micropithecus* and *Lomorupithecus* (*19,* *21, 29, 36, 37*). However, *Pliobates* differs from these taxa (and more closely resembles hylobatids) by displaying a more well-defined muzzle (especially compared to *Epipliopithecus*) with long and more horizontal nasals, a higher zygomatic root (moderately high as in hylobatids, but less so than in hominids), an interorbital pillar nearly orthogonal to the frontal squama (as in hylobatids and chimpanzees), a high degree of orbital convergence and frontation (as in all extant hominoids), and thin and anteriorly-projecting (telescopic) orbital rims [to a greater extent than in *Epipliopithecus* (*36*), and thus most closely resembling hylobatids and, as far as it can be ascertained due to incomplete preservation, *Micropithecus* (*29*)]. *Pliobates* also displays derived hominoid features in the basicranium (Fig. 3; fig. S6), including the absence of postglenoid foramen with a large and ventrally-visible jugular foramen (as in all extant hominoids), the foramen ovale situated anteriorly and laterally to the Eustachian aperture (as in hylobatids and African apes), the fusion between the auditory meatus and the postglenoid process (as in hylobatids and African apes), and the horizontal and anteriorly-directed carotid canal in the petrosal bone (as in hylobatids).Estimated cranial capacity for *Pliobates* is 69-75 cm3, which coupled with our body mass estimates (text S1) yields a monkey-like degree of encephalization (*38*), much higher than in the stem catarrhine *Aegyptopithecus*, and slightly above that of *Victoriapithecus* and the extant cercopithecoid average, but only slightly below that of hylobatids and *Proconsul* (text S4; fig. S7; tables S9-S10).

The humerus (Fig. 4) resembles that of extant crown catarrhines, proconsulids and dendropithecids by lacking, unlike *Epipliopithecus*, an entepicondylar foramen (*17, 20, 21, 29, 36, 39, 40*). *Pliobates* more closely resembles extant hominoids in the laterally-facing bicipital tuberosity in the radius (*39, 41*) (Fig. 4), as well as the configuration of the humeroradial articulation (*39, 40, 42*) (Fig. 5), including: in the humerus, the lack of capitular tail [present in *Epipliopithecus*, dendropithecids and cercopithecoids (*42*)] and the moderately globulous (although not posterolaterally expanded) capitulum with a well-developed zona conoidea [lacking in *Epipliopithecus* and dendropithecids (*39-42*)]; and, in the radius, the little tilted and pseudocircular radial head with a small and flat area, a reduced lateral lip, and a bevelled surface for the humeral zona conoidea. *Pliobates* also displays a hominoid-like diarthrodial distal radioulnar joint (*43-45*), with a two-faceted expanded semilunar articulation in the ulnar head (Fig. 5). In this regard, *Pliobates* clearly departs from *Epipliopithecus*, dendropithecids and cercopithecoids (*17*, *36, 40*), and more closely resembles *Proconsul* (*46*), although the ulnar head is less extensive than in extant hominoids.In contrast with these derived features, the humeral shaft and humeroulnar joint are plesiomorphic, with the former (Fig. 4) being anteriorly straight and somewhat proximally retroflexed, and the latter (Fig. 5) lacking the stabilizing features of extant hominoids (*41, 47*) (being characterized by a narrow ulnar trochlear notch without a median keel, in agreement with the absence of spooling and the poorly-defined trochlear lateral keel in the humerus). Although computations of relative forelimb length in fossilsmust be taken with care because they depend on the accuracy of body size estimates, our results suggest that the forelimb of *Pliobates*, unlike that of *Epipliopithecus*, is somewhat elongated relative to body size, although less extremely than in hylobatids and more closely resembling the atelid condition (text S5; fig. S8; tables S11-S12). *Pliobates* further displays a high arm angle (8º), clearly greater than average in most anthropoids except *Hylobates* (9.8º), *Pongo* (6.3º) and *Ateles* (6.5º) (*48*). Estimated humeral torsion (text S6) is moderate (101º), most similar to that of *Dendropithecus* and non-atelid platyrrhines, but only slightly lower than in hylobatids and atelids (*49*).

The ulnocarpal articulation of *Pliobates* is completely remodelled compared to *Epipliopithecus* and dendropithecids (*17, 36, 50*), including a partially developed ulnar fovea (Fig. 5), which in extant hominoids is the attachment area of the triangular disc ligament and the intra-articular meniscus (*43-45*). The ulnar styloid process is relatively long and slender, with no discernible articular surfaces for the pisiform or triquetrum. This agrees with the lack of articular facet for the styloid process on the pisiform, as in extant hominoids but unlike in monkeys and *Proconsul* (*51*). However, in contrast to *Pierolapithecus* (*52*), the triquetrum of *Pliobates* shows a proximal articular facet, more developed than that displayed by hylobatids and sometimes *Pan* (*45, 48*), but less so than in monkeys. This suggests that ulnotriquetral contact might have been reduced by some kind of intra-articular tissue, similarly to some *Ateles* (*53*). Moreover, as in apes, the triquetrum of *Pliobates* is small relative to hamate size (fig. S9), indicating a reduced loading on the ulnar side of the wrist. However, as in monkeys and *Proconsul*, the triquetrum of *Pliobates* differs from that of extant apes and *Pierolapithecus* (*52*)by possessing a proximally-protruding beak-like process (Fig. 6). The hamate of *Pliobates* is “Miocene ape-like” (*51, 52*), although it more closely resembles that of hylobatids by possessing a dorsopalmarly narrow and proximodistally long triquetral articular surface that is proximally globular, as well as a distally-projecting hamulus (Fig. 6). *Pliobates* further resembles hylobatids and *Ateles* by displaying an oblong and mediolaterally narrow capitate head that, like the facet for the hamate, is proximodistally aligned. This morphology contrasts with the more globulous, wider and ulnarly-inclined capitate head of other catarrhines, including *Proconsul* (*46, 51*) and *Pierolapithecus* (*52*), although in *Pliobates* it is not radially inclined as in hylobatids. Moreover, the capitate facet for the second metacarpal is divided by a deep ligamentary notch (Fig. 6), as in extant hominoids and *Pierolapithecus* (*52*), but unlike in other catarrhines (including *Proconsul*), in which the facet for the second metacarpal is dorsopalmarly continuous and occupies the whole lateral aspect of the capitate (*51*) (Fig. 6). In fact, *Pliobates* displays a complex articulation between the third metacarpal and capitate, as in extant apes, but unlike in *Proconsul* (*51*), although as in *Pierolapithecus* (*52*) the capitate of *Pliobates* lacks a hook-like process.

**Phylogeny and evolutionary implications**

Our cladistic analysis based on both craniodental and postcranial characters recovers a single most parsimonious tree (Fig. 7; tables S13-S15), indicating that *Pliobates* is more closely related to crown hominoids than other Miocene small-bodied catarrhines and *Proconsul*. With a moderate support (bootstrap 71%, Bremer index 3), our results contradict the view of some authors that all these taxa are stem catarrhines (preceding the divergence with Old World monkeys) (*17, 21*), and concur instead with some previous cladistic analyses indicating a hominoid status for both *Proconsul* (*2, 8, 22*) and, at least, dendropithecids (*8, 22*). Our analysis is inconsistent with the current consensus that *Epipliopithecus* is a pliopithecoid (*20, 28, 37, 54*), although, in fact, the internal phylogeny of pliopithecoids and dendropithecids is not well settled by our results (being recovered by the most parsimonious tree but not by the bootstrap 50% majority rule consensus). Similarly, the phylogenetic relationships between the analyzed dryopithecines (*Hispanopithecus* and *Pierolapithecus*) are neither well resolved (with the closer link between *Pierolapithecus* and crown hominids having a Bremer index of 1 and bootstrap support of 56%). In contrast, our analysis recovers with a very high support (bootstrap 93-100%, Bremer indices 7-11) both the molecular phylogeny of extant hominoids (*1, 6*) and the stem hominid status of *Pierolapithecus* and *Hispanopithecus* (*9, 52*). In turn, the position of *Pliobates* as a stem hominoid more derived than *Proconsul* is relatively well supported (bootstrap 78%, Bremer index 2). When the analysis is repeated by excluding all the fossil taxa with a large amount of missing data (fig. S10), the position of *Pliobates* as a stem hominoid more derived than *Proconsul* is much better supported (bootstrap 100%, Bremer index 20), being even more robust than the monophyly of crown hominoids (bootstrap 98%, Bremer index 11) or than the great-ape status of *Pierolapithecus* and *Hispanopithecus* (bootstrap 100%, Bremer index 13).

Given that our analyses support *Pliobates* as a stem hominoid more derived than *Proconsul*, the mosaic of primitive and derived features displayed by the former taxon is of utmost relevance for interpreting the evolution of several key features among catarrhine primates. Many authors agree that homoplasy has played an important role in hominoid postcranial evolution (*5, 9, 12, 52*), but *Pliobates* shows a mosaic of primitive and derived features both in the cranium and the postcranium. For the cranium, this is best illustrated by the short tubular (but incompletely ossified) external auditory meatus with a V-shaped end, which would imply the independent acquisition of a more completely ossified ectotympanic in cercopithecoids and hominoids. This was already suspected by some previous authors (*20*), as suggested to some extent by the stem catarrhine *Saadanius* (*22*), the stem Old World monkey *Victoriapithecus* (*33*) and the stem ape *Proconsul* (*55*), in which the ectotympanic, albeit slightly more developed, is still short, does not laterally exceed the postglenoid process, and lacks a completely closed terminal ventral tip (fig. S6). In contrast, several other cranial features of *Pliobates* are derived towards the crown-hominoid condition, generally more closely resembling hylobatids than hominids. Some of the similarities with gibbons (e.g., short face with a distinct muzzle and anteriorly-situated telescopic orbits) may be size-related to a large extent (*56*), but others (horizontal and anteriorly-directed carotid canal) are otherwise only known in hylobatids. Coupled with the fact that *Pliobates* chronologically fits within the long ghost lineage of hylobatids, since their divergence from hominids ca. 17 Ma (*1*) until their putative oldest record (*Yuanmoupithecus*)at 8-7 Ma (*10, 57*), these similarities raise the possibility that *Pliobates* might be a stem hylobatid. This hypothesis is not favored by our cladistic analyses based on total (craniodental+postcranial) evidence, which support instead a stem hominoid status for *Pliobates*, mostly due to the lack of various crown-hominoid postcranial synapomorphies. However, its hylobatid cranial features and small body sizesuggest that, at least in some respects, the last common ancestor of crown hominoids might have been more gibbon-like (or less great ape-like) than generally assumed (*6, 16*).

Furthermore, *Pliobates* supports the view that some small-bodied catarrhines played a more important role in the emergence of crown hominoids than generally assumed during the last decades. The postcranial evidence provided by Miocene great apes such as *Pierolapithecus* and *Sivapithecus* (*19, 52, 58*) indicates that the last common ancestor of crown hominoids must have been postcranially more primitive than inferred based on extant forms. This supports some degree of parallel evolution in the postcranium between extant hylobatids and hominids (*5*), although not to such a great extent as if *Pliobates* was interpreted as a crown hominoid. As a stem ape, *Pliobates* cannot resolve whether many of the postcranial derived features shared by extant hylobatids and hominids are homologous (6) or homoplastic (*5*), although it suggests that a suite of features of the humeroradial and wrist joints might be indeed homologous. In these anatomical regions, *Pliobates* displays much more extensive postcranial synapomorphies of crown hominoids than those convergently displayed by atelids, including a diarthrodial radioulnar joint, an expanded ulnar head, an incipient ulnar fovea, a long and thin styloid process with reduced contact with the relatively small triquetrum, and a distally-projecting hamulus on the hamate. Thus, although *Pliobates* retains a primitive morphology of the proximal humerus suggestive of generalized above-branch quadrupedalism (*59*), given the emphasis on pronation/supination capabilities, the reduced compressive forces transferred across the ulnar side of the wrist, and the important ulnar deviation and rotatory capabilities at the wrist joint, its overall postcranial bodyplan is more compatible with a locomotor repertoire including a large amount of cautious and eclectic climbing (*45, 60*), in agreement in previous hypotheses on the original locomotor adaptations of hominoids (*60, 61*). Recent interpretations of *Proconsul* similarly depicted this taxon as an arboreal quadruped with adaptations for cautious climbing and clambering (*12, 46*), including an incipient distal radioulnar diarthrosis that is however still associated to a non-retreated ulnar styloid process (*46*). The reduced ulnocarpal articulation of *Pliobates* thus more closely foreshadows the condition of extant hominoids, although to a lesser extent than in the stem great ape *Pierolapithecus* (*52*), indicating a decreased emphasis on forearm use under weight-bearing conditions compared to *Proconsul* (*46*). Several characteristics of *Pliobates* (particularly, the elongated forearm, the high arm angle, and the laterally-facing bicipital tuberosity) further suggest some degree of below-branch forelimb-dominated suspensory behaviors (*48*). Based on currently available evidence, it is not possible to conclusively ascertain whether these incipient suspensory adaptations were inherited by the last common ancestor of crown hominoids (and later secondarily lost in some fossil great apes such as *Sivapithecus*), or whether they merely represent an independent acquisition of *Pliobates*. In any case, the lack of hominoid-like elbow stabilizing features in the humeroulnar joint (*41, 47*), the generalized metacarpophalangeal proportions, and the lack of marked phalangeal curvature suggest that *Pliobates* was not specifically adapted to perform the acrobatic suspensory behaviors (ricochetal brachiation) displayed by extant gibbons.

**Conclusions**

*Pliobates* provides the first evidence of crown-hominoid postcranial synapomorphies in a Miocene small-bodied catarrhine, thus documenting a greater diversity in postcranial morphology and positional behaviors than previously recognized among this paraphyletic assemblage of taxa. Three decades ago, the degree of parallel evolution required to evolve hylobatids from small-bodied catarrhines such as dendropithecids, albeit conceivable, was considered unwarranted in the light of the then available evidence (*18*), due to the numerous parallelisms that would be required in crown-hominoid (and even crown-catarrhine) features between hylobatids and hominids. Although the evidence provided by *Pliobates* reduces this morphological gap, this taxon still falls short of being supported as a hylobatid by our cladistic analyses, which still strongly favor instead the monophyly of extant hominoids with the exclusion of all fossil small-bodied catarrhines. However, unlike dendropithecids, currently interpreted as stem catarrhines (*21*) or hominoids more basal than *Proconsul* (*22*), *Pliobates* is unambiguously interpreted as more closely related to crown hominoids. Given its chronology and geographic location, as well as the retention of plesiomorphic dental and some postcranial features resembling small-bodied catarrhines such as dendropithecids, *Pliobates* is likely to be a late-surviving offshoot of a small African stem hominoid more closely related to crown hominoids than *Proconsul* is. This has significant implications for reconstructing the ancestral morphotype from which extant hominoids evolved, by suggesting that some small-bodied catarrhines could have played a much more significant role in ape evolution than previously thought, and that the last common ancestor of crown hominoids must not be necessarily great ape-like.

**Methods**

***Studied material***

The partial skeleton IPS58443 is composed of 70 bones and bone fragments (table S1) found in close spatial association that, given the lack of repeated elements, are attributed to a single individual. After the recovery of the main cranial fragments, postcranial elements were found at the field during excavation of the same stratigraphic level, and the remaining postcranial small bones and other small fragments were recovered by screen-washing the excavated sediments.

***Age and geological background***

The Abocador de Can Mata (ACM) local stratigraphic composite series (*62-64*)is located in the area of els Hostalets de Pierola within the Vallès-Penedès Basin (NE Iberian Peninsula), a NNE-SSW half-graben limited by the Catalan Coastal Ranges that was generated by the rifting of the NW Mediterranean during the Neogene (*65, 66*). The basin infill mostly consists of marginal alluvial fan sediments that have provided a rich fossil record of Miocene terrestrial vertebrates (*67*). The area of els Hostalets de Pierola displays thick Middle to Late Miocene sequences deposited in distal-to-marginal, inter-fan zones of coalescing alluvial fan systems (*64*). The ACM composite series, about 250 m in thickness, includes more than 250 formally-defined localities that can be accurately dated based on lithostratigraphic, magnetostratigraphic and biostratigraphic correlation (*26, 63, 64*). The whole series is late Aragonian and, based on updated chron boundaries *(68)*, it spans from ca. 12.6 to 11.5 Ma. Locality ACM/C8-A4 is correlated to chron C5r.2n (11.657–11.592 Ma), with an interpolated age of 11.628 Ma, close to the Middle/Late Miocene boundary, as defined by the base of the Tortonian and currently dated to 11.625 Ma (*68*).

***Cranial reconstruction***

The cranium was preserved in a main piece (IPS58443.1) including parts of the neurocranium, basicranium, muzzle and right maxilla (fig. S1), a medium-sized fragment with the left maxilla (IPS58443.2), and other smaller fragments that were found in close spatial association or recovered by screen-washing the surrounding sediments. These other fragments include part of the occipital and right parietal (IPS58443.3), the right glenoid region (IPS58443.4), the right occipital condyle (IPS58443.5), a fragment of the right orbital margin (IPS58443.6), the left orbital margin and temporal process of the zygomatic (IPS58443.12), a parietal fragment (IPS58443.11), and several other minor fragments whose location cannot be determined (IPS58443.7 to IPS58443.10, IPS58443.13 and IPS58443.37). The mandible is not preserved, except for a fragment of the right ramus with the condyle (IPS58443.14). In turn, the main fragment (IPS58443.1) is composed of several bone fragments that are crushed against each other and somewhat displaced from their anatomical position, but (like the remaining specimens) not plastically distorted.

Several bone fragments of IPS58443.1 were individualized through careful mechanical preparation, but their fragility and state of preservation precluded a complete isolation of many bone fragments from each other and/or from the embedding matrix. Therefore, for conservational reasons, no complete preparation of the specimen was performed, and a virtual 3D reconstruction was undertaken instead. The larger specimens (IPS58443.1 and IPS58443.2) were scanned at the American Museum of Natural History (New York) with a high-resolution computed tomograph (CT) GE phoenix v|tome|x s180 (GE Measurement & Control Solutions, Hanover, Germany), using a nanofocus X-ray tube. Two different protocols were used for each cranial fragment (IPS58443.1 and IPS58443.2, respectively): 160 kV voltage, 1.4 mA current, 0.2 mm Cu filter and magnification of 2.10013075, obtaining 1.600 slices of 0.2 mm in thickness and a pixel size of 0.09523217 mm; and 145 kV voltage, 1.3 mA current, 0.1 mm Cu filter and a magnification of 2.93159482, obtaining 1.500 slices of 0.2 mm in thickness and a pixel size of 0.06822225 mm. Raw CT data were imported into VG studio Max 2.1 and exported (as a stack of tiff files) to Avizo 7.0 and Geomagic 2012 for segmentation, repositioning, mirroring and/or visualization. CT-scanned bone fragments were segmented slice by slice by digitally removing the matrix with the aid of differential bone/sediment densities using the semiautomatic thresholding tools of Avizo 7.0. Additional small isolated bones fragments not surrounded by matrix were scanned with a 3D desktop laser scanner (NextEngine) at high definition (HD) and with a dimensional accuracy of 0.13 mm (Macro Mode); the resulting 3D models were exported to Geomagic 2012 to align and repair the meshes. The preserved bone fragments generally displayed clean fractures that could be easily matched with other fragments. Up to 39 3D virtual models of bone fragments, including pieces of the premaxillae and maxillae with teeth, lacrimals, zygomatics, frontal, parietals, temporals, occipital and pterygoids, were therefore digitally assembled and repositioned using Avizo 7.0 and Geomagic 2012 on the basis of preserved morphology, fracture congruence and bilateral symmetry. Once the various preserved fragments were adequately positioned, areas preserved only in one side of the cranium were mirrored. The individual models were finally merged to obtain the definitive 3D virtual model, which was also 3D-printed with a ZPrinter®450 at the Universitat Autònoma de Barcelona for visualization and comparative purposes. See text S3 for the anatomical details regarding the steps followed in the reconstruction.

***Dental measurements and body mass estimation***

Standard dental measurements of mesiodistal length (MD) and maximum buccolingual breadth (BL) were taken (in mm) to assess dental size and proportions by means of comparative bivariate plots of log-transformed BL vs. MD for each of the upper molars. Data for extant and extinct small-bodied catarrhines were taken from the literature (*17, 25, 30-32, 34, 36, 56, 69-75*) or measured by one of the authors (D.M.A.). Based on MD and BL measurements, tooth square area (A, in mm2) was computed in postcanine teeth, in order to estimate the body mass (BM, in kg) of *Pliobates* using allometric equations of BM vs. A (*76*). BM of *Pliobates* and, for comparative purposes, *Epipliopithecus vindobonensis* was also estimated based on allometric equations using postcranial estimators (*77*) for a sample of hominoids and catarrhines (hominoids+cercopithecoids) separately, based on the mean/sex species data. Six postcranial BM estimators were employed (*78*), including three surface areas (for the tibia, humerus and radius) and three linear measurements (for the humerus and radius); see tables S3-S4 for further details.

***Humeral torsion and arm angle***

Humeral torsion, i.e., orientation of the humeral head relative to the mediolateral axis of the distal humerus (*49*) cannot be directly computed in the described skeleton because the humeral head is missing. Accordingly, humeral torsion was kindly estimated by Susan Larson, by following her own methodology (*49*) for incomplete humeri lacking the proximal end (based on the bisector of the bicipital groove, indicating the orientation of the humeral head), as well as based on the posterior buttress for the humeral head (taken as a reference for the head axis). Measurements were obtained from a cast of the two humeral diaphyseal fragments of the holotype specimen. This humerus was originally preserved as a single specimen with a crack filled with sediment at about midshaft level, the two fragments being slightly crushed against each other in proximodistal direction. After manual separation of the matrix, the original shape of the diaphysis was reconstructed by correctly aligning casts of the two fragments.

The arm angle (or carrying angle at the elbow joint), which measures the angle between the long axes of the humerus and ulna (arm angles < 0º imply medial deviation of the ulna) (*48*), was computed from a photograph of the re-articulated original specimens.

***Postcranial proportions***

The degree of elongation of the forearm, the arm and the forelimb as a whole were assessed by means of allometric regressions of radius, humerus and radius+humerus length (in mm), respectively, relative to BM (in kg). Allometric equations (table S11) were derived based on sex-species mean data taken from the literature (*77, 79-81*) or kindly provided by E. Sarmiento to S.M.S. Regressions for anthropoid primates were based on N = 54, corresponding to 31 species from 17 genera; hylobatids, orangutans, *Ateles* and *Brachyteles* were excluded from the regressions because they are clear outliers. Allometric residuals were computed for the studied sample as well as *Pliobates* and *Epipliopithecus*; humeral length in the former, given the lack of the humeral head, was estimated by taking into account the proportions of the humerus of *Epipliopithecus*.

To assess the size of the triquetrum relative to the hamate, the size of each bone was computed as the geometric mean of three measurements representing their maximum dimensions: maximum mediolateral breadth (BTB), dorsopalmar height (HTB) and proximodistal length (LTB), for the triquetrum; and maximum proximodistal length (LHB), dorsopalmar height (HHB) and mediolateral breadth (BHB), for the hamate. Comparative data were kindly provided by Tracy Kivell, her metrics and sample (including 28 anthropoid species from 16 genera) being described in the literature (*82, 83*).

***Cranial capacity and encephalization***

Due to preservational reasons, it was not possible to compute cranial capacity (CC, in cm3) from the virtual endocast. Therefore, CC was estimated using published allometric equations based on various external neurocranial measurements (*84*): maximum width of braincase base (CW, in mm); vertical height of braincase (CH, in mm); chord of midline suture through occipitals, parietals and frontals (CL, in mm); modulus of the above-mentioned linear measurements (CO, in mm), computed as CO = CW + CH + CL; product of the above-mentioned linear dimensions (PR, in mm3), computed as PR = CW x CH x CL; and foramen magnum area (FMA, in cm3), computed as FMA = (π/4) x FMW x FML, where FMW is foramen magnum width (in mm) and FML is foramen magnum length (in mm). To assess encephalization, we relied on lower taxonomic level metrics of relative brain size, which are significantly correlated with general domain cognitive abilities in primates (*38, 85*). Encephalization residuals (ER) were computed as ER = ln CC (observed) – ln CC (predicted), by using the ordinary least-squares cercopithecoid allometric regression (ln CC = 0.4778 ln BM + 3.457), whereas encephalization constants (EC) were computed as EC = CC / BM0.28 (*38, 85*). Mean/sex species data for extant species were taken from the literature (*38*). Besides the estimates derived for *Pliobates* in this study, various extinct catarrhines (female *Aegyptopithecus zeuxis*, male *Victoriapithecus macinnesi*, female *Proconsul nyanzae*, male *Oreopithecus bambolii* and female *Hispanopithecus* *hungaricus*) were also included in the analyses, based on published data (*33, 34, 38, 86, 87*).

***Dental microwear***

Paleodietary reconstruction was based on dental microwear analysis (*88*). The M1 of *Pliobates* was selected, since it exhibits more clear and larger Phase II crushing/grinding facets than the remaining molars. Occlusal surfaces were examined through Environmental Scanning Electron Microscope (ESEM) at 500x magnification in secondary emissions mode and at 20 kV following established procedures (*88*). An area of standardized size, corresponding to 0.02 mm2 onthe original facet (*89*), was analyzed using the custom software package Microware 4.02© (*90*). The following three microscopic variables were measured: percentage of pits; breadth of striations; and breadth of pits. Striations and pits were categorized by following an arbitrarily set length to width ratio of 4:1 (*54, 87, 91, 92*). Our results were compared with those previously derived for a sample of 11 extant anthropoids with well-known diets (*87, 93, 94*), partitioned into three distinct dietary categories (*54*), as well as with those reported for extinct catarrhines (*54, 89, 91, 92, 95*), including both pliopithecoids and hominoids. Microwear data were analyzed by means of Canonical Variates Analysis (CVA) using SPSS 19.

***Phylogenetic analysis***

A cladistic analysis based on maximum parsimony was performed with PAUP\* 4.0 for Unix (*96*), with the search command ‘branch-and-bound’, based on a taxon-character data matrix of 319 characters and 20 taxa (tables S13-S14) that was coded anew by the authors, although being partially based on character statements taken from the literature (*8, 22, 37, 97-99*). All but 10 characters were treated as unordered, whereas inapplicable characters were treated as missing data. Clade robusticity was assessed by means of bootstrap analysis (10,000 replicates) and Bremer support indices. For most parsimonious cladograms, the following metrics were computed: CI = Consistency Index (excluding uninformative characters); RI = Retention Index; and RC = Rescaled Consistency Index. Character polarity was determined using the outgroup method, with the stem catarrhine *Aegyptopithecus* being employed as such. Ingroup taxa include the stem catarrhine *Saadanius*, two cercopithecoids (the extant *Macaca* and the extinct *Victoriapithecus*), extant hylobatids, extant (*Pongo*, *Gorilla* and *Pan*) and extinct (*Pierolapithecus* and *Hispanopithecus*) great apes, and a wide representation of small-bodied fossil catarrhines from Africa (two dendropithecids, including *Micropithecus* and *Dendropithecus*+*Simiolus* coded simultaneously) as well as Eurasia (six pliopithecoids, including *Pliopithecus*, *Epipliopithecus*, *Dionysopithecus*, *Barberapithecus*, *Anapithecus* and *Plesiopliopithecus*). The phylogenetic placement of *Saadanius*, *Micropithecus* and most pliopithecoids (except *Epipliopithecus*) should be viewed with great care, because they have a large proportion of missing data. Therefore, the analysis was also rerun by removing these taxa.

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Fig. 1. Dental morphology*.* (A–B) Detail of the right maxilla with postcanine teeth of the holotype (IPS58443) of *Pliobates* cataloniae gen. et sp. nov., in occlusal (A) and buccal (B) views. Mesial is to the right.

**Fig. 2**. **Cranial reconstruction.** Virtual reconstruction of the holotype (IPS58443) cranium of *Pliobates cataloniae* gen. et sp. nov. including mirrored fragments, in frontal (**A**), lateral (**B**), posterior (**C**), basal (**D**) and superior (**E**) views.See fig. S2 and text S3 for further details.

Fig. 3. Basicranial morphology*.* Drawing of the left basicranium of the holotype (IPS58443) of *Pliobates cataloniae* gen. et sp. nov. as preserved. The jugular foramen appears artifactually larger, due to the displacement of the temporal and occipital portions along the occipitotemporal suture (corrected in the reconstruction of Fig. 2). The course of the carotid canal is depicted with a dashed line, based on CT images. Original artwork by Marta Palmero. Legend: AE, articular eminence; CAF, carotid foramen; COF, condylar fossa; EA, Eustachian aperture; EAM, external auditory meatus; EP, Eustachian process; ET, ectotympanic; FM, foramen magnum; FO, foramen ovale; GF, glenoid fossa; JF, jugular foramen; OC, occipital condyle; OTS, occipitotemporal suture; PGP, postglenoid process.

**Fig. 4.** **Forelimb long bones.**Humerus, radius and ulna of the holotype (IPS58443) of *Pliobates cataloniae* gen. et sp. nov. (**A–E**) partial left humerus in medial (A), posterior (B), lateral (C), anterior (D) and distal (E) views.(**F–K**) left radius in medial (F), posterior (G), lateral (H), anterior (I), proximal (J) and distal (K) views. (**L–O**)proximal half of left ulna in medial (L), posterior (M), lateral (N) and anterior (O) views. (**P–T**) distal fragment of left ulna in medial (P), posterior (Q), lateral (R), anterior (S) and distal (T) views.

Fig. 5. Elbow and wrist morphology. Most diagnostic features of the elbow and wrist joints of *Pliobates cataloniae* gen. et sp. nov. (IPS58443) denoted by arrows in drawings of the distal humerus, proximal radius and distal ulna compared to selected extant and extinct anthropoids. (A–D) anterior (top) and distal (bottom) views of the distal humerus in *P. cataloniae* (A), *Epipliopithecus vindobonensis* Individual I (B, reversed), ?*Dendropithecus* sp.KNM-MO 17022A (C) and *Hylobates moloch* (D). (E–H) view perpendicular to the radial tuberosity (top) and proximal view (bottom) of the proximal radius in *P. cataloniae* (E), *E. vindobonensis* Individual I (F), *Simiolus enjiessi* KNM-MO 63 (G, reversed) and *H. moloch* (H). (I–M) medial (top) and distal (bottom) views of the distal ulna in *P. cataloniae* (I), *E. vindobonensis* Individual I (J), *H. moloch* (K), *Ateles paniscus* (L) and *Cercopithecus aethiops* (M). Legend: 1, absence of entepicondylar foramen; 2, absence of capitular tail; 3, lack of spool-shaped trochlea; 4, well-developed bevelled surface for the zona conoidea; 5, small and flat area in the radial head; 6, ulnar fovea; 7, two-faceted, expanded semilunar articular surface in the ulnar head. Specimens are depicted as from the left side and not to scale. Artwork by Marta Palmero.

Fig. 6. Carpal bones. Line drawings of carpal bones in *Pliobates cataloniae* gen. et sp. nov. (IPS58443), compared to a sample of selected anthropoid genera. (A–E) Left capitate, in radial (top) and proximal (bottom) views, of *Cercopithecus aethiops* (A), *Ateles paniscus* (B), *Pierolapithecus catalaunicus* (C), *Hylobates lar* (D) and *P. cataloniae* (E); gray colour denotes articular areas for the second metacarpals, and striped areas those for the third metacarpal. (F–J) Left hamate, in radial (top) and ulnar (bottom) views, of *C. aethiops* (F), *A. paniscus* (G), *Pi. catalaunicus* (H), *H. lar* (I) and *P. cataloniae* (J). (K–O) Left triquetrum, in proximomedial (top) and distal (bottom) views, of *C. aethiops* (K), *A. paniscus* (L), *Pi. catalaunicus* (M), *H. lar* (N) and *P. cataloniae* (O). Not to scale.

Fig. 7. Results of the cladistic analysis. Single most parsimonious tree of 645 steps based on a taxon-character data matrix of 319 characters and 20 taxa (table S13-S14). CI = 0.5912 (excluding uninformative characters); RI = 0.6897; RC = 0.4213. Values below nodes correspond to Bremer indices, and numbers above nodes to bootstrap support values (only when ≥50%). Node numbers refer to clades in the list of apomorphies reported in table S15.

Table 1. Dental measurements. Standard dental measurements taken to the nearest 0.1 mm in the holotype (IPS58443) of *Pliobates cataloniae* gen. et sp. nov. to assess dental size and proportions. Abbreviations: MD, mesiodistal length (in mm); BL, buccolingual width (in mm); BLI, breadth/length index (in %), computed as BL / MD x 100.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Catalog No.** | **Tooth** | **Side** | **MD** | **BL** | **BLI** |
| IPS58443.1 | P3 | Right | >2.8 | >4.5 | — |
| IPS58443.1 | P4 | Right | 3.2 | 5.3 | 165.6 |
| IPS58443.1 | M1 | Right | 5.0 | 5.9 | 118.0 |
| IPS58443.1 | M2 | Right | 5.3 | 6.5 | 122.6 |
| IPS58443.1 | M3 | Right | 4.6 | 6.4 | 139.1 |
| IPS58443.2 | M2 | Left | >5.0 | — | — |
| IPS58443.2 | M3 | Left | 4.5 | 6.7 | 148.9 |

Supplementary Materials:

Texts S1-S6

Figures S1-S10

Tables S1-S15

Movie S1