

A New Species of *Pliopithecus* Gervais, 1849 (Primates: Pliopithecidae) from the Middle Miocene (MN8) of Abocador de Can Mata (els Hostalets de Pierola, Catalonia, Spain)

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ABSTRACT *Pliopithecus (Pliopithecus) canmatensis* sp. nov. is described from several Late Aragonian localities from Abocador de Can Mata (ACM) in els Hostalets de Pierola (Vallès-Penedès Basin, Catalonia, Spain), spanning from ~11.7 to 11.6 Ma (C5r.3r sub-chron), and being correlated to the MN8 (reference locality La Grive L3). The ACM remains display a pliopithecine dental morphology with well-developed pliopithecine triangles on M/2 and M/3. This, together with other occlusal details, negates an attribution to the subgenus *Epipliopithecus*. Although slightly smaller, the ACM remains are most similar in size to comparable elements of *P. piveteaui* and *P. antiquus*. Several occlusal details (such as the greater development of the buccal cingulid in lower molars) and dental proportions (M/3 much longer than M/2), however, indicate greater

similarities with *P. antiquus* from Sansan and La Grive. The ACM remains, however, differ from *P. antiquus* in dental proportions as well as occlusal morphology of the lower molars (including the less peripheral position of the protoconid and more medial position of the hypoconulid, the more mesial position of the buccal cuspids as compared to the lingual ones, the narrower but distinct mesial fovea, the higher trigonid, and the more extensive buccal cingulid, among others). These differences justify a taxonomic distinction at the species level of the ACM pliopithecid remains with respect to *P. antiquus*. Previous pliopithecid findings from the Vallès-Penedès Basin, previously attributed to *P. antiquus*, are neither attributable to the latter species nor to the newly erected one. *Am J Phys Anthropol* 141:52–75, 2010. © 2009 Wiley-Liss, Inc.

The superfamily Pliopithecoidea includes several genera of Early to Late Miocene Eurasian catarrhines [see Begun (2002) for the most recent review]. The phylogenetic relationships between pliopithecoids and other catarrhines are far from clear. Once considered to be phylogenetically related to hylobatids due to some superficial resemblances (e.g. Hürzeler, 1954; Zapfe, 1958), in fact, pliopithecoids do retain some very primitive features that clearly indicate an earlier divergence, predating the cercopithecoid-hominoid splitting. Given their dental formula (with only two premolars), they are usually considered to be stem catarrhines (Harrison et al., 1991; Andrews et al., 1996; Begun, 2002), which would constitute a clade of their own on the basis of a few putative synapomorphies, such as P/3 morphology.

Ever since the work by Ginsburg and Mein (1980), pliopithecoids have been customarily classified into a single family with two distinct subfamilies: Pliopithecinae and Crouzeliinae. The occlusal dental morphology of crouzeliines is generally considered to be derived as compared to pliopithecines, being further related to a more folivorous diet [e.g. Harrison in Andrews et al. (1996)]. After the recognition that the Early Miocene *Dionysopi-*

thecus Li, 1978 and *Platodontopithecus* Li, 1978 from Asia show pliopithecoid affinities (Harrison and Gu, 1999), a new subfamily Dionysopithecinae was erected within the Pliopithecidae, further distinguishing the Pliopithecini and Crouzeliini at the tribe level within the subfamily Pliopithecinae. Later on, Moyà-Solà et al. (2001) distinguished these groups as three distinct

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subfamilies within a single family Pliopithecidae. Most recently, Begun (2002) elevated the Crouzeliinae to the family level (Crouzeliidae), while Harrison (2005) granted a family status for the Dionysopithecinae (i.e. Dionysopithecidae) but not for the Crouzeliinae. This minor taxonomic disagreements stem from the fact that the phylogenetic relationships between and within the several family-level groups of pliopithecoids are far from clear. We agree with Harrison and Gu (1999) and Harrison (2005) that, on the basis of currently available evidence, pliopithecines and crouzeliines probably share a common ancestor with the exclusion of dionysopithecines. However, given the uncertainties regarding the phylogenetic relationships between the several groups—as illustrated by the different systematic schemes used by different authors—we provisionally follow here the arrangement of three pliopithecoid subfamilies employed by Moyà-Solà et al. (2001). It should be taken into account that, because the earliest crouzeliines (*Plesio-pliopithecus* spp.) are insufficiently known (Zapfe, 1961; Bergounioux and Crouzel, 1965; Ginsburg and Mein, 1980; Welcomme et al., 1991), significant taxonomic disagreements remain regarding the distinction between the two pliopithecoid subfamilies. This is best exemplified by the dentally derived genus *Egarapithecus* Moyà-Solà et al., 2001, which has been considered a crouzeliine by most researchers (Andrews et al., 1996; Moyà-Solà et al., 2001; Harrison et al., 2002), although Begun (2002) considered it to be a derived pliopithecine that has converged into a crouzeliinelike occlusal morphology.

Such taxonomic disagreements notwithstanding, on the basis of currently available anatomical, paleobiogeographic and biostratigraphic data, the most likely evolutionary scenario for pliopithecoids reads as follows (Harrison, 2005). Earliest pliopithecoids were the first catarrhines to disperse from Africa into Eurasia, where they experienced an evolutionary radiation in a continent apparently devoid, at least initially, of other anthropoids. The African catarrhine *Lomuropithecus harrisoni* Rossie and MacLachy, 2006 has been interpreted as a pliopithecoid. This taxon, however, lacks a pliopithecine triangle on lower molars, while other putative derived features of pliopithecoids related to incisor and P/3 morphology cannot be evaluated (Rossie and MacLachy, 2006). Accordingly, the pliopithecoid status of *Lomuropithecus* is very uncertain, and the ancestry of pliopithecoids among African stem catarrhines remains an open question. Be that as it may, undoubted pliopithecoids are first recorded by dionysopithecines from the Early Miocene of Asia (Harrison and Gu, 1999). Soon after the initial radiation of this group in Asia, pliopithecines would have presumably originated from a dionysopithecinelike ancestor in Asia, later dispersing into Europe by the Middle Miocene (Harrison and Gu, 1999; Harrison, 2005). Crouzeliines, on the contrary, appear to have locally evolved in Europe from a pliopithecinelike ancestor by the Middle Miocene, later dispersing into Asia by the Late Miocene (Harrison, 2005).

In the Iberian Peninsula, pliopithecoids are only recorded at the Vallès-Penedès Basin, where they are represented by both pliopithecines and crouzeliines. Before excavations began at Abocador de Can Mata in late-2002 (Alba et al., 2006b), the most informative pliopithecoid remains from this basin corresponded to a partial upper and lower associated dentition from Castell de Barberà (latest Middle Miocene, MN8, ~11.5 Ma). These remains were first reported by Crusafont-Pairó

(1975, 1978), and partially described, together with an isolated dP4 from the late Middle Miocene (MN8) locality of Can Feliu (Sant Quirze), by Crusafont-Pairó and Golpe-Posse (1981, 1982). These authors noted similarities with *Pliopithecus* [now *Plesio-pliopithecus*] *lockeri*, but refrained from making a taxonomic assignment other than *Pliopithecus* sp. (i.e., Pliopithecidae indet., following the more restricted current usage of the genus *Pliopithecus*). Ginsburg (1986) attributed these specimens to Crouzeliinae indet. nov., while most recently they have been attributed to *Pliopithecus antiquus* by Andrews et al. (1996), to Pliopithecinae gen. et sp. indet. (new) by Begun (2002), and to *P. cf. antiquus* by Harrison et al. (2002; footnote 1). Providing a detailed description of the Castell de Barberà material is beyond the scope of this work (see Alba and Moyà-Solà, in preparation), but for the time being, it will be here referred to as Pliopithecidae nov. Another pliopithecoid is represented by an isolated M2/ from the Middle Miocene locality (MN8) of Sant Quirze, which has been attributed to *Pliopithecus* sp. by Harrison et al. (2002). Finally, *Egarapithecus narcisoi* Moyà-Solà et al., 2001 is further recorded from the Late Miocene (MN10, ~9 Ma) locality of Torrent de Febulines (Terrassa). Initially attributed to *Pliopithecus* sp. by Golpe Posse (1982), the crouzeliine affinities of the Terrassa material were already noted by Andrews et al. (1996), and have been confirmed in the formal description of the genus and species (Moyà-Solà et al., 2001) and most later accounts [Harrison et al., 2002, footnote 2; but see Begun (2002) for a different interpretation].

In this paper, we describe the pliopithecoid dentognathic remains recovered from several localities of the stratigraphic section of Abocador de Can Mata (ACM), where significant discoveries of fossil great apes have been also made during recent years (Moyà-Solà et al., 2004, 2009). Paleontological fieldwork in this area has been carried out from late-2002 to mid-2003, and from early 2004 onwards (and it is still ongoing), resulting in the discovery of more than a 100 localities of large and small mammals and other terrestrial vertebrates (Alba et al., 2006a,b, 2007). The pliopithecoid remains described in this work were excavated during the field campaigns of 2005 and 2007. They include 19 records from five different sites (Table 1), ranging from mandibles and maxillary fragments to isolated teeth, and including a minimum number of individuals of eight: two from C4-A1 (=C4-Ae), two from C4-Cb, two from C5-A8, one from C5-C2 (=C5-Cb), and one from C5-C3 (=C5-Cc). When these localities are combined, 61 teeth are available for measurement and analysis, comprising all the definitive upper and lower dentition except by I1/ and the M3/, and including an isolated dP4/ as the single representative of the deciduous dentition. These remains correspond to a relatively restricted temporal range and are all attributed to a new species of the genus *Pliopithecus*.

STRATIGRAPHY AND AGE

The pliopithecoid finds reported in this article (Table 1) come from several localities of ACM (Table 2), which is located in the area of els Hostalets de Pierola, in the Vallès-Penedès Basin (Catalonia, Spain). The fauna and biostratigraphic background of ACM have been recently updated (Alba et al., 2006b; Casanovas-Vilar et al., 2008), and the geological context and magnetostratigraphy has been also published by Moyà-Solà et al. (2009).

TABLE 1. *Dentognathic remains of Pliopithecus (Pliopithecus) canmatensis sp. nov. from the local series of Abocador de Can Mata (Catalonia, Spain)*

Museum record no.	Field record no.	Field campaign	Locality	Short description
IPS35036	ACM6422	2005	ACM/C4-A1	Mandible with righth series C/1-M/3 and left P/3-M/3 series; male
IPS41715	ACM9157	2005	ACM/C4-A1	Left P4/ crown with partial roots
IPS41717	ACM8784	2005	ACM/C4-A1	Left C/1 crown with root; female
IPS41718	ACM9356	2005	ACM/C4-A1	Right M2/ crown with partial roots
IPS41719	ACM8802	2005	ACM/C4-Cb	Two mandibular fragments with right and left P/3-M/3 series; female (?)
IPS41720	ACM8867	2005	ACM/C4-Cb	Eroded left M/2 with partial roots
IPS41721	ACM8836	2005	ACM/C4-Cb	Left C/1 crown with nearly complete root; male
IPS41722	ACM8890	2005	ACM/C4-Cb	Right buccal fragment of upper premolar crown with root
IPS41956	ACM18742	2007	ACM/C5-A8	Right M/3 crown
IPS41960	ACM18914	2007	ACM/C5-A8	Righth M/2 crown with partial roots
IPS41959	ACM18922	2007	ACM/C5-A8	Right (?) I/1
IPS41957	ACM18895	2007	ACM/C5-A8	Left C/1 root and nearly complete crown; female
IPS41958	ACM18716	2007	ACM/C5-A8	Right maxillary fragment with series I2/-P3/; female
IPS41955	ACM18888	2007	ACM/C5-A8	Left lower series C/1-M/1; male
IPS41976	ACM19111	2007	ACM/C5-C2	Right dP4/ crown
IPS41954	ACM20807	2007	ACM/C5-C3	Left C/1 root and crown base; male
IPS41981	ACM20896	2007	ACM/C5-C3	Partial mandible (lacking the two canines and left I/2); male
IPS41983	ACM21044	2007	ACM/C5-C3	Left maxillary fragment with partial P3/-M1/
IPS41984	ACM21718	2007	ACM/C5-C3	Left M2/ with roots and partial crown

TABLE 2. *Stratigraphic position of the pliopithecoid localities included in this paper (in bold type) within the local series of Abocador de Can Mata (Catalonia, Spain), proposal of local biozonation and biostratigraphic correlation*

Paleomastologic age	MN biozone	Local biozone	Stratigraphic position	Sites
Early Vallesian	MN9	<i>Megacricetodon ibericus</i> + <i>Hipparion</i> s.l.	390 m	Can Mata III
Late Aragonian	MN8	<i>Megacricetodon ibericus</i> + <i>Democricetodon crusafonti</i>	350 m 292 m 211 m 195 m 191 m 175 m 174 m 171 m	Can Mata I ACM/CCV1 ACM/C4-A1 ACM/C5-A8 ACM/C5-C2 ACM/C4-Cb ACM/C5-C3 ACM/C3-A2
	?	?	170 m 155 m	ACM/C3-Ae ACM/C3-Az
	MN7	<i>Megacricetodon ibericus</i> + <i>Democricetodon larteti</i>	142 m 39 m	ACM/BCV1 ACM/C9-A1
	MN6 ?	<i>Megacricetodon crusafonti</i> ?	29 m	ACM/BDL1

The first and last ACM localities surely correlated with the several local biozones are also included, together with other primate localities from Hostalets de Pierola [including those recently published by Moyà-Solà et al. (2004, 2009)]. Updated from Alba et al. (2006b).

Accordingly, only some remarks regarding the pliopithecoid localities treated in this work are given below.

On the basis of previous magnetostratigraphic correlation (Moyà-Solà et al., 2009), all these pliopithecoid localities are attributable to the C5r.3r subchron, with an estimated age of 11.9–11.5 Ma. Moreover, on the basis of biostratigraphic data, these localities correspond to the *M. ibericus* + *D. crusafonti* local biozone (Alba et al., 2006b), which can be correlated to the MN8 sensu Mein and Ginsburg (2002), for which the site of La Grive L3 is the reference locality. The pliopithecoid localities reported in this work are therefore younger than the hominoid localities previously reported from the local stratigraphic series of ACM (Moyà-Solà et al., 2009); these include BCV1 (the type locality of *Pierolapithecus catalaunicus* Moyà-Solà et al., 2004), for which a revised estimated

age of 11.9 Ma has been attributed on the basis of paleomagnetic and biostratigraphic data; C3-Az, with a slightly younger estimated age of also 11.9 Ma; and C3-Ae, with an estimated age of 11.8 Ma. On the basis of the stratigraphic position of these localities, and by taking into account an estimated mean sedimentation rate of 24 cm/kyr for the ACM series (Moyà-Solà et al., 2009), the pliopithecoid localities reported in this work would be situated about 0.2 myr above BCV1, ranging approximately from 11.7 to 11.6 Ma.

SYSTEMATIC PALEONTOLOGY

Order PRIMATES Linnaeus, 1758
Suborder ANTHROPOIDEA Mivart, 1864

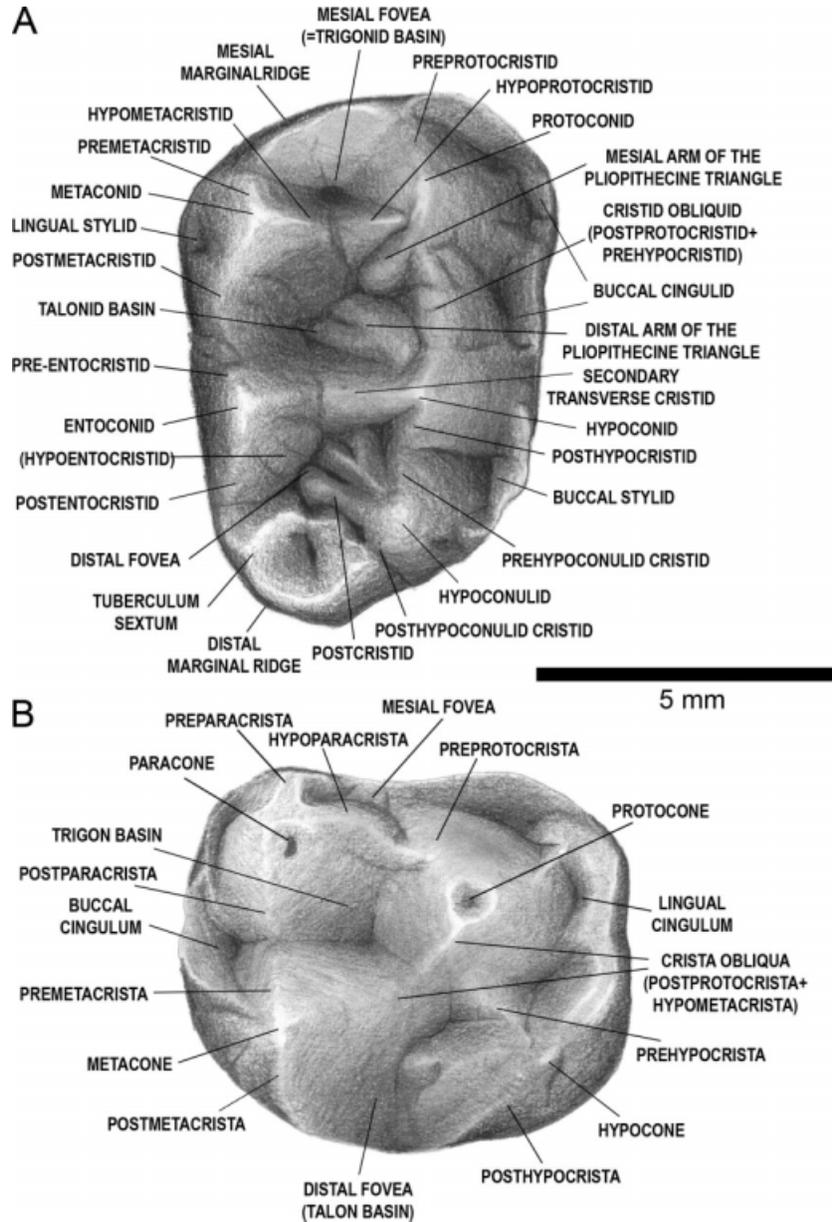


Fig. 1. Dental terminology used in this work (in occlusal view) on upper and lower molars, as exemplified in two specimens of *Pliopithecus* (*Pliopithecus*) *canmatensis* sp. nov.: (A) Right M/3 (IPS41956); and (B) Right M2/ (IPS41718). Mesial is on top. Original art by Marta Palmero. Dental terminology after Harrison and Gu (1999).

Infraorder CATARRHINI É. Geoffroy Saint-Hilaire, 1812
 Superfamily PLIOPITHECOIDEA Zapfe, 1961
 Family PLIOPITHECIDAE Zapfe, 1961
 Subfamily PLIOPITHECINAE Zapfe, 1961
 Genus *Pliopithecus* Gervais, 1849
 Subgenus *Pliopithecus* Gervais, 1849
Pliopithecus (*Pliopithecus*) *canmatensis* sp. nov.
 (Figs. 1–10 and 11C–E).

Differential diagnosis

Small-sized species of *Pliopithecus*, most comparable in dental size to *P. antiquus* but slightly smaller on average. *P. canmatensis* differs from dionysopithecines (*Dionysopithecus* and *Platodontopithecus*) by the following

features: (1) postcanine teeth with higher crowns; (2) molar occlusal morphology with less-rounded cusps and more pronounced occlusal relief; (3) more lingually situated protocone and more voluminous hypocone on upper molars; (4) relatively broader lower premolars, especially P/4; (5) shorter mesial foveae on lower molars; (6) M/3 absolutely longer and relatively narrower than the M/2 (instead of slightly shorter but equally broad); (7) M2/ absolutely longer than the M1/; and (8) M1/ relatively broader than M2/. *P. canmatensis* further differs from *Platodontopithecus* by the much smaller dental size of the former, being more similar to *Dionysopithecus*, from which it differs by the absolutely longer M/3 and M2/.

P. canmatensis differs from all crouzeliines (including *Egarapithecus*) by the following features: (1) less peripheralized and less buccolingually compressed cusps; (2)

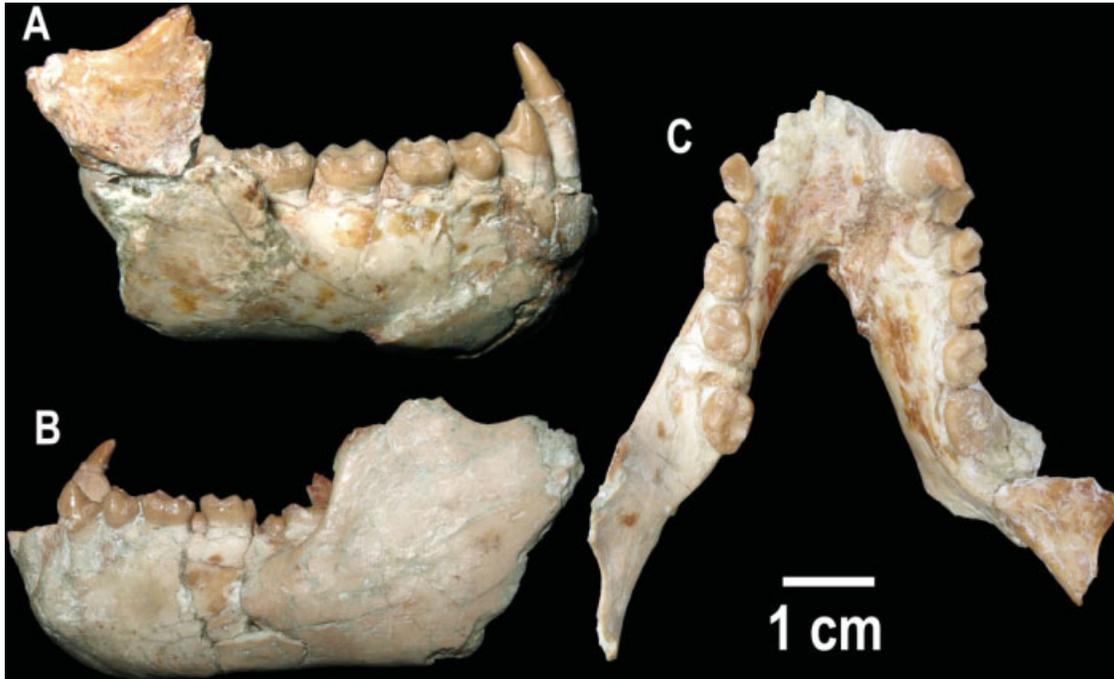


Fig. 2. Male mandible of *Pliopithecus (Pliopithecus) canmatensis* sp. nov. (IPS35036; holotype) from ACM/C4-A1, in right buccal (A), left buccal (B), and occlusal (C) views. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

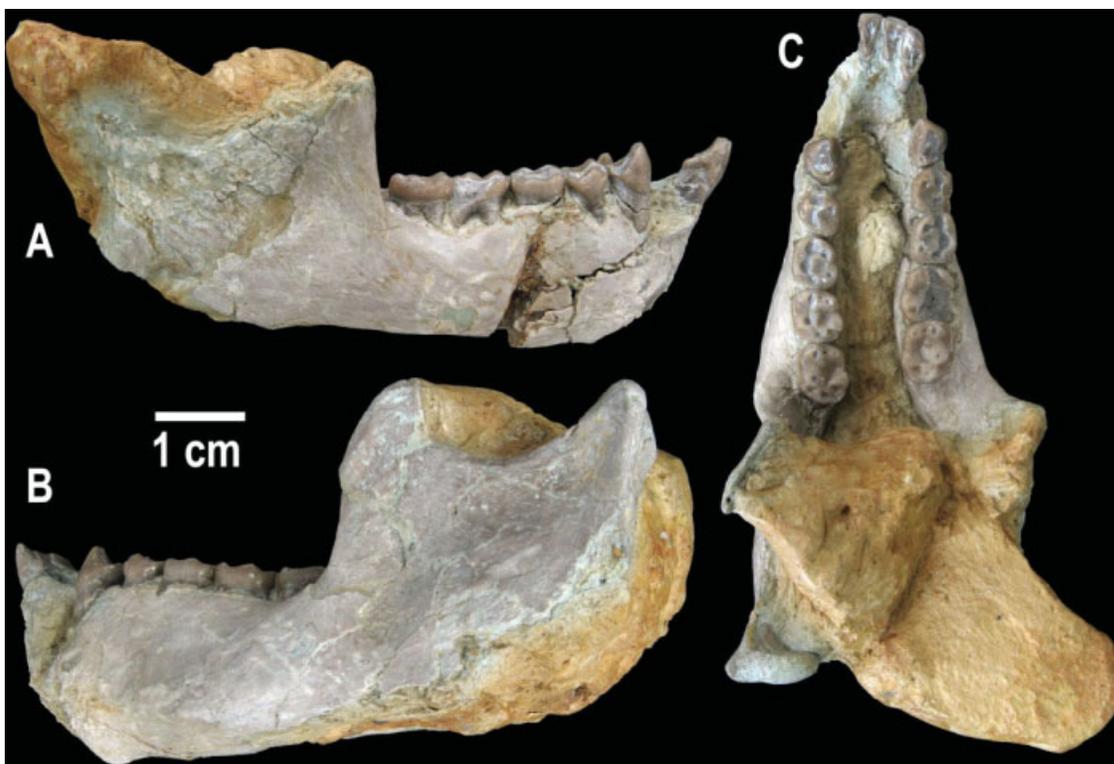


Fig. 3. Male mandible of *Pliopithecus (Pliopithecus) canmatensis* sp. nov. (IPS41981; paratype) from ACM/C5-C3, in right buccal (A), left buccal (B), and occlusal (C) views. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

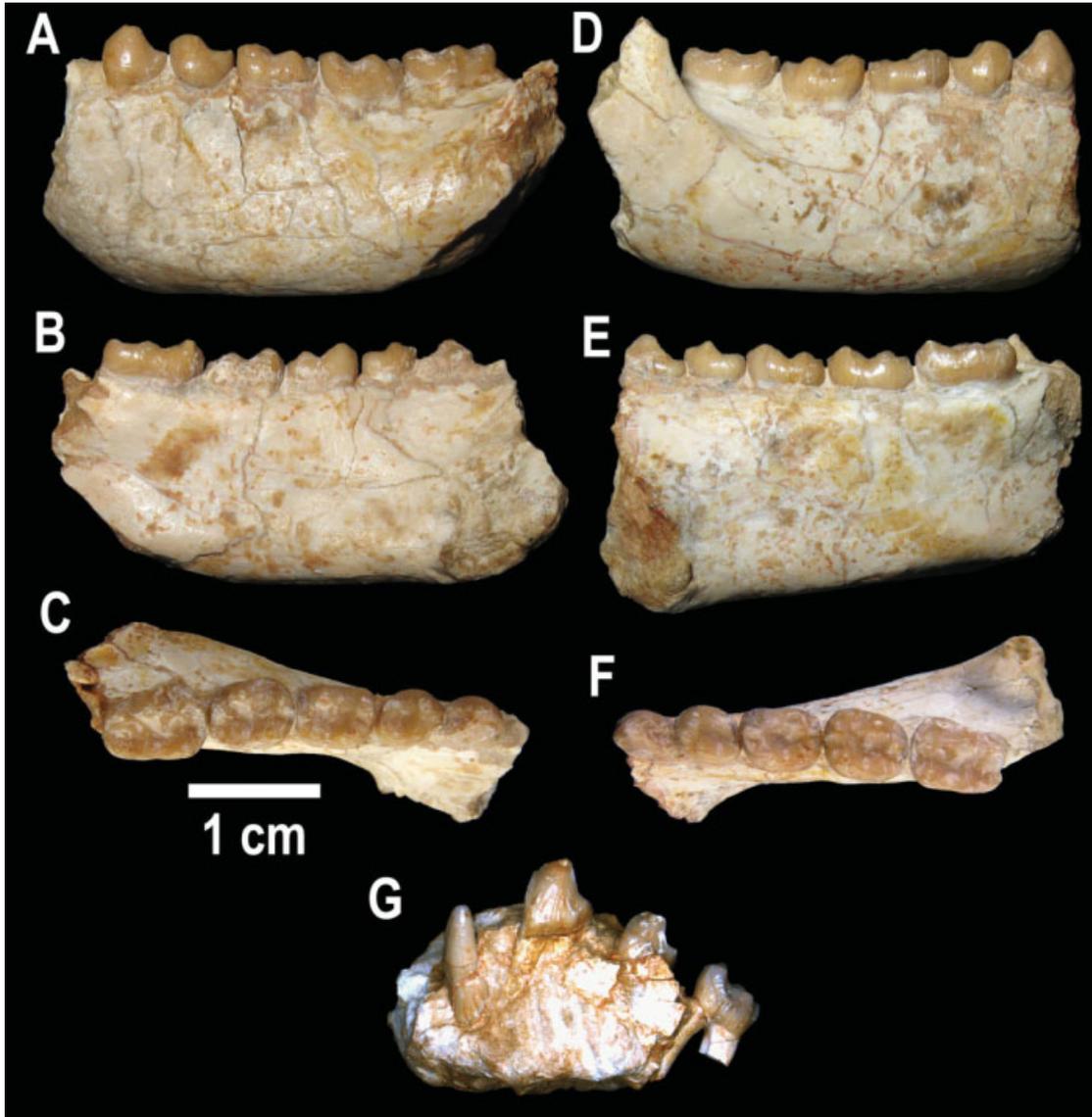


Fig. 4. Mandibular fragments of *Pliopithecus (Pliopithecus) canmatensis* sp. nov.: (A–F) Female right and left mandibular corpora (IPS41719; paratype) from ACM/C4-Cb, in left buccal (A), left lingual (B), left occlusal (C), right buccal (D), right lingual (E), and right occlusal (F) views; (G) Male left lower series with C/1–M/2 (IPS41955; paratype) from ACM/C5–A8, in buccal view. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

less extensive and shallower occlusal basins, except for the distal fovea on upper and lower molars; (3) upper molars with the hypocone situated farther from the protocone; (4) lower molars relatively broader (except for the M/1 of *Laccopithecus* Wu and Pan, 1984), with the trigonid only moderately more elevated than the talonid, shorter and more restricted mesial foveae, only slightly oblique cristid obliqua, distinct and more extensive distal foveae (especially in M/3), broader buccal cingulids, and nonreduced hypoconulid that is more buccally placed at least in M/3 (where it is aligned with the remaining buccal cusps). *P. canmatensis* further differs from *crouzeliines* by the smaller size of the former, except when compared to *Plesiopliopithecus* Zapfe, 1961, from which it differs by the absolutely longer M/2.

P. canmatensis differs from *P. (Epipliopithecus) vindobonensis* Zapfe and Hürzeler, 1957 by: (1) the presence

of a well-developed pliopithecine triangle on M/2 and M/3; (2) the more medially situated hypoconulid on M/1 and M/2; (3) a relatively narrower M2/, which is narrower instead of broader than the remaining upper molars; (4) the lower-crowned lower incisors; and (5) smaller dental size. *P. (P.) canmatensis* differs from other *Pliopithecus* s.s. spp. by: (1) the absolutely shorter P/3; and (2) the relatively narrower P/4, M/1 and, to lesser extent, M/2. With regard to dental size, *P. (P.) canmatensis* differs from *P. zhanxiangi* Harrison et al., 1991 and, to a lesser extent, *P. platyodon* Biedermann, 1863 by being smaller, thus most closely resembling *P. antiquus*, although being slightly smaller. *P. canmatensis*, like *P. antiquus*, differs from *P. piveteaui* Hürzeler, 1954 by displaying an absolutely longer M/3 that is also much longer than the M/2 (instead of being similarly-long or even slightly shorter). *P. canmatensis* differs from both *P. antiquus*

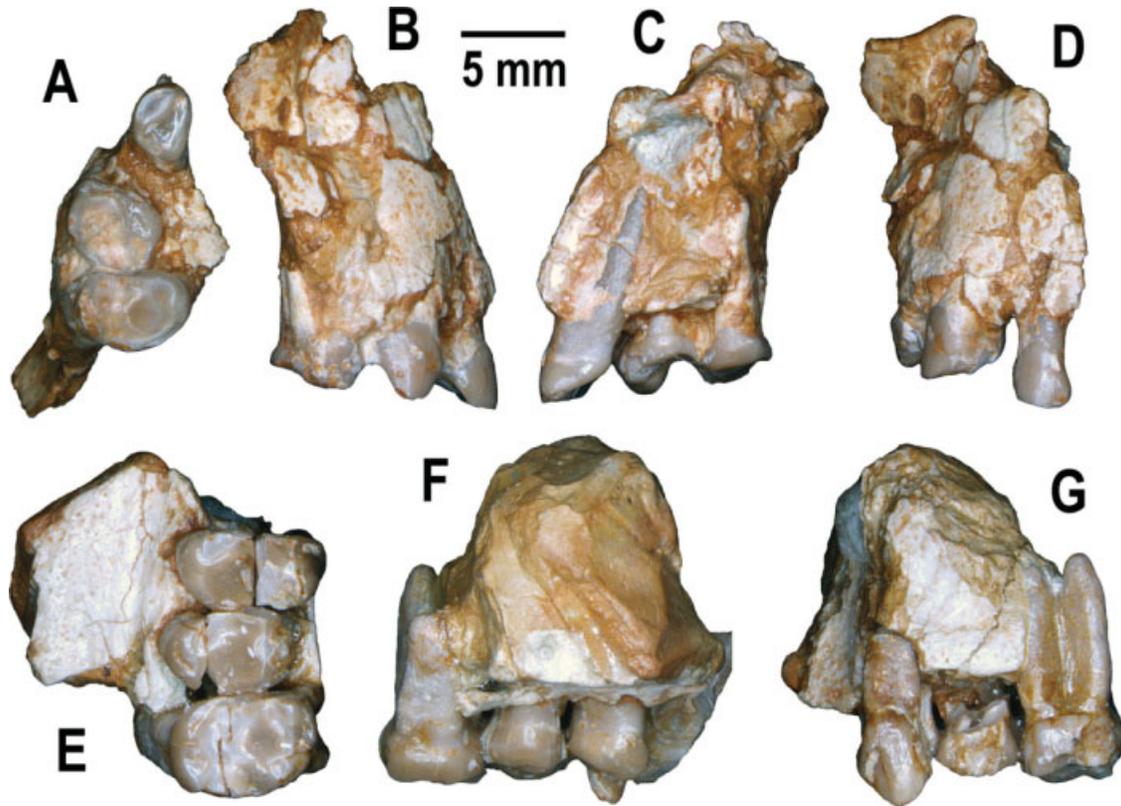


Fig. 5. Maxillary fragments of *Pliopithecus (Pliopithecus) canmatensis* sp. nov.: (A–D) Right female maxillary fragment with I2/P3/ (IPS41958; paratype) from ACM/C5-A8, in occlusal (A), buccal (B), lingual (C) and frontal (D) views; (E–G) Left maxillary fragment with P3/M1/ (IPS41983) from ACM/C5-C3, in occlusal (E), lingual (F), and buccal (G) views. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

and *P. piveteaui* by occlusal details of the lower molars, including: (1) larger hypoconid; (2) trigonid of the lower molars relatively larger and much higher as compared to the talonid; (3) more mesially positioned buccal cusplids as compared to the corresponding buccal ones (especially the protoconid as compared to the metaconid); and (4) wider buccal cingulid on lower molars, particularly in males, becoming clearly ledgelike between the protoconid and hypoconid (especially in M/3). Specifically, *P. canmatensis* further differs from *P. piveteaui* by: (1) absolutely shorter M/2; (2) relatively narrower P/4 and lower molars (particularly, the M/1), on average; and (3) apparently, the absence of a well-developed pliopithecine triangle on the M/1. Finally, *P. canmatensis* further differs from *P. antiquus* by: (1) lower molars with the protoconid less peripherally situated, resulting in a narrower mesial fovea mostly positioned on the lingual moiety of the crown; (2) hypoconulid not only medially situated in the M/1, but also in the M/2; (3) secondary cusplid (tuberculum sextum) on the distolingual corner of M/3; and (4) C/1, P/4, M/1 and M/2 relatively narrower and, except for the P/4, absolutely shorter, on average.

Holotype

Mandible IPS35036 (Figs. 2, 6A–C, 7A–B, 9A,B,H,I, N,O, and 11C) housed at the Institut Català de Paleontologia in Sabadell (Catalonia, Spain). See measurements in Tables 3 and 5.

Paratypes

Mandible IPS41981 (Figs. 3, 7F–G, 9E,F,L,R,S, and 11E), lower dental series IPS41719 (Figs. 4A–F, 7C–D, 9C,D,J,K,P,Q, and 11D) and IPS41955 (Fig. 4G, 7E, and 9G), maxillary fragments IPS41958 (Fig. 5A–D) and IPS41983 (Fig. 5E–G and 10C), and isolated upper and lower teeth IPS41715 (Fig. 10A), IPS41717 (Fig. 6I–M), IPS41718 (Fig. 1B, 8A–C, and 10D), IPS41720 (not figured), IPS41721 (Fig. 6D–H), IPS41722 (not figured), IPS41954 (not figured), IPS41956 (Fig. 1A, 8G–I, and 9T), IPS41957 (Fig. 6N–R), IPS41959 (Fig. 6S–W), IPS41960 (Fig. 8D–F and 9M), IPS41976 (Fig. 10B), and IPS41984 (Fig. 10E). See Table 1 for a short description and stratigraphic provenance of these remains and Tables 3–5 for measurements. Dental dimensions and proportions have been graphically depicted in Figures 12 and 13. All the paratypes are housed at the same institution as the holotype.

Type locality

ACM/C4-A1 (“Abocador de Can Mata, Cell 4, Sector A, Locality 1”), from the local stratigraphic series of Abocador de Can Mata (els Hostalets de Pierola, Catalonia, Spain).

Distribution

Species only recorded in several localities situated quite close to one another, within the limits of the new

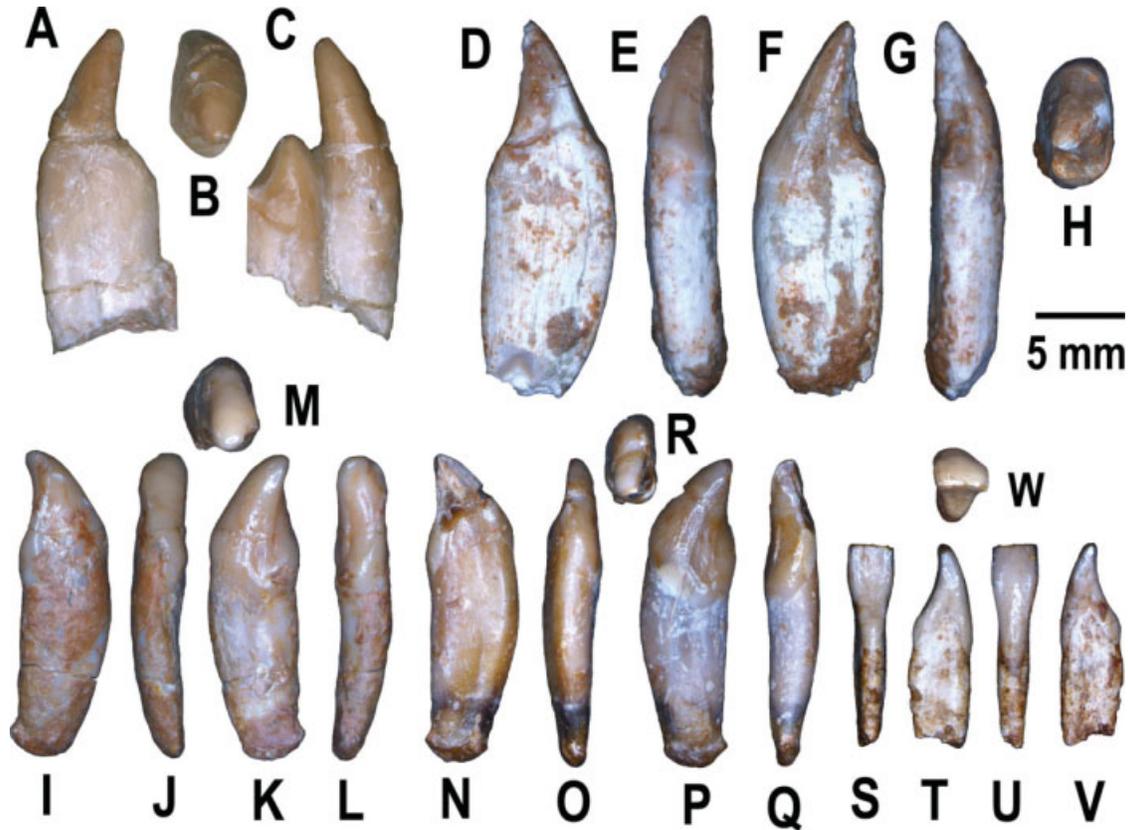


Fig. 6. Lower canines and incisors of *Pliopithecus (Pliopithecus) canmatensis* sp. nov.: (A–C) Right male C/1 (IPS35036; holotype) from ACM/C4-A1, in lingual (A), occlusal (B), and buccal (with P/3) (C) views; (D–H) Left male C/1 (IPS41721; paratype) from ACM/C4-Cb, in lingual (D), mesial (E), buccal (F), distal (G), and occlusal (H) views; (I–M) Left female C/1 (IPS41717; paratype) from ACM/C4-A1, in lingual (I), mesial (J), buccal (K), distal (L), and occlusal (M) views; (N–R) Left female C/1 (IPS41957; paratype) from ACM/C5-A8, in lingual (N), mesial (O), buccal (P), distal (Q), and occlusal (R) views; (S–W) Lower central incisor (IPS41959) from ACM/C5-A8, in lingual (S), mesial (T), labial (U), distal (V), and occlusal (W) views. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

phase of the Abocador de Can Mata in the Vallès-Penedès Basin (Catalonia, Spain).

Stratigraphic range

C5r.3r subchron, from ~11.7 to ~11.6 Ma, corresponding to the Mammal Neogene biozone MN8 [sensu Mein and Ginsburg (2002)], Late Aragonian (Middle Miocene) in the continental chronostratigraphic scale.

Etymology

From the local toponym “Can Mata de la Garriga”, which gives name to the rubbish dump where the type locality is situated.

DESCRIPTION

Preservation of the specimens

The collection of pliopithecoid dentognathic remains from ACM includes two relatively complete mandibles, two postcanine tooththrows belonging to a single individual, a partial lower series, several maxillary fragments, and many isolated teeth. When all these specimens are considered together, all the permanent dentition can be described, except for the I1/ and the male C1/, whereas a

single dP/4 is the only representative of the deciduous dentition.

Remains from ACM/C4-A1 (the type locality) include a male mandible with right and left postcanine series and right canine (IPS35036; holotype); a left P4/crown with partial roots (IPS41715), showing a moderate degree of wear; a left female C/1 (IPS41717), which only shows a very slight degree of wear; and a right M2/ crown (IPS41718) displaying a slight degree of wear with dentine exposure at the tips of the two mesial cusps, and preserving most of the distobuccal root, whereas the mesiobuccal root and the fused lingual root are broken at the base. These specimens from C4-A1 were not found closely associated, but scattered across an area of 20–25 m². As indicated by canine morphology, at least two individuals (a male and a female) are represented. However, there is no reason to assume that the two isolated upper cheek teeth belong to one of these individuals, or even to the same individual. The mandible IPS35036 is a quite completely preserved mandible with a few associated small bone fragments. It preserves the two postcanine tooththrows and the right canine, which is placed more lingually than the P/3 due to bone distortion. All the incisors from this mandible, as well as the left canine, are missing; the alveoli of these teeth are partially preserved and filled with sediment, indicating that these teeth were lost post mortem. On the basis of canine size

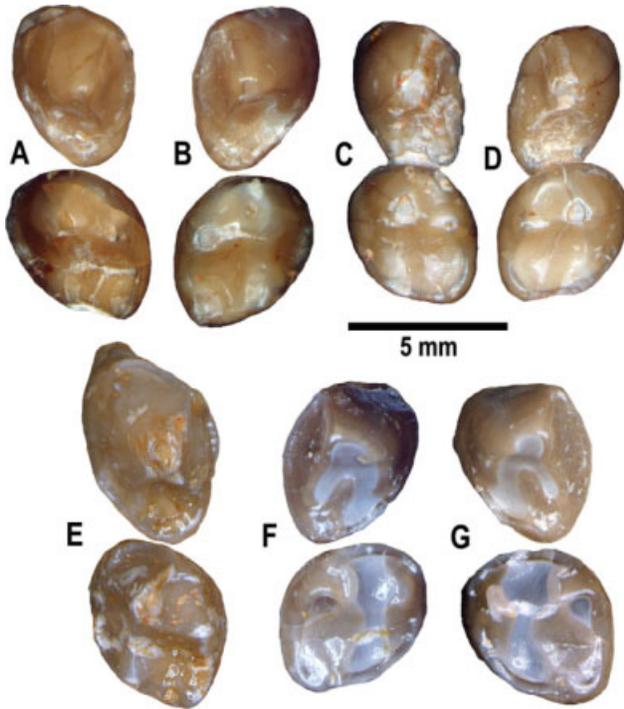


Fig. 7. Lower premolars (P/3-P/4) of *Pliopithecus (Pliopithecus) canmatensis* sp. nov., in occlusal view: (A, B) Male individual (IPS35036; holotype) from ACM/C4-A1, left (A) and right (B) sides; (C, D) Female individual (IPS41719; paratype) from ACM/C4-Cb, left (C) and right (D) sides; (E) Male individual (IPS41955; paratype) from ACM/C5-A8, left side; (F, G) Male individual (IPS41981; paratype) from ACM/C5-C3, left (F) and right (G) sides.

and shape, this specimen is attributable to a male individual. It must correspond to a fully adult specimen, because all the molars as well as the canine are fully erupted and display a moderate to medium degree of wear. This specimen preserves the two mandibular corpora and the symphysis, as well as a considerable part of the two rami (particularly on the left side) up to the sigmoid notch. Both rami are damaged at the gonion level; they also lack the uppermost part of the mandibular condyle, the coronoid apophysis, and the distalmost part of the ramus, although the right one is more incompletely preserved, further lacking the mesialmost part of the ramus. This specimen is distorted, particularly at the right side, due to multiple oblique, diagenetically generated fractures. The latter run from the lower part of the ramus at the level of M/2 toward the roots of P/3 and C/1 on both the lingual and buccal sides and to the lowermost point of the mandibular symphysis as well. They are partially infilled with sediment, which is particularly marked in the crack that runs between the alveoli of the right I/2 (missing) and C/1, which is as much as 2-mm wide on the buccal side and about 3–4 mm on the lingual side. As a result, the P/3 and C/1 are upwardly and somewhat buccally displaced, whereas most of the right corpus and ramus are buccally inclined outwards and slightly upwardly displaced. This causes the right tooth-row to be displaced from the occlusal plane toward the buccal side. Unlike the right mandibular body, the left one is only minimally distorted, although it also displays several diagenetic vertical fractures, at the mesial and distal levels of the M/2. Despite these cracks, no significant distortion or loss of bone has occurred, so that the several mandibular fragments fit together perfectly. Displacement only affects the position of the left M/3 inside

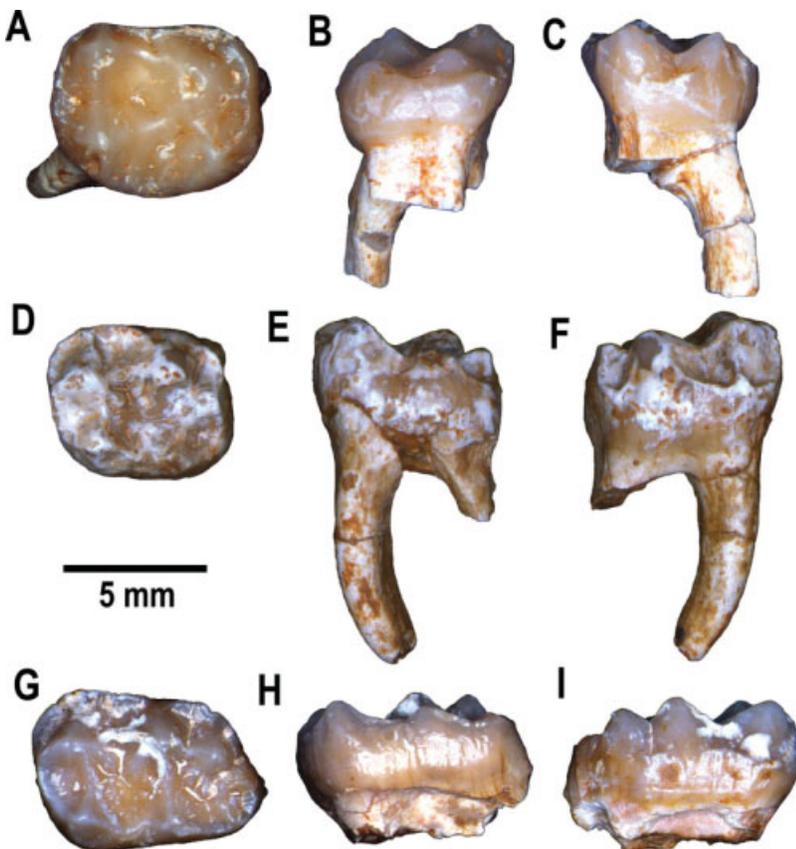


Fig. 8. Detailed morphology of upper and lower molars of *Pliopithecus (Pliopithecus) canmatensis* sp. nov.: (A–C) Right M2/ (IPS41718; paratype) from C4-A1 (type locality), in occlusal (A), lingual (B), and buccal (C) views; (D–F) Right M2 (IPS41960; paratype) from ACM/C5-A8, in occlusal (D), lingual (E), and buccal (F) views; (G–I) Right M3 (IPS41956; paratype) from ACM/C5-A8, in occlusal (G), lingual (H), and buccal (I) views.

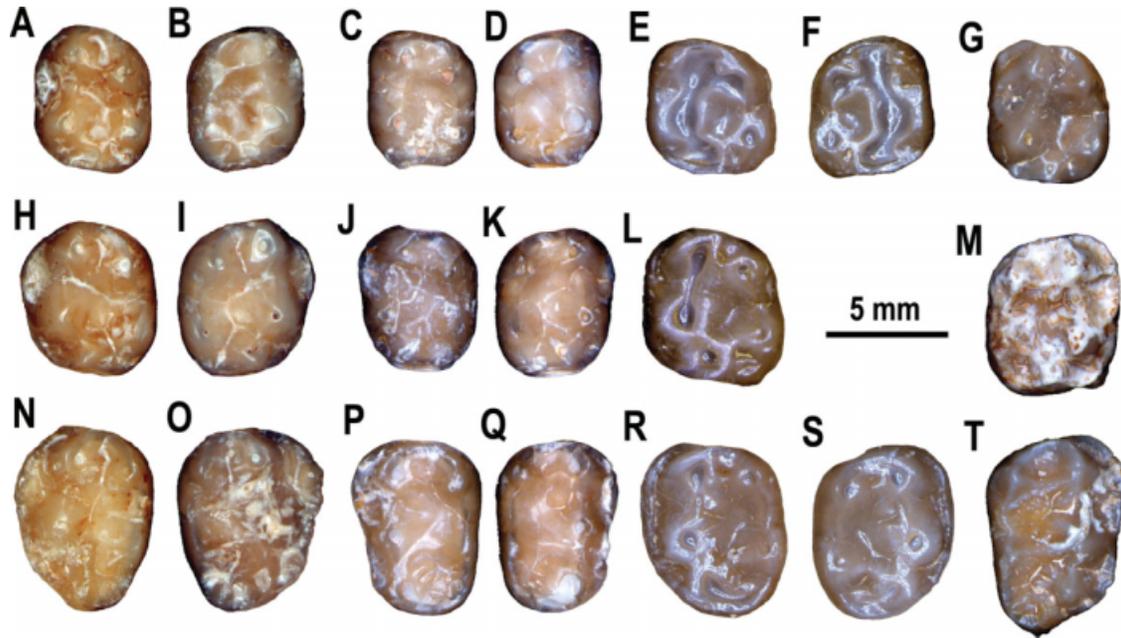


Fig. 9. Lower first (A–G), second (H–M), and third (N–T) molars of *Pliopithecus* (*Pliopithecus*) *canmatensis* sp. nov., in occlusal view: Right and left, male (IPS35036; holotype) from ACM/C4-A1 (A, B, H, I, N, O); right and left, female (IPS41719; paratype) from ACM/C4-Cb (C, D, J, K, P, Q); right and left, male (IPS41981; paratype) from ACM/C5-C3 (E, F, L, R, S); left, male (IPS41955; paratype) from ACM/C5-A8 (G); right, unsexed (IPS41960; paratype) from ACM/C5-A8 (M); right, unsexed (IPS41956; paratype) from ACM/C5-A8 (T).

its alveolus, being somewhat distolingually resituated from anatomical position. As a result, the occlusal surface of this tooth is artifactually positioned outside the occlusal plane defined by the remaining postcanine teeth, and an artifactually generated gap is produced between left M/2 and M/3.

Remains from ACM/C4-Cb include two mandibular fragments (IPS41719) as well as three isolated teeth: a left M/2 crown (IPS41720) with partial roots, with an eroded and badly damaged occlusal surface (no description is possible); a complete left male C1/ (IPS41721); and a fragment of right upper premolar with partial root (IPS41722). The two postcanine series were found very closely associated with one another, and there can be no doubt that they belong to the same individual. On the contrary, the isolated remains were not found in close association. At least two different individuals must be represented at this site, because both the canine IPS41721 and the isolated molar IPS41720 cannot belong to the same individual as IPS41719. The latter includes two (right and left) partial mandibular corpora with complete postcanine series, attributable to a female individual on the basis of overall size and morphology of the P/3. The symphysis of this specimen is lacking except for its lowermost portion. The left fragment is basally broken at the level of M/2–M/3, where it preserves the origin of the mesial margin of the ramus, as well as at the level of distal C/1, where it preserves a distal portion of the C/1 root and base of the crown, the lower part of the incisors' alveoli, and the lowermost part of the symphysis. The right mandibular fragment is broken distally from the M/3, where it preserves a larger portion of the basal part of the mesial margin of the

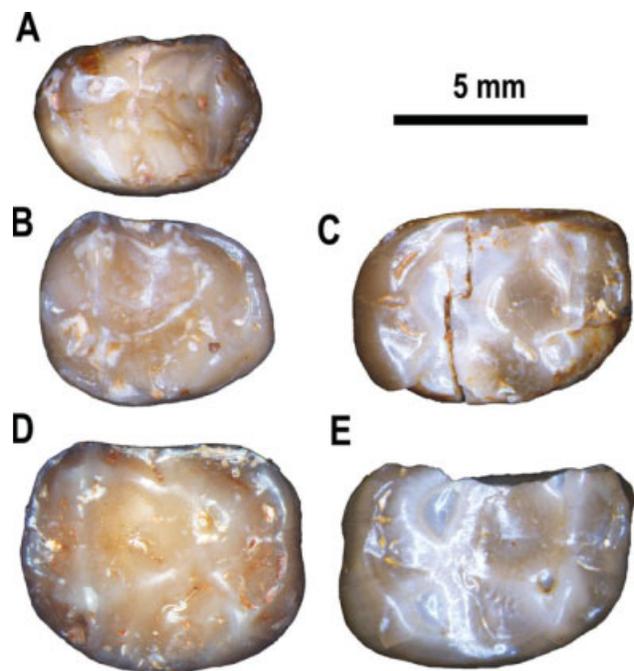


Fig. 10. Upper cheek teeth of *Pliopithecus* (*Pliopithecus*) *canmatensis* sp. nov., in occlusal view: (A) Left P4/ (IPS41715; paratype) from ACM/C4-A1 (type locality); (B) Right dP4/ (IPS41976; paratype) from ACM/C5-C2; (C) Left M1/ (IPS41983; paratype) from ACM/C5-C3; (D) Right M2/ (IPS41718; paratype) from ACM/C4-A1 (type locality); (E) Partial left M2/ (IPS41984; paratype) from ACM/C5-C3.

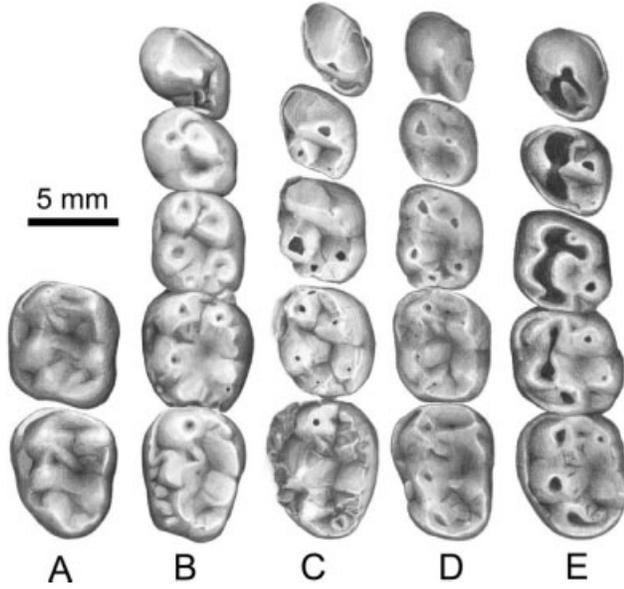


Fig. 11. Drawings of the lower postcanine series of *Pliopithecus antiquus* from France (A, B) and *P. (P.) canmatensis* sp. nov. from ACM (C-E): (A) male (?) left (reversed) M2-M/3 from La Grive PB A (holotype of *P. a. chantrei*, here considered a junior synonym of the nominal subspecies); (B) male left P/3-M/3 from Sansan (holotype of *P. antiquus*); (C) male right (reversed) P/3-M/3 (IPS35036) from ACM/C4-A1 (holotype of *P. canmatensis*); (D) female left P/3-M/3 (IPS41719) from ACM/C4-Cb (paratype); and (E) male left P/3-M/3 (IPS41981) from ACM/C5-C3 (paratype). Original art by Marta Palmero; French specimens were drawn from good quality cast, whereas the remaining ones were drawn from original specimens.

ramus; mesially, it is broken just mesial to the P/3, although it still preserves the lowermost part of the symphysis.

Remains from ACM/C5-A8 include some isolated specimens as well as mandibular and maxillary fragments with partial series: a right (?) complete I/1 (IPS41959), which only displays a slight degree of wear with no dentine exposure; a right M/2 crown (IPS41960) that is completely preserved except for very small enamel fragments close to the cemento-enamel junction, and which further preserves the entire mesial root and the basal-most part of the distal one; a right M/3 crown (IPS41956) with only minimal damage on the tip of the entoconid and some accessory cuspid, but with no appreciable wear, the roots being broken at the cemento-enamel junction; a left female C/1 (IPS41957), preserving the root and a large portion of the crown (except for a lingual portion, above the cemento-enamel junction); a left male series C/1-M/1 (IPS41955); and a right female maxillary fragment (IPS41958). Although some mandibular bone fragments are preserved in IPS41955, particularly those attached to the roots of P/4, the teeth that compose this dental series are not exactly in life position, standing together with one another merely because sediment has not been completely removed. The M/1 is displaced distally, while the P/3 is displaced mesially; the canine is apparently more basally positioned, and probably it only consists of the unworn germ that was still

TABLE 3. Dental measurements (in mm) of *Pliopithecus (Pliopithecus) canmatensis* sp. nov. from the local series of Abocador de Can Mata (Catalonia, Spain)

Museum record no.	Tooth	MD	BL(m)	BLd	B/L (%)
IPS35036	r C/1	6.6	3.9		59.1
IPS35036	r P/3	5.3	3.7		69.8
IPS35036	l P/3	5.3	3.9		73.6
IPS35036	r P/4	4.6	4.5		97.8
IPS35036	l P/4	4.6	4.4		95.7
IPS35036	r M/1	5.6	5	4.9	89.3
IPS35036	l M/1	6.2	4.8	4.8	77.4
IPS35036	r M/2	6.5	5.7	5.3	87.7
IPS35036	l M/2	6.7	5.5	5.3	82.1
IPS35036	r M/3	7.4	6.1	5.4	82.4
IPS35036	l M/3	7.8	6.6	6.3	84.6
IPS41715	P4/	4.2	5.9		140.5
IPS41717	C/1	5.0	3.1		62.0
IPS41718	M2/	6.2	7.5		121.0
IPS41719	r P/3	5.0	3.6		72.0
IPS41719	l P/3	4.6	3.4		73.9
IPS41719	r P/4	4.6	4.1		89.1
IPS41719	l P/4	4.5	4.0		88.9
IPS41719	r M/1	5.5	4.4	4.4	80.0
IPS41719	l M/1	5.7	4.4	4.3	77.2
IPS41719	r M/2	6.0	4.9	4.9	81.7
IPS41719	l M/2	6.0	5.0	4.7	83.3
IPS41719	r M/3	6.9	5.0	4.6	72.5
IPS41719	l M/3	7.1	5.2	4.6	73.2
IPS41720	M/2	>6.2	>4.6	>4.8	
IPS41721	C/1	7.1	3.9		54.9
IPS41955	C/1	-	>9.8		
IPS41955	P/3	6.2	4.3		69.4
IPS41955	P/4	5.8	4.3		74.1
IPS41955	M/1	6.0	4.7	5.0	83.3
IPS41956	M/3	8.6	5.7	5.2	66.3
IPS41957	C/1	5.0	3.0		60.0
IPS41958	I2/	3.2	3.4		106.3
IPS41958	C1/	5.0	4.5		90.0
IPS41958	P3/	3.9	6.4		164.1
IPS41959	I/1	2.6	3.4		130.8
IPS41960	M/2	6.8	5.4	5.3	79.4
IPS41976	dP4/	5.1	6.4		125.5
IPS41954	C/1	6.5	3.8		58.5
IPS41981	r I/1	2.7	4.1		151.9
IPS41981	l I/1	2.8	3.9		139.3
IPS41981	r I/2	2.9	4.2		144.8
IPS41981	r P/3	5.2	4.6		88.5
IPS41981	l P/3	5.3	4.2		79.2
IPS41981	r P/4	4.8	4.8		100.0
IPS41981	l P/4	5.0	4.8		96.0
IPS41981	r M/1	5.7	5.0	5.3	93.0
IPS41981	l M/1	5.9	5.0	5.3	89.8
IPS41981	r M/2	6.1	5.6	(5.9)	96.7
IPS41981	l M/2	6.1	5.5	5.8	95.1
IPS41981	r M/3	7.2	5.9	5.9	81.9
IPS41981	l M/3	7.3	5.8	5.9	80.8
IPS41983	P3/	4.1	7.0		170.7
IPS41983	P4/	4.2	(6.6)		152.4
IPS41983	M1/	(5.3)	7.3		137.7
IPS41984	M2/	>5.7	7.8		

The locality of provenance of each specimen is specified in Table 1. *Abbreviations:* MD, mesiodistal; BL, buccolingual; B/L, breadth (BL)/length (MD) \times 100; m, mesial; d, distal; r, right; l, left.

inside the crypt or only becoming to emerge when the animal died. All the postcanine teeth display only a very slight degree of wear, and the canine shows no wear at all. Although not completely formed, the canine is quite high crowned, indicating that it belonged to a male spec-

TABLE 4. Descriptive statistics of canine and cheek teeth measurements (in mm) of *Pliopithecus* (*Pliopithecus*) *canmatensis* sp. nov. from the local series of *Abocador de Can Mata* (Catalonia, Spain)

Tooth	Mesiodistal length (MD)				Buccolingual breadth (BL)				Breadth/length index (%)			
	N	Mean	SD	Range	N	Mean	SD	Range	N	Mean	SD	Range
dP4/	1	5.10			1	6.40			1	125.5		
C1/f	1	5.00			1	4.50			1	90.0		
P3/	2	4.00	0.14	3.9–4.1	2	6.70	0.42	6.4–7.0	2	167.4	4.67	164.1–170.7
P4/	2	4.20	0.00	4.2–4.2	2	6.25	0.49	5.9–6.6	2	148.8	11.74	140.5–157.1
M1/	1	5.30			1	7.30			1	137.5		
M2/	1	6.20			2	7.65	0.21	7.5–7.8	1	121.0		
C/1 m	3	6.73	0.32	6.5–7.1	3	3.87	0.06	3.8–3.9	3	57.5	2.27	54.9–59.1
C/1 f	2	5.00	0.00	5.0–5.0	2	3.05	0.07	3.0–3.1	2	61.0	1.41	54.9–59.1
P/3	7	5.27	0.48	4.6–6.2	7	3.96	0.43	3.4–4.6	7	75.2	6.71	69.4–88.5
P/4	7	4.84	0.45	4.5–5.8	7	4.41	0.31	4.0–4.8	7	91.7	8.80	74.1–100.0
M/1	7	5.80	0.24	5.5–6.2	7	4.89	0.38	4.4–5.3	7	84.3	6.43	77.2–93.0
M/2	7	6.31	0.34	6.0–6.8	7	5.46	0.39	4.9–5.9	7	86.6	6.9	79.4–96.7
M/3	7	7.47	0.57	6.9–8.6	7	5.77	0.54	5.0–6.6	7	77.4	6.8	66.3–84.6

All measurements are for mixed sexes except the canines.
 Abbreviations: N, sample size; SD, standard deviation; m, male; f, female.

TABLE 5. Mandibular measurements (in mm) of *Pliopithecus* (*Pliopithecus*) *canmatensis* sp. nov. from the local series of *Abocador de Can Mata* (Catalonia, Spain)

	IPS41981	IPS41719	IPS35036
Symphysis height	22.5		23.5
Corpus height at P/3 (right) ^a	18.3	15.4	22.5 (20.8) ^d
Corpus height at P/3 (left) ^a	17.8	15.2	20.2
Corpus height at P/4 (right) ^a	16.5	13.8	19.9 (12.2) ^d
Corpus height at P/4 (left) ^a	17.3	14.4	18.3
Corpus height at M/1 (right) ^a	(15.8) ^d	13.7	16.7
Corpus height at M/1 (left) ^a	16.7	13.4	15.9
Corpus height at M/2 (right) ^a	14.5	12.3	14.2
Corpus height at M/2 (left) ^a	14.8	12.4	14.9
Corpus height at M/3 (right) ^a	13.4	12.8	14.2
Corpus height at M/3 (left) ^a	12.1		14.5
Length of postcanine series (right)	28.6	27.4	30.8 (29.5) ^d
Length of postcanine series (left)	30.0	27.5	32.8 (29.5) ^d
Ramus height (left) ^b	(21.0) ^d		(24.0) ^d
Mandibular length (left) ^c	68.3		>67.5

^a Measured on the buccal side and perpendicular to the alveolar plane.
^b Measured on the buccal side from the lowermost point of the sigmoid notch to the lowermost edge of the ramus, perpendicular to the alveolar plane.
^c Measured from infradentale to the posteriormost point of the mandibular condyle (not in the sagittal plane).
^d Estimated values between parentheses.

imen. The crown of the canine displays a diagenetic fracture, and a postdepositional fracture without loss of material and minimal distortion; the crown of the P/3 is also damaged at the tip. The maxillary fragment IPS41958 preserves the I2-/P3/ series. These teeth display a relatively advanced degree of wear, with abundant dentine exposure particularly on the buccal moiety

of the crowns. On the basis of canine basal dimensions (height cannot be measured), this specimen is attributable to a female individual. The bone is somewhat diagenetically crushed and distorted, with the several fractures filled with sediment. Nonetheless, the degree of distortion is slight. The nasal aperture rim is not preserved, but there is a portion of the lower orbital rim, which is situated 16 mm above the alveolar level. At the alveolar level, the specimen is broken just beneath the distobuccal and the lingual roots of the P3/ (the former being only partially preserved), while the portion of the lower orbital rim further continues somewhat distally. All these remains from C5-A8 were not found in close association, and at least two individuals (a male and a female) must be represented.

Locality ACM/C5-C2 has only yielded an isolated right dP4/ crown with the basalmost part of the roots preserved (IPS41976), displaying a slight degree of wear.

Finally, locality ACM/C5-C3 has yielded another relatively complete mandible (IPS41981), a left maxillary fragment with partial series (IPS41983), and two isolated teeth: a left male C/1 (IPS41954) with root and unworn partial crown (only the base is preserved, since the apex is broken away); and a left M2/ (IPS41984) with almost complete roots (only a very small apical portion of the distobuccal root is missing) and partial crown (lacking the mesial portion of the protocone, the mesio-buccal aspect of the paracone, and the mesial fovea), which displays a moderate degree of wear with dentine exposure on the four main cusps (particularly the lingual ones). The mandible IPS41981 preserves the two mandibular corpora, the partial two rami, and the symphysis. There are two major fractures, one affecting the right corpus below M/1 (with some loss of bone below the alveolar level), and the other one affecting the left C/1 alveolus. The teeth display a relatively advanced degree of wear; the two canines and the left I/2 are missing, and apparently they were not originally preserved, because their alveoli (externally broken in the case of the canines) appear filled with sediment. The left ramus is completely preserved except for the gonial region, whereas the right one further lacks the condyle, the coronoid process, and the sigmoid notch. The symphyseal region is somewhat superficially eroded, but its shape can be readily ascertained. Overall, this mandible shows

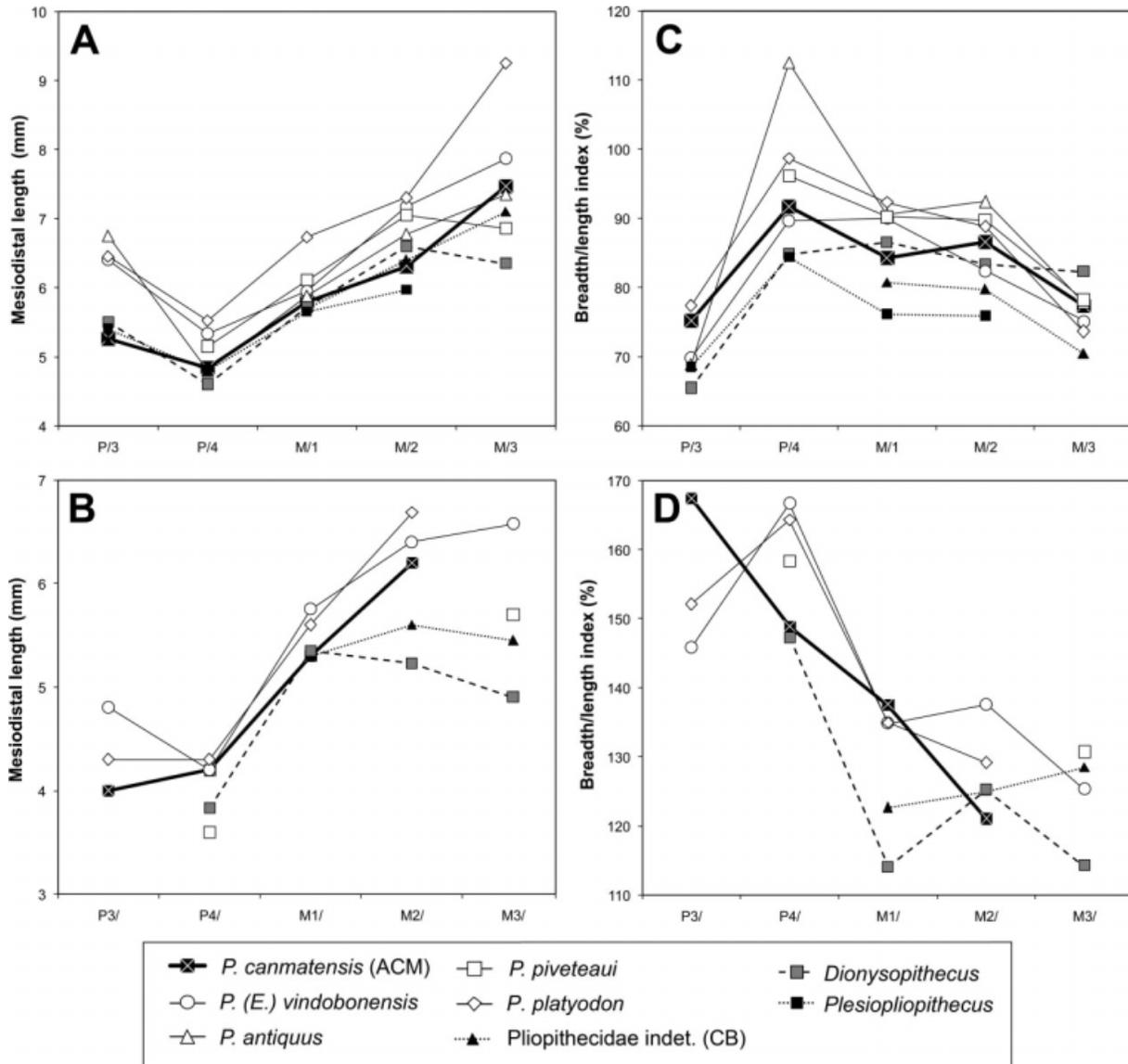


Fig. 12. Upper and lower cheek-teeth length and proportions in *Pliopithecus* (*Pliopithecus*) *canmatensis* sp. nov. from the local series of Abocador de Can Mata (Catalonia, Spain), as compared to other, similarly sized pliopithecids: (A) Mesiodistal length (in mm) of lower series; (B) Mesiodistal length (in mm) of upper series; (C) Breadth/length index (%) of lower series; (D) Breadth/length index (%) of upper series. Measurements were taken from the following sources: Zapfe (1960) for *P. (E.) vindobonensis*; Harrison and Gu (1999) for *Dionysopithecus shuangouensis*; Hürzeler (1954) and taken from casts for *P. (P.) antiquus*; Ginsburg (1975) and Ginsburg and Mein (1980) for *P. (P.) piveteaui*; Harrison et al. (1991) and taken from casts for *P. (P.) platyodon*; Zapfe (1961), Ginsburg and Mein (1980) and taken from casts for *Plesiopliopithecus* spp.; Alba and Moyà-Solà (in preparation) for *Pliopithecidae* indet. from Castell de Barberà; and this study for *P. (P.) canmatensis*.

some distortion, with the left body and ramus being slightly displaced downwards and inwards with respect to the rest of the mandible. On the basis of overall size and P3 morphology, the mandible IPS41981 most likely belongs to a male specimen, although this cannot be unambiguously assessed, because the canines are missing. With regard to the maxillary fragment IPS41983, it preserves a P3-M2/ series with an advanced degree of wear. The crowns of the three preserved cheek teeth are broken at the middle, but only very minor portions of the occlusal surface are missing, so that measurements can be readily taken. The buccal root of P4/ is also missing, while the remaining ones are largely preserved. Enamel fragments are missing from the buccal moiety of the P3/,

small mesiolingual and distolingual portions of the crown and buccal wall of the paracone of P4/, and the mesiolingual, distolingual, and distobuccal walls of the crown of M1/. Not much maxillary bone is preserved, except for a portion of the palate at the level of the premolars.

Description of the mandible and maxilla

Currently available evidence of the face of *Pliopithecus canmatensis* sp. nov. is quite restricted (see Fig. 5). The maxillary fragment IPS41958 displays two infraorbital foramina at the level of P3-/C1/ and overall indicates the presence of a short face with a shallow clivus (although the morphology of the subnasal floor is not preserved).

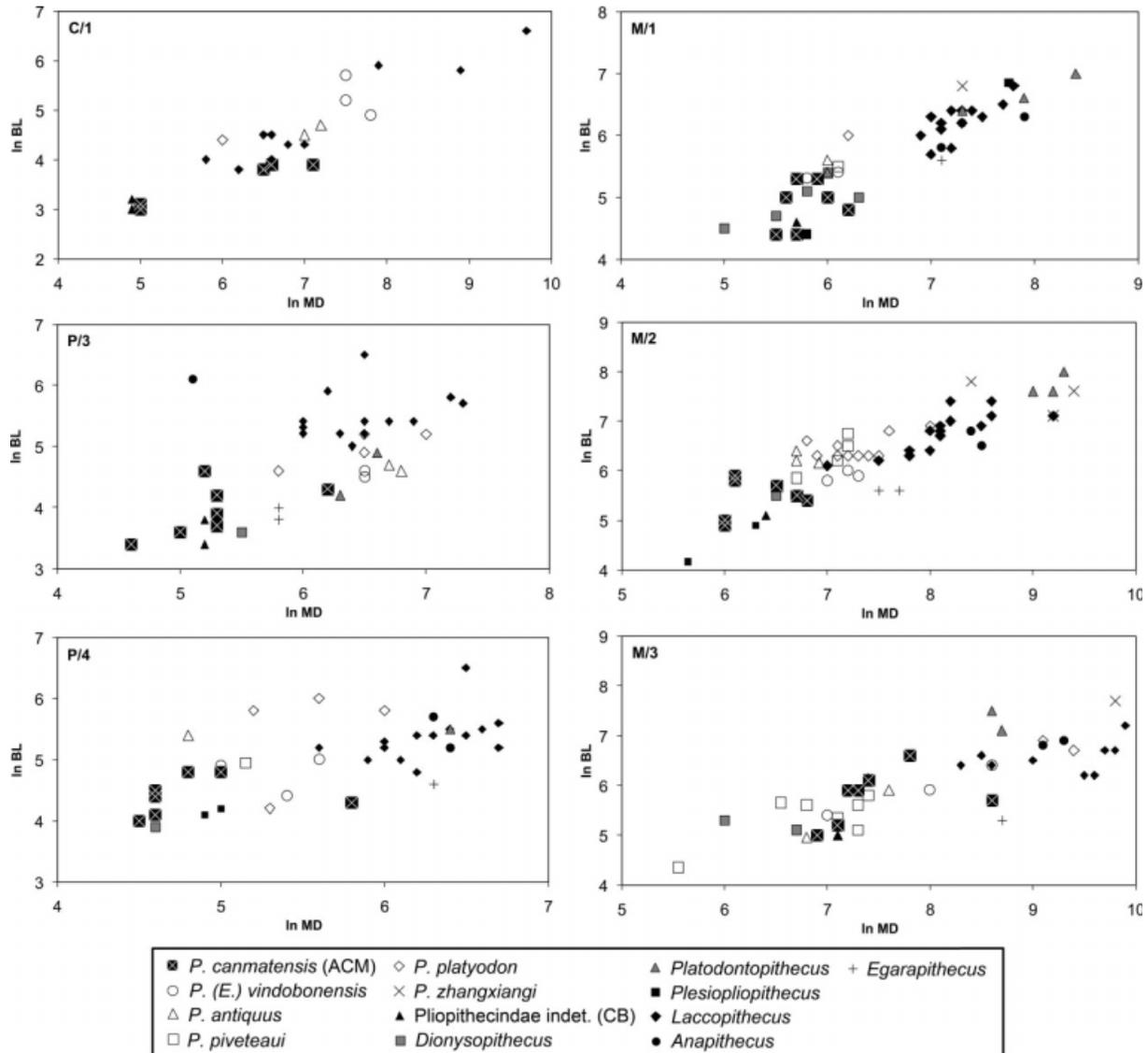


Fig. 13. Bivariate plots of buccolingual breadth (BL) versus mesiodistal length (MD) in lower cheek teeth of *Pliopithecus* (*Pliopithecus*) *canmatensis* sp. nov. from the local series of Abocador de Can Mata (Catalonia, Spain) and other pliopithecids. Measurements were taken from the same sources indicated in Figure 12, as well as Pan et al. (1989) for *Laccopithecus robustus*; Harrison and Gu (1989) for *Platodontopithecus jianghuaiensis*; Moyà-Solà et al. (2001) for *Egarapithecus narcisoi*; Welcomme et al. (1991) for *Plesiopithecus priensis* (not included in Figure 12); Harrison et al. (1991) for *Pliopithecus zhangxiangi* (not included in Figure 12); and taken from casts for *Anapithecus hernyaki*.

In this specimen, attributed to a female individual, the canine crown is separated from the lateral incisor by a narrow diastema (2 mm long on the alveolar level) that must have accommodated the crown of the lower canine.

Mandibular morphology can be much more readily ascertained, because three relatively complete specimens have been thus far recovered (Figs. 2–4). On this basis, the mandible of this taxon can be described as long and relatively shallow with regard to the corpora and, especially, the rami. The mandibular body is highest at the symphysis, which is quite deep, progressively becoming shallower distally until M/2 and M/3. As shown by IPS41981, the incisors are quite vertically implanted (i.e. only slightly procumbent). Both IPS35036 and IPS41981 show that, in lateral view, the symphysis displays a convex profile, with its apicalmost portion being relatively

straight, but progressively curving toward its lowermost portion, until ending approximately below the mental foramen (IPS41981 and IPS41719) or slightly distally (IPS35036), that is, at the level of P/3 or P/4. On the lingual side, the symphysis displays a moderately steep, shelflike torus that occupies the upper two thirds and extends until the level of P/4-M/1, whereas the lower third is vertical and displays no simian shelf. The mental foramen is situated at about the level of the P/3, approximately midway between the base of the corpus and the alveolar level (IPS41981 and IPS35036), or slightly closer to the base of the corpus (IPS41719). Apparently, there is no diastema between C/1 and P/3, although this assertion should be taken cautiously, because this region is distorted and/or severely damaged on the several available specimens. The P/3 is moderately sectorial, and its main

axis is slightly oblique (buccally rotated) with regard with the main mesiodistal axis of the remaining postcanine teeth. The sectoriality of the P/3 is more marked in the male specimens (IPS35036, IPS41981, and IPS41955) than in the female ones (IPS41719). This can be best appreciated in the unworn specimen IPS41955. The remaining male P/3 already display a broad and steep wear facet on the mesial wall of the crown (with abundant dentine exposure in IPS41981, which displays the most advanced degree of wear), whereas on the female specimens, on the contrary, wear is restricted to the mesial crest of the crown. Overall, available evidence indicates the existence in male specimens of a honing complex for shearing the upper canine against the lower third premolar, whereas the lower canine was shorn against the mesial aspect of the upper canine.

Although the shape of the dental arcades in occlusal view cannot be readily reconstructed due to distortion, it must have been approximately U-shaped and quite narrow, with the right and left postcanine series being parallel or only slightly diverging. The corpus is narrow at the level of premolars and M/1 and much broader at the level of M/2 and M/3. The mesial margin of the ramus originates at the level of mid to distal M/3, but it soon becomes vertical, so that in lateral view it only does not overlap with the M/3 (IPS41981) or only overlaps with its distal portion (IPS35036 and, apparently, IPS41719 as well). The extramolar sulcus between the mesial portion of the ramus and the distobuccal aspect of the M/3 is very wide. The ramus is low, especially as compared to the length of the mandible. Approximately at the alveolar level of the incisors, the mesial margin of the ramus abruptly curves backwards and then abruptly descends vertically, so that the coronoid process is clearly asymmetrical. The sigmoid notch is long and moderately shallow, while the condyle is slightly less protruding than the coronoid process. The distal margin of the ramus is apparently less verticalized than the mesial one. On the lingual side of the ramus, as judged from IPS35036, the mandibular foramen is situated at about two thirds of ramus height, at about the level of the lowest point of the mandibular notch. A marked endocoronoid ridge originates from the distolingual aspect of the third molar and progressively curves upwards until the level of the mandibular foramen, just mesial to it and below the distalmost aspect of the coronoid process, where it becomes much badly defined and further originates an ill-defined crest directed toward the mandibular condyle.

Description of the lower dentition

Lower incisors. Spatulate teeth with a waisted morphology (mesiolingually compressed root and crown base), with the crown progressively expanding mesiodistally and becoming labiolingually compressed toward the apex (see Fig. 6S–W). There is a moderately developed, bulbous basal thickening at the lingual aspect of the crown base, whereas on the mesial and distal sides, the cemento-enamel junction displays an inverted-V shape. In occlusal view, the labial contour of the crown wall is slightly convex, whereas the lingual side above the basal thickening is somewhat concave, further displaying two slight marginal ridges, which descend from the mesial and distal ends of the crown apex toward the basal thickening. The I/1 is a spatulate and nearly symmetrical tooth, whereas the I/2 displays a more asymmetrical crown, being higher on the mesial than on the distal occlusal end. In the I/1, the marginal lingual ridges define

a V shape, whereas on the I/2 they rather define a U, with the distal ridge markedly curving, in lingual view, along the distal edge of the crown, until merging with the distal end of the occlusal edge. At least in the I/2, there is a weak lingual vertical pillar above the basal thickening, which separates the marked concavity on the distal moiety of the crown from the much flatter mesial moiety.

Lower canines. IPS41957 and IPS41717 are attributable to female specimens on the basis of their low crown (8.1–8.5 mm on the buccal side) as well as occlusal morphology (see Fig. 6A–R). The female canine displays a blunt occlusal edge instead of a pointed apex. The crown base is buccolingually compressed (breadth-length index 60–62%), assuming that the mesiodistal axis is defined by the largest basal crown dimension; the root, which is somewhat higher than the crown, is also buccolingually compressed throughout its length. The crown displays an elliptical basal outline, whereas the root tends to display a biconvex contour on the buccal side, and a flat profile on the lingual one. The crown is much higher on the buccal than on the lingual side. The cemento-enamel junction is approximately horizontal on the buccal side, whereas on the lingual side it displays an inverted-V shape. In occlusal view, the crown is convex on the mesial and buccal aspects, but it progressively becomes flatter toward the lingual side, until becoming concave at the distolingual aspect of the crown. A fine cristid descends from the apex in mesiolingual direction, merging with the subtle lingual cingulid situated on the distolingual corner of the crown, just above the cemento-enamel junction. In IPS41717, a wear facet for the I2/ can be discerned on this area. Another fine cristid descends from the apex of the crown across the buccal wall of the crown, progressively disappearing before reaching the crown base; there is no distinct buccal cingulid.

The male lower canine, represented by four available specimens, is much stouter and pointed than the female specimens, further being somewhat higher than the female canine. The best-preserved specimen IPS41721, showing a moderate degree of wear, displays a buccal crown height of 8.1 mm, whereas the root is about 14.0 mm high. The IPS35036 specimen is generally comparable to the above-mentioned specimen in both size and shape, whereas the partial specimen IPS41954, as far as it can be appreciated, appears to be similarly stout but displays a shorter crown base and root. Nevertheless, the unworn specimen IPS41955 indicates that crown height on the buccal side was of about 10 mm, indicating a moderate degree of canine height sexual dimorphism. The crown base is about as buccolingually compressed (breadth/length index 55–59%) as in female specimens (assuming that the major crown basal dimension represents the mesiodistal axis) and displays an elliptical outline in occlusal view. On buccal or lingual view, the mesial profile of the crown is slightly convex, whereas the distal one is slightly concave, although it flattens as wear increases (as in IPS35036); a short but conspicuous vertical medial sulcus can be still appreciated in IPS41721. This distal portion of the crown is delimited by two cristids, the distolingual one being sharper and reaching the crown apex (as shown by IPS41955); in the apparently unworn but broken specimen IPS41954, these two fine cristids can be discerned close to the base on the distal aspect of the crown. Unlike the buccal side of the crown, which is clearly convex, the lingual aspect

of the crown is almost flat, being mesially delimited by a sharp mesiolingual cristid that descends from the apex and ends in a conspicuous triangular thickening of the enamel before reaching the crown base. This thickening is broken away in IPS41721, but can be clearly ascertained in IPS31036 and IPS41955. A very tenuous and shallow mesial sulcus can be appreciated on the lower moiety of the crown in IPS41727. IPS35036 shows a small wear facet for the I2/ on the mesial aspect of the crown apex. Regarding the crown base, in male canines, as in female ones, the cemento-enamel junction somewhat ascends on the lingual side, shaping an inverted V, whereas on the buccal side it is rather horizontal. From the above-mentioned enamel thickening at the end of the mesiolingual cristid, both a very tenuous mesial cingulid, and a somewhat more marked but similarly narrow lingual cingulid, converge; distally, the latter becomes continuous with the distal marginal ridge. At least in IPS41954, there is also a short and subtle remnant of buccal cingulid, which is separated from the distal marginal ridge by the distobuccal cristid.

Lower premolars. The P/3 is a unicuspid and high-crowned tooth, with the single cuspid more protruding than the highest cusps of the remaining postcanine teeth, at least in male individuals (IPS35036, IPS41955 and, presumably, IPS41981), although less protruding than the canine (see Fig. 7). In the female specimen (IPS41719), this tooth is somewhat smaller and less high-crowned as compared to the remaining postcanine teeth. In all specimens, the crown is longer than broad, even though slightly less buccolingually compressed than the lower canines (breadth/length index 69–74%, excluding IPS41981 where the advanced degree of wear distorts this measurement). The main (mesiodistal) axis of the crown is somewhat buccally rotated relative to the main longitudinal axis defined by the remaining postcanine teeth. Moreover, the enamel somewhat extends onto the mesiobuccal aspect of the root relative to the rest of the crown and, in male individuals, there is a conspicuous honing facet for the upper canine on the mesiolingual wall of the crown. Accordingly, this tooth must be considered clearly sectorial, even though the extension of the enamel along the mesiobuccal root is quite restricted. As a result of wear on the mesiobuccal aspect of the crown, the rather elliptical occlusal outline that can be appreciated in IPS41955 progressively becomes suboval or even subtriangular in more worn specimens, such as IPS35036 and IPS41981, respectively. In both male and female specimens, three different cristids steeply descend in different directions from the apex of the single main cuspid: a sharp and short preprotocristid descends in mesiolingual direction toward lingual cingulid, which at this level reaches about midcrown height; a somewhat poorly defined postprotocristid runs in distobuccal direction toward the buccal end of the distal marginal ridge; and a similarly long hypoprotocristid runs in distolingual direction toward the lingual end of the distal marginal ridge. The distal marginal ridge is relatively well-developed, being continuous with the above-mentioned two latter cristids, and distally delimits a moderately developed distal fovea. Cingulids are clearly more developed in male specimens, particularly with regard to the lingual cingulid; this can be divided into two distinct portions (mesiolingual and distolingual), which become continuous with one another at the end of the preprotocristid. The mesiolingual portion of

this cingulid is only preserved in IPS41955, whereas, on the other specimens, it has been eroded by wear. The distolingual portion, on the contrary, is preserved in all the male specimens, in which it terminates before reaching the end of the hypoprotocristid, except in IPS35036, where it reaches this point and the lingual end of the distal marginal ridge. There is no buccal cingulid except for a short stylid on the distobuccal corner of the crown of IPS35036 and IPS41955 (although it may have been present but worn away in IPS41981). The distolingual wall of the crown is flat to slightly concave, while the mesiolingual (before being flattened by wear, as in IPS41955) and the buccal walls are convex; the distal portion of the crown, comprised between the hypo- and postprotocristid, is markedly concave; this can be clearly appreciated in IPS41955 and IPS41719, whereas in IPS35036 and, especially, IPS41981, it has been progressively flattened by wear. At the distobuccal corner of the crown, where the distobuccal stylid (if present), the distal marginal ridge, and the distobuccal cristid converge, there is a small thickening of the enamel that may be interpreted as a poorly developed hypoconid (this cannot be discerned in IPS41981 due to wear); however, there is no comparable poorly developed distolingual cuspid, except in the female specimen IPS41719.

The P/4 is a tetracuspid tooth, with the two mesial cuspid (protoconid and metaconid) moderately high and well-developed, and the two distal cuspid (hypoconid and entoconid) much smaller and poorly developed, further being situated on the distobuccal and distolingual corners of the crown, respectively. The crown displays a suboval to subrectangular occlusal profile, being slightly longer than broad (breadth/length index 74–100%), and with all the several sides convex except for the distal side, which is rather straight. The lingual cuspid are much more peripherally situated than the buccal ones, especially as compared to the protoconid. Occlusal morphology can be best ascertained in the almost unworn specimen IPS41955, and to lesser extent in IPS41719 and IPS35036, whereas IPS41981 is too worn to provide much reliable information. The short preprotocristid and premetacristid, mesially originating respectively from the apex of the protoconid and the base of the metaconid, soon converge with the fine mesial marginal ridge. These crests define a roughly quadrangular and well-developed, but relatively shallow, mesial fovea (trigonid basin), with is mostly situated on the lingual moiety of the crown. This fovea is further enclosed distally by the short but broader hypoprotocristid and hypometacristid, which do not completely join each other, being separated by a mesiodistal groove that runs across the mesial fovea. The extensive and rectangular talonid basin, being slightly longer than broad, and somewhat displaced toward (but not restricted to) the lingual moiety of the crown, is also much deeper than the trigonid basin, with the fine postprotocristid and postmetacristid descending steeply until merging with the almost horizontal preprotocristid and prehypocristid that further delimit the talonid basin. The distal marginal ridge is only minimally developed, and there is no apparent development of secondary enamel wrinkling on the talonid basin. There is no lingual cingulid, except for a very slight remnant on the mesial aspect of the metaconid in male specimens. The marked buccal cingulid is much better-developed, but discontinuous, being divided into two distinct portions: a mesiobuccal one, curving from the end of the preprotocristid and mesial marginal ridge across the

mesiobuccal corner of the crown; and a distobuccal one between the protoconid and hypoconid.

Lower molars. The nomenclature employed for the description of the occlusal morphology of lower molars (see Figs. 8D–I and 9) has been summarized in Figure 1A. The first two lower molars display a subrectangular occlusal outline, being slightly longer than wide (breadth-length index 77–93% in the M/1 and 79–97% in the M/2). The M/1 and M/2 of some specimens (IPS41955 and IPS41981) display a slightly wider distal lobe, whereas in the remaining specimens (IPS35036, IPS41719, and IPS41960) the mesial lobe is similar or slightly wider than the distal one. In all specimens, the M/3 is absolutely longer but relatively narrower than the preceding molars (breadth-length index 66–85%), displaying a suboval (IPS41719, IPS41981, and IPS41956) to clearly oval (IPS35036) occlusal contour, with the mesial lobe somewhat wider than the central lobe (except in IPS41981, where they are approximately equal), and both lobes being much wider than the otherwise well-developed distal lobe. In both the M/1 and M/2, mesiodistal crown length tends to be slightly greater on the buccal than on the lingual moiety of the crown, due to the very mesial position of the protoconid. The latter is also true for M/3, although in this tooth, the buccal moiety of the crown is not longer than the lingual moiety, due to the greater development of the distolingual corner of the crown, as compared to the preceding molars.

The occlusal morphology of the lower molars can be best ascertained in IPS41955 (M/1), IPS41960 (M/2), and IPS41956 (M/3), and to a lesser degree in the partial mandibles IPS35036 and IPS41719; the advanced degree of wear in IPS41981, on the contrary, precludes a detailed assessment. The crown of the lower molars displays five main cusps, which are rather pyramidal in shape, as well as buccolingually compressed (particularly the lingual ones), more markedly in the M/3 than in the preceding molars. The trigonid is quite large and much higher than the talonid. The mesial cuspids (especially the protoconid) are higher and less peripheral than the hypoconid and, especially, the entoconid; the latter is the most peripheralized cuspid except in the M/3, where the metaconid is also much peripheralized. On the M/1 and M/2, the hypoconulid is centrally situated on the distal end of the crown, whereas on the M/3 it is more buccally situated, although being, like the protoconid, less peripheral than the hypoconid. The hypoconid is more extensive than the remaining cusps, whereas the hypoconulid is the lowest and most restricted one, except in the M/3, where it can be comparable to the entoconid. The buccal cusps are more mesially situated than the corresponding lingual ones, especially the protoconid as compared to the metaconid.

The short preprotocristid, together with the somewhat longer premetacristid, the short mesial marginal ridge, and the fine and transverse cristid constituted by the hypoprotocristid and hypometacristid, define a moderately well-developed, although short and shallow, mesial fovea (trigonid basin). The two latter transverse cristids are continuous in some specimens (IPS41960, IPS41955, and IPS41956), whereas in other cases (IPS35036 and IPS41719) their contact is partially interrupted by a mesiodistal groove that runs from the mesial fovea toward the trigonid basin. The mesial fovea, which is somewhat situated toward (but not restricted to) the lin-

gual moiety of the crown, is somewhat wider than long, although quite narrow as compared to crown width. This can be best appreciated in IPS41955, IPS41719, and IPS41956, but as wear proceeds further, the mesial fovea appears narrower, being only preserved as a fissurelike fovea that curves between the base of the protoconid and the mesial marginal ridge, and which corresponds in fact to the deepest portion of a somewhat wider and more extensive fovea. The central fovea (talonid basin), in any case, is much deeper and more extensive than the mesial one, being somewhat wider distally than mesially, due to the more peripheral position of the hypoconid and entoconid as compared to the mesial cusps. This central fovea, which is longer than wide, is laterally delimited by the relatively broad postprotocristid and postmetacristid, which respectively originate from the base of the protoconid and the apex of the metaconid as well as by the somewhat shorter prehypocristid and preentocristid. The cristid obliquid, formed by the postprotocristid and the prehypocristid, is slightly oblique. On M/1 and M/2, the merging of the two lingual and the two labial cristids surrounding the talonid basin with one another is partially interrupted by fine transverse grooves. Almost no secondary enamel wrinkling can be appreciated on the talonid basin in M/1 and M/2, except for a few short and shallow secondary grooves; the nearly unworn specimen IPS41960, however, do indeed suggest that some development of secondary enamel wrinkling was present at least in the M/2 of this particular specimen. This is more apparent on M/3, as can be appreciated from the isolated unworn specimen IPS41956. In M/1 and M/2, the deepest points of the talonid basin define a Y-pattern with the base of the hypoconid contacting with the bases of the remaining cusps, although the three arms of the Y, converging toward the center of the basin, are less discernible in M/2, and become completely obliterated by enamel wrinkling in M/3.

On the M/1, there is no pliopithecine triangle, that is, there are no distinct mesial and distal arms, although two subtle grooves or a depression are present where these arms would have been situated if they were present; only in IPS35036, there is some hint of a tenuous and badly developed distal arm of the triangle. Unlike in M/1, a well-developed complete pliopithecine triangle is present in the M/2, at least in some specimens (especially in IPS41960 and IPS41719, where both the mesial and distal arms can be discerned), and in all available M/3. The mesial arm of the triangle emerges from the base of the protoconid (where the hypoprotocristid originates), whereas the distal arm emerge from the base of the hypoconid (close to the origin of the prehypocristid). Together with the postprotocristid and prehypocristid, these secondary ridges define a triangle that encloses within it a Y-shaped groove pattern (with the arms directed buccally). The ends of the mesial and distal arms do not contact each other, so that the stem of the Y continues toward the rest of the central fovea. Despite a slightly to much considerably advanced degree of wear in the M/2 and M/3 of IPS35036 and IPS41981, respectively, the presence of a pliopithecine triangle, and especially of a well-developed distal arm of the triangle, can be still inferred.

Besides a marked and well-defined triangle, the M/2 IPS41960 and, to a greater degree, the M/3 IPS41956, further display a considerable development of secondary enamel wrinkling, which is manifested in several grooves and ridges that radiate from the center of the

talonid basin. In the M/2 IPS41960, there is a very thick secondary cristid that runs from the mesiolingual aspect of the apex of the hypoconid toward the center of the talonid basin, being longer, broader, and more distally situated than the distal arm of the pliopithecine triangle, which runs parallel to it; a similar, but somewhat shorter secondary ridge can be discerned on the right M/2 of IPS41719, although it is less conspicuous due to wear. In the M/3, a similar secondary cristid is present in some specimens, although it is more transversely directed toward the hypoentocristid; they together separate the talonid basin from the distal fovea. In M/1 and M/2, the talonid basin is distally closed by the base of the hypoconulid as well as by the extremely short posthypocristid, prehypocristid, postcristid, and hypoentocristid. In these molars, the posthypocristid and prehypocristid almost entirely merge with one another, thus partially interrupting the moderately shallow groove that runs from the central fovea toward the buccal stylid that is situated on the distobuccal corner of the crown. On the distolingual corner of the crown, there is a small distal fovea entirely restricted to the lingual moiety of the crown, which is lingually delimited by an ill-defined postentocristid that progressively curves until becoming continuous with the subtle distal marginal ridge. This distal fovea is slightly wider and deeper in M/2 than in M/1. In one specimen (IPS41955), the postcristid and hypoentocristid joint with one another, thus completely separating the talonid basin from the distal fovea; in other specimens, however, the ends of both cristids are separated by the deep (IPS41719) to apparently shallow (IPS35036, IPS41981, and IPS41960) groove that runs in distolingual direction, thus communicating both foveae. In IPS41981, there is a secondary enamel ridge that runs close to the distal marginal ridge and occupies most of the distal fovea, although a secure assessment is precluded by the advanced degree of wear of this specimen. In both the M/1 and M/2, there is no distinct posthypocristid.

The M/3 mainly differs from the preceding molars by the more buccolingually compressed lingual cuspids, which are very peripheralized; by the much more buccal position and greater development of the hypoconulid, which unlike in the preceding molars is more protruding than the entoconid; and especially by the much larger distal fovea, which further displays a greater development of secondary enamel folds and ridges than the talonid basin, particularly at the base of the entoconid, hypoconulid, and the distal marginal ridge. In the M/3 IPS41956, the distal fovea is completely separated from the trigonid basin by a transverse, sharp, and continuous secondary cristid that runs from the apex of the hypoconid until the apex of the entoconid. Despite more advanced wear, this configuration can be still ascertained in IPS35036 and in IPS41719, although in the latter specimen, this secondary transverse cristid does not originate from the apex of the hypoconid, but rather from the junction between the posthypocristid and prehypocristid, which are longer than in IPS41956. In M/3, the latter two cristids are mesiodistally instead of obliquely directed as in the preceding molars, due to the more peripheral situation of the hypoconulid. At least in some specimens (especially IPS41956), the posthypocristid and the prehypocristid are partially interrupted from one another by a groove that runs toward the buccal stylid that is situated close to the distobuccal corner of the crown. There is a short posthypocristid

distally directed toward the distal marginal ridge, whereas a longer and broader postcristid further originates from the hypoconulid toward the hypoentocristid. In all specimens, these two cristids are interrupted by a deep groove; in IPS35036, the postcristid and the hypoentocristid are very broad but simple, whereas in IPS41956, the presence of numerous secondary ridges makes it almost impossible to discern these cristids from other secondary ridges that radiate from the entoconid and the hypoconulid. Behind these cristids, the development of enamel wrinkling is further exaggerated, particularly in IPS41956, where two enamel folds even isolate a small "fovea" on the distalmost portion of the distal fovea. Because of the greater development of the distolingual corner of the crown, in the M/3, the postentocristid is longer than in the preceding molars. At the junction of the postentocristid with the distal marginal ridge, where some secondary enamel folds further converge in some specimens, there is a distinct thickening of the distal marginal ridge on the distolingual corner of the crown that constitutes a secondary accessory cuspid (*tuberculum sextum*).

The lingual cingulid is restricted in most specimens to a short and triangular lingual stylid just next to the juncture of the postmetacristid and preentocristid, which is better developed in M/1, but restricted to a barely discernible vertical and short groove in M/2 and M/3. In some specimens (IPS35036, IPS41960, and IPS41956), there is also a shallow depression on the distolingual aspect of the metaconid that may be interpreted as another remnant of lingual cingulid; in most specimens, some development of subtle secondary enamel folds and ridges can be further appreciated on some parts of the lingual crown wall. The buccal cingulid is much better developed, although discontinuous, in all available M/1 and M/2, and in some M/3. Next to the hypoconulid, on the distobuccal corner of the crown, there is a short stylid that displays a progressively greater development from M/1 to M/3, being wide and shelflike only in the latter molar. Besides this distobuccal stylid, there is a marked and much longer buccal cingulid that runs from the mesial aspect of the protoconid (where the mesial ridge and the preprotocristid converge) until the mesiobuccal aspect of the hypoconid. Only in two M/3 (the right M/3 of IPS41981 and the right M/3 of IPS41956), the distobuccal stylid is uninterrupted from the former portion, thus constituting a continuous buccal cingulid; in other instances, both portions of the cingulid are separated by the buccal wall of the hypoconid or by secondary vertical ridges that originate from it. In M/1, the mesial and longer portion of the buccal cingulid, isolated from the distobuccal stylid, is further completely subdivided into two distinct portions by a relatively thick secondary cristid that originates from the buccal aspect of the protoconid, next to the apex, and progressively descends slightly distalwards. As such, this secondary cristid separates a marked but moderately narrow mesial portion of the cingulid around the protoconid, and a much wider, ledge-like (almost basinlike) mesial portion that is situated between the protoconid and hypoconid. In the M/1 of IPS41719, this secondary cristid progressively curves distalwards, whereas in other specimens, it appears more verticalized, but in all instances the ledge-like portion of the cingulid tends to be somewhat longer than the narrower, more mesial portion. In the M/2, the buccal cingulid is more extensive and wide, although two distinct portions (a narrow mesial one, and a ledge-like

more distal one) can be still discerned. The secondary, vertical cristid on the buccal wall of the protoconid is similar than in the M/1, even though slightly shorter, so that the narrow and the ledge-like portions of the cingulid become continuous with one another, except in IPS41960, where the secondary vertical cristid briefly interrupts them from one another. In M/3, the secondary vertical cristid on the buccal wall of the protoconid is variably developed: in the female specimen IPS41719, it is present and apparently interrupts the two portions of the buccal cingulid only on the right side; on the contrary, in the remaining (presumably male) specimens, this secondary cristid, even though present or even double, fails to interrupt the ledge-like portion of the cingulid from the narrower, more mesial portion, which in IPS41956 and especially IPS35036 becomes ledge-like. Like in the lingual side, there is also some development of secondary vertical grooves and ridges on the buccal crown wall in all lower molars and particularly in the buccal cingulid of the M/3.

Description of the upper dentition

Upper incisors. The single available upper incisor, a I2/ from IPS41958, is moderately spatulate, with a mesiodistally compressed root with an elliptical section, and a crown progressively expanding mesially from base to apex, where the crown displays considerable apical wear (see Fig. 5A–D). The cemento-enamel junction is V-shaped on the labial side, but straight on the mesial aspect of the tooth. In occlusal view, this tooth displays a subtriangular profile. The labial side is moderately convex, while the lingual one is concave and, besides some secondary enamel wrinkling that has not been entirely eroded by wear, it further displays two asymmetrical marginal ridges (the mesial one being less curved and thicker than the distal one), which converge toward a basal lingual thickening. The basal portion of the distal marginal ridge displays a wear facet against the lower canine.

Upper canines. There is only a single C1/, available from IPS41958, and presumably belonging to a female specimen (see Fig. 5A–D). The crown displays a subrhomboidal occlusal contour, being slightly longer than broad (breadth/length index 90%), with the main axis somewhat buccally rotated. Because of the advanced degree of wear, few details of occlusal morphology can be ascertained except by the presence of a well-developed lingual cingulum. There are two wear facets with profuse dentine exposure: a mesial one due to shearing against the lower canine, and a much larger one that occupies most of the central and distal portions of the crown, due to wear against the P/3.

Upper premolars. These teeth are bicuspid and display a suboval to elliptical contour, being clearly wider than long (breadth/length index 164–171% in the P/3 and 141–157% in the P/4), but with the lingual moiety of the crown being slightly longer than the buccal one in the P/3 (see Fig. 10A). The crown base is somewhat inflated on the buccal side. In occlusal view, the crown displays markedly convex buccal and lingual contours and straighter mesial and distal ones. Occlusal morphology is difficult to ascertain given the advanced degree of wear and/or the damaged nature of the specimens, except in the P4/ IPS41715. The paracone is much more protruding than the protocone. The preparacrista and postparacrista are mesiodistally directed and approximately equally longer, whereas the more obliquely

directed preprotocrista is shorter than the postprotocrista, due to the more mesial position of the protocone as compared to the paracone. Subtle transverse ridges (hypoparacrista and hypoprotocrista), separated by a transverse groove that runs in mesiodistal direction, separate the short and restricted mesial fovea from the more extensive, but shallow, trigon basin, which in IPS41983 further displays some development of secondary enamel wrinkling. The mesial and distal marginal ridges are poorly developed. There are no well-developed lingual or buccal cingula, although there is a narrow mesiobuccal cingulum in the P3/ of IPS41983, a discontinuous and slight mesiobuccal and distobuccal cingulum in the P4/ IPS41715 and a short and narrow lingual cingulum on the two available P4/ (IPS41715 and IPS41983).

Upper molars. The nomenclature used for the description of the occlusal morphology of upper molars (see Figs. 8A–C and 10C–E) has been summarized in Figure 1B. No M3/ is available. The remaining upper molars display a subrectangular occlusal outline, with a moderately convex buccal contour and a slightly biconvex lingual profile. They are somewhat broader than long (breadth/length index 138% in M1/ and 121% in M2/), and the buccal moiety of the crown is mesiodistally slightly longer than the lingual one. The M1/ is smaller than the M2/. Occlusal morphology can be best ascertained in the M2/ IPS41718, although the morphology of the remaining, more worn, and/or damaged specimens is compatible with the former. There are four main cusps, the buccal ones being more peripherally and more mesially situated than the corresponding lingual ones, which are also less buccolingually compressed than the buccal ones. The protocone is the most extensive cusp, while the paracone is the most protruding one. The two distal cusps (and particularly the hypocone, which is situated close to the distolingual corner of the crown) are smaller than the two mesial ones.

The preparacrista is shorter and less obliquely directed than the preprotocrista. The mesial marginal ridge is not very marked, but there is an enamel thickening at the distal end of the preprotocrista, where the lingual cingulum originates, that may be interpreted as rudimentary protoconule (=paraconule). The hypoparacrista originates from the mesial aspect of the base of the paracone and runs in lingual direction until reaching the preprotocrista. This hypoparacrista thus constitutes a fine but continuous crest that distally closes the mesial fovea, which is short, narrow as compared to crown breadth, and somewhat shallower than the trigon basin; this mesial fovea is mostly situated on the buccal moiety of the crown (especially in the M2/). The trigon basin, which is somewhat wider than long, is buccally delimited by the narrow postparacrista and premetacrista, which respectively originate from the apices of the paracone and metacone. This triangular, moderately deep and relatively extensive, central fovea is further separated from the distal fovea by a continuous crista obliqua formed by the postprotocrista and the hypometacrista. The crista obliqua is rather straight, being obliquely situated with respect to the mesiodistal axis of the crown. There is a short and oblique posthypocrista that runs until the slightly developed distal marginal ridge, and a short and mesially directed prehypocrista that runs toward the base of the protocone. The short postmetacrista also runs distally until merging with the distal marginal

ridge. The distal fovea is as wide as and even deeper than the trigon basin, although somewhat shorter. This fovea is distally partially open and displays somewhat more developed secondary enamel folds and grooves than the mesial fovea.

In the M1/, the buccal cingulum is narrow and discontinuous, although damage on the distobuccal corner of the crown precludes a complete assessment. In the M2/, the buccal cingulum is somewhat broader and more marked, even becoming ledgelike between the paracone and metacone, although still being interrupted by secondary enamel grooves and crests on the buccal walls of the paracone and, especially, the metacone. The C-shaped lingual cingulum is much more extensive than the buccal one in both the M1/ and M2/, being clearly ledgelike between the protocone and the hypocone, and only being partially interrupted by short secondary enamel folds that radiate from the base of the protocone.

In IPS41984, besides the very stout and pyramidal lingual root, there are two mesiodistally compressed buccal roots partially separated by two deep grooves on either side (i.e., only fused with one another along the middle portion). In IPS41718, on the contrary, the two buccal roots are fused close to the base, being mostly separated from one another.

Deciduous dentition. There is a single deciduous tooth available from the sample, IPS41976, which corresponds to a dP4/ (see Fig. 10B). It is a small molariform tooth, only slightly shorter than the available M1/, but absolutely and relatively narrower (breadth/length index 126). This, coupled with its lower crown as compared to the definitive molars, and its subtriangular occlusal outline (with the buccal moiety being clearly longer than the lingual one), indicate that this specimen corresponds to a deciduous premolar. Its occlusal morphology generally resembles that of the definitive molars, with well-defined but somewhat finer cristids. The buccal cingulum is narrow and discontinuous (constituted by short and narrow stylids interrupted from one another by the bases of the two buccal cusps), whereas the C-shaped lingual cingulum is more marked and continuous, as in the definitive molars. The roots of this tooth are broken close to the base, and it is not clear whether besides the single fused lingual root, the two buccal roots were fused with one another or not.

DISCUSSION

The material from ACM clearly displays the main putative synapomorphies of the Pliopithecoidea (Andrews et al., 1996; Harrison and Gu, 1999; Begun, 2002). In particular, the lower incisors mesiodistally waisted toward the base of the crown; the mesiodistally short and relatively high-crowned P/3, with a steep mesiobuccal sectorial face that, even though sexually dimorphic, does not extend much inferiorly to form a sectorial flange even in males; and the relatively narrow lower molars with a relatively well-developed mesial fovea and a well-developed pliopithecine triangle (especially in M/2 and M/3)—although the latter feature is variably expressed or even secondarily lost in several pliopithecoid genera.

Both occlusal morphology and dental proportions suggest pliopithecine affinities for the ACM material, by displaying among others a more marked occlusal relief and more pyramidal (less globulous) cusps than dionysopithecines, but at the same time lacking crouzeliine-derived features, such as sharper crests and very buccolingually

compressed and peripheralized cusps, with large and deep mesial and central foveae (Ginsburg and Mein, 1980; Harrison et al., 1991; Andrews et al., 1996; Moyà-Solà et al., 2001; Begun, 2002).

The Pliopithecinae have been traditionally considered a monotypic subfamily (e.g. Andrews et al., 1996), being represented by the single genus *Pliopithecus*. Begun (2002), however, classified *P. vindobonensis* into a distinct genus *Epipliopithecus* Zapfe and Hürzeler, 1957, which was originally erected a subgenus of *Pliopithecus*. Begun (2002) justified this taxonomic distinction on the basis of several dental differences basically related to incisor morphology and the lack of a distinct pliopithecine triangle in *Epipliopithecus*. This contrasts with Harrison's taxonomic opinion (Harrison et al., 2002; Harrison, 2005), which placed the type species of *Epipliopithecus* into the genus *Pliopithecus* with no subgeneric distinction. Given the currently available evidence, we prefer to provisionally retain *Epipliopithecus* merely as a distinct subgenus within a broader *Pliopithecus* s.l.

The pliopithecine material from ACM can be attributed to the genus *Pliopithecus* s.l. on the basis of the following characters (after Harrison et al., 1991; Begun, 2002): (1) lower incisors waisted and quite narrow, spatulate, and moderately to relatively high-crowned; (2) upper incisors waisted, relatively high-crowned and with a distinct buccal cingulum; I1/ more spatulate than I2/, which is narrower and more asymmetrical; (3) lower and upper canines relatively high-crowned and buccolingually compressed, with marked size and shape sexual dimorphism; (4) lower premolars not very elongated; P/3 high-crowned and, in males, moderately sectorial with a steeply-inclined mesiobuccal honing face against the upper canine, but lacking a truly sectorial extension of the enamel onto the mesiobuccal root; (5) short and relatively broad upper premolars, with heteromorphic cusps (the paracone much more prominent than the paracone); (6) long and relatively narrow lower molars that increase in size from M/1 to M/2 (and generally M/3), with relatively low and moderately rounded cusps, not very sharp cristids, a relatively well-developed buccal cingulum, and usually with a well-developed pliopithecine triangle in M/2 and M/3 (except in *Epipliopithecus*); (7) short and relatively broad mesial fovea in lower molars, with the protoconid being more mesially placed than the metaconid; long and moderately extensive talonid basin, with a slightly obliquely oriented cristid obliqua; distinct and well-defined distal fovea, with a relatively large and progressively more buccally situated hypoconulid from M/1 to M/3; (8) short and relatively broad upper molars, with M2/ much larger than M1/; trigon basin generally broader than long, with a continuous crista obliqua but usually without a distal transverse ridge connecting the hypocone with the metacone; well-developed (usually shelflike) lingual cingulum, and variably developed buccal styler shelves.

The morphology of the ACM material agrees with the diagnosis of *Pliopithecus* given above. Moreover, both the presence of a well-defined pliopithecine triangle on M/2 and M/3 and the lower-crowned lower incisors as compared to *P. (Epipliopithecus) vindobonensis* indicate that this material must be attributed to the subgenus *Pliopithecus* s.s. According to Begun (2002), four different species of *Pliopithecus* s.s. can be distinguished: *P. antiquus* (de Blainville, 1839); *P. piveteaui* Hürzeler, 1954; *P. platyodon* Biedermann, 1863; and *P. zhanxiangi* Harrison et al., 1991. The type species of this (sub)genus is *P.*

antiquus, being recorded at the French localities of Sansan (MN6) and La Grive [Peyre et Beau quarry, PB A, which is correlated to MN8 according to Mein and Ginsburg (2002)]. Isolated material from other Aragonian and Vallesian localities has been also referred to this species on tentative grounds (Begun, 2002), including MN6 sites from Germany and Switzerland, MN7 and MN8 sites from Poland, and MN9 sites from France. With regard to the remaining species of this subgenus, only *P. zhanxiangi* (Harrison et al., 1991), recorded from the MN6 locality of Maerzuizigou (China), can be clearly distinguished on the basis of its larger size. There are also details of occlusal morphology and dental proportions that further distinguish this relatively large-bodied species of *Pliopithecus* from the remaining ones (Harrison et al., 1991; Begun, 2002). However, given the great size discrepancy between *P. zhanxiangi* and the pliopithecoid material from ACM, these differences will be no further mentioned here.

P. antiquus, on the contrary, as represented by the remains from Sansan (de Blainville, 1839) and La Grive (Depéret, 1887), is the species most similar to the ACM material on the basis of size. *P. antiquus* is apparently the smallest species of the genus, although as noted by Begun (2002), there is an extensive overlap amongst the several European species, particularly between *P. piveteaui* and *P. antiquus*. The two latter species must be therefore distinguished from one another on other basis of morphological criteria, whereas *P. platyodon*, recorded from the type locality of Elgg (MN5) in Switzerland, is somewhat larger on average—thus being most similar to *P. (E.) vindobonensis* as far as size is concerned. In fact, most of the specimens currently included within the hypodigm of *P. platyodon* come from the MN6 locality of Göriach (Austria). Hürzeler (1954) attributed the Göriach sample to *P. cf. antiquus*, but both Hürzeler (1954) and Zapfe (1960) suggested that this sample might alternatively represent *P. platyodon*, to which it was formally transferred by Harrison et al. (1991)—an opinion that has been subsequently followed by other workers (Andrews et al., 1996; Begun, 2002). Besides size, *P. platyodon* also differs from the remaining pliopithecine species by several morphological details (Andrews et al., 1996), especially by displaying a very long M/3 as compared to the preceding lower molars.

On the contrary, *P. piveteaui* from Manthelan (type locality) and other sites from the Loire Valley in France (MN5) just show the opposite condition. The latter taxon was formerly considered a junior synonym of *P. antiquus* by several researchers (Harrison et al., 1991; Andrews et al., 1996). Andrews et al. (1996), in particular, considered that the holotype of *P. piveteaui* is unusual for a pliopithecoid in having an M/3 smaller in size (area) than the M/2, while in other pliopithecoids the M/3 is similar or greater in size as compared to the M/2 [see also Begun (2002)]. The former authors argued that this difference may be explained as resulting from normal pliopithecoid variation, with other species showing wide ranges of variation in M/3 size, and with several M/3 of *P. piveteaui* being larger than the M/3 of the holotype. Although the M/3 is usually more variable than the preceding molars, when all the available published measurements are taken into account (Ginsburg, 1975; Ginsburg and Mein, 1980), it emerges that the M/3 of *P. piveteaui* is, on average, shorter than the M/2 (see Fig. 12A): thus, mean length for the M/3 is of 6.85 mm (range, 5.55–7.4; $n = 7$), whereas that of the M/2 is of 7.05 mm

(range, 6.7–7.2; $n = 4$). This was already noted by Ginsburg and Mein (1980, p. 69): “It is said that in *Pl. piveteaui* the M/2 is longer than the M/3. This fact has been not only shown on the type specimen, but further confirmed on the basis of the length means of isolated teeth, which are currently numerous enough in order the results to be significative” (our translation from the French original). In fact, these mean values alluded by Ginsburg and Mein (1980) are very close to the values displayed by the holotype specimen (M/3 6.8 mm and M/2 7.1 mm), so that the latter cannot be considered unusual for the species. This permits to conclude that *P. piveteaui* displays an M/3 that is similar in size (or even slightly smaller) than the M/2, whereas in *P. antiquus* and, more markedly, in *P. canmatensis*, the former tooth is clearly longer than the latter: 7.35 mm (range, 6.8–7.6; $n = 4$) versus 6.77 mm (range, 6.7–6.9; $n = 3$) in *P. antiquus*, and 7.47 mm (range, 6.9–8.6; $n = 7$) versus 6.31 mm (range, 6.0–6.8; $n = 7$) in *P. canmatensis*. Interestingly, *P. piveteaui* shares with dionysopithecines the lack of an increased M/3 length as compared to the M/2 (see Fig. 12A), which suggests that, as already prefigured by Ginsburg and Mein (1980), the latter feature may be a synapomorphy shared by all European species of *Pliopithecus* except for *P. piveteaui*, which is the oldest and apparently most primitive species. Interestingly, the M/2-M/3 size discrepancy is more exaggerated in the ACM specimens than in those from *P. antiquus*.

Besides the relative size between the M/3 and M/2, there are other differences in occlusal morphology that warrant a distinction of *P. piveteaui* from *P. antiquus* at the species level (Hürzeler, 1954; Ginsburg, 1975, 1986; Ginsburg and Mein, 1980; Begun, 2002): (1) more buccolingually compressed cuspids, larger foveae, and more marked cristids in the lower molars (particularly M/2 and M/3); (2) M/3 very distally tapering, with a reduced entoconid and a narrower buccal cingulid; (3) M/2 somewhat distally tapering and with a reduced buccal cingulid; and (4) M/3 not longer than M/2. These differences are usually interpreted as reflecting the more plesiomorphic status of *P. piveteaui* (e.g. Ginsburg, 1975; Begun, 2002). To some regards, such as the buccolingually compressed cuspids, *P. canmatensis* resembles the condition displayed by *P. piveteaui*, but in other respects, the ACM specimens more closely resemble *P. antiquus* (see comparison of lower cheek teeth in Fig. 11) or even show a more exaggerated condition—such as regarding the development of the buccal cingulid on the lower molars, which in *P. canmatensis* is very extensive and becomes clearly ledge-like between the protoconid and the hypoconid (especially in M/3). Be that as it may, as shown in the differential diagnosis, *P. canmatensis* simultaneously differs from both *P. piveteaui* and *P. antiquus* by several details of occlusal morphology (the larger and higher trigonid, the larger hypoconid, and the more mesially positioned protoconid as compared to the metaconid), which may be interpreted as autapomorphic for the new taxon.

Further characters specifically distinguish *P. canmatensis* from either *P. piveteaui* or *P. antiquus*. Dental proportions, in particular, enable the distinction of the new species from *P. piveteaui*, with the former displaying an absolutely shorter M/2 (Fig. 12A) as well as relatively narrower lower cheek teeth (Fig. 12C). To the latter regard, the proportions displayed by *P. canmatensis* are intermediate between other *Pliopithecus* spp. and the taxon from Castell de Barberà, with *Plesiopliopithecus*

displaying the most extreme condition. Nevertheless, given the roughly similar proportions displayed by *Dio-nyssopithecus* with regard to the M/1 and M/2, the condition shown by *P. canmatensis* is difficult to interpret from an evolutionary viewpoint. *P. piveteaui* might also differ from *P. canmatensis* by displaying a well-formed pliopithecine triangle not only in the M/2 and M/3, but also in the M/1 [see Ginsburg (1975, Plate Fig. 2)]; nevertheless, given that this observation is based on a single first molar, the possibility remains that this feature is variable in the former species. Other features, such as the degree of distal tapering of the M/2 and M/3, are quite variable within the ACM sample, so that their taxonomic usefulness as a distinctive character remains doubtful. With regard to *P. antiquus*, regrettably, the exclusion from the hypodigm of this species of material currently attributed to *P. platyodon* and *P. piveteaui*, and the uncertainties regarding the attribution to this species of material from localities other than Sansan and La Grive, leave only a limited sample to which the ACM material can be compared. Nevertheless, as already listed in the differential diagnosis, *P. canmatensis* differs from the Sansan and La Grive material by several features, which besides the distinctive features from both *P. antiquus* and *P. piveteaui* (see discussion earlier) further include the less peripherally situated protoconid (thus resulting in a narrower mesial fovea mostly positioned on the lingual moiety of the crown), the more medially positioned hypoconulid in the M/2, the development of a tuberculum sextum in the M/3, and the size and relative proportions of the C/1 (in males), P/4, M/1, and M/2.

Interestingly, the new species from ACM shares several of the differential characters with respect to *P. antiquus* mentioned above with the undescribed material of Pliopithecidae nov. from Castell de Barberà (MN8) (Crusafont-Pairó and Golpe-Posse, 1981, 1982). Particularly noteworthy is the relatively large trigonid, the metaconid and entoconid placed distally with respect to the protoconid and hypoconid, the trigonid much higher than the talonid, and the large hypoconid. In spite of the similar size, however, both dental proportions and several occlusal details do not permit an attribution of the material from Castell de Barberà to the newly described species from ACM. In the past, the pliopithecid remains from Castell de Barberà have been attributed to *P. antiquus* by Andrews et al. (1996), to *P. aff. antiquus* by Moyà-Solà et al. (1990), and to *P. cf. antiquus* by Harrison et al. (2002). Begun (2002) went one step further by attributing this material to a new pliopithecine taxon, to which the isolated dP/4 from the MN8 locality of Can Feliu (Crusafont-Pairó and Golpe-Posse, 1981, 1982) might also belong (Begun, 2002). The latter author noted several morphological differences between the material from Castell de Barberà and that attributed to *P. antiquus* by him, including more buccolingually compressed cusps with well-developed crests and large occlusal basins. To these regards, the pliopithecid from Castell de Barberà also differs from *P. canmatensis* sp. nov. Begun (2002) interprets the occlusal morphology of the taxon from Castell de Barberà as more reminiscent of *P. piveteaui*, but being more accentuated. Several other authors, however, have previously noted some similarities of the Castell de Barberà taxon with the crouzeiines (Ginsburg, 1986), particularly with *Plesiopliopithecus* (Crusafont-Pairó and Golpe-Posse, 1981, 1982). Clarifying the systematic affinities (either pliopithecine or crouzeiine) of the taxon from Castell de Barberà is out-

side the scope of this work. In any case, however, this study clearly shows that the pliopithecid material from ACM is more similar and surely congeneric to French specimens from Sansan and La Grive, whereas specimens from Castell de Barberà represent a new taxon that will be described shortly (Alba and Moyà-Solà, in preparation).

CONCLUSIONS

A new species of fossil catarrhine primate, *Pliopithecus canmatensis* (Pliopithecidae: Pliopithecinae) is described from several localities of Abocador de Can Mata. These localities correspond to the C5r.3r subchron, with an estimated age ranging from 11.7 to 11.6 Ma, and can be correlated to the Late Aragonian (Middle Miocene) MN8 biozone (sensu Mein and Ginsburg, 2002). The new species is represented by several mandibles and mandibular fragments, as well as some maxillary fragments and isolated teeth, which together record all the permanent dentition except for the I1/ and M3/, as well as the dP/4. On the basis of dental size and morphology, the new species is more similar to *P. piveteaui* and, especially, *P. antiquus*, although it can be distinguished from both species by several occlusal details and dental proportions, particularly regarding the lower molars.

The fragmentary nature of the available maxillary specimens only permits to describe the face as short and with a shallow nasoalveolar clivus. The mandible, in its turn, is long and relatively shallow, with a deep symphysis that internally displays a shelflike upper torus but shows no simian shelf on the lower third. The mental foramen is situated below the P/3, and the corpora progressively shallow distalwards from the symphysis, being broadest at the level of M/2-M/3. The dental arcade is narrow and displays only slightly diverging post-canine tooththrows. The ramus is low, shows a steep mesial margin, and originates from mid to distal M/3, only partially overlapping (at most) with the distal portion of M/3, and further displaying a wide extramolar sulcus. The coronoid process is slightly more projecting than the mandibular condyle, and the sigmoid notch is long and shallow.

Regarding dental morphology, the lower incisors are spatulate, narrow, waisted, and relatively high-crowned, with a moderately developed lingual basal thickening; the lateral one is somewhat asymmetrical, like the narrow upper lateral one. The upper canine is only slightly buccolingually compressed at the base and displays a marked lingual cingulum, whereas the lower one is very buccolingually compressed and shows marked size and shape sexual dimorphism. Thus, male lower canines are high-crowned, pointed, and relatively stout, further displaying a conspicuous triangular thickening at the end of a mesiolingual cristid, whereas female ones are lower and display a rather blunt occlusal edge. The lower premolars are somewhat longer than broad, particularly the P/3, which is unicuspid, high-crowned, somewhat buccally rotated and, in males, moderately sectorial, with a steep buccolingual honing facet against the upper canine. The P/4 displays well-developed mesial cuspids and rudimentary distal ones, with a shallow mesial fovea. In both teeth, the mesial fovea is shorter and more restricted than the distal one and displays a paracone that is much more protruding than the paracone.

The lower molars are long and relatively narrow, with rather pyramidal and somewhat buccolingually com-

pressed cuspids, particularly the more peripheralized lingual ones. The buccal cuspids are more mesially situated than the corresponding lingual ones, particularly the protoconid as compared to the metaconid; there is no distinct paraconid. The trigonid is relatively large and markedly higher than the talonid, with a short and shallow but distinct mesial fovea. The talonid basin is much longer and deeper, with a slightly oblique cristid obliqua and some development of wrinkling (particularly in the M/3). The hypoconid is large as compared to the remaining cuspids. There is only a well-developed pliopithecine triangle in the M/2 and M/3, with the ends of the mesial and distal arms of the triangle being separated by a transverse groove. The M/1 and M/2 display a relatively small and quite medially situated hypoconulid (especially in the M/1), as well as a small but distinct distal fovea, which is entirely restricted to the distolingual corner of the crown and separated from the talonid basin by the postcristid and hypoentocristid. The M/3 differs from the preceding molars by displaying a buccally situated and larger hypoconulid that is linearly arranged with the remaining buccal cuspids as well as a much more extensive and wrinkled distal fovea; the latter is separated from the talonid basin by a secondary transverse cristid that runs from the entoconid and which displays a small tuberculum sextum on the distolingual corner of the crown. The buccal cingulid of the lower molars is well-developed and becomes increasingly wider from M/1 to M/3, although it is discontinuous—with the ledge-like portion between the protoconid and hypoconid being separated from the distobuccal stylid—except in some M/3. Finally, the upper molars are much wider than long, with the M1/ being clearly smaller than the M2/. The buccal cusps are more peripherally and mesially situated, and more buccolingually compressed, than the lingual ones. There is a short mesial fovea with a vestigial protoconule and a more extensive and deeper trigon basin, which is somewhat wider than long. The somewhat smaller distal fovea is separated from the trigon basin by a continuous crista obliqua and displays no transverse distal ridge connecting the hypocone with the metacone.

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