

A NEW AMPHICYONINE (CARNIVORA: AMPHICYONIDAE) FROM THE UPPER MIOCENE OF BATALLONES-1, MADRID, SPAIN

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Typescript received 4 July 2007; accepted in revised form 17 September 2007

Abstract: The vertebrate community of the late Miocene locality of Batallones-1, Madrid Province, Spain, is mainly composed of mammals of the order Carnivora, which represents 98 per cent of the total number of macro-mammal fossils. Here, we describe craniodental remains of approximately 12 individuals of a new, highly specialized member of the Amphicyonidae, previously assigned to *Amphicyon* sp. cf. *A. castellanus*. A phylogenetic analysis of Amphicyoninae shows that this new form, named *Magericyon*

anceps gen. et sp. nov., is markedly distinct from all other known Amphicyoninae, specifically in its hypercarnivorous features (strongly compressed upper canines, absence of dP1/dp1 and P2/p2, single-rooted p3, absence of a metaconid on the lower molars, and reduction of M2 relative to M1).

Key words: Carnivora, Amphicyonidae, Spain, Miocene, Vallesian, carnivore trap, Batallones.

SINCE 1991, the localities of Cerro de los Batallones in Madrid Province, Spain (Text-fig. 1), especially Batallones-1, have been intensively excavated, resulting in the discovery of thousands of fossils of fishes, amphibians, reptiles, birds, and mammals (Morales *et al.* 2004). The exceptional richness of this fossiliferous area was recently demonstrated by the discovery of four additional localities (Batallones-7–9 in 2004, Batallones-10 in 2007). The faunas from the localities are extremely rich and diverse, although the Carnivora (which comprise 98 per cent of the total number of remains of large mammals) are by far the most abundant mammals (Morales *et al.* 2004, table 1). Their high proportion suggests that Batallones-1 acted as a natural trap, attracting carnivorans because of the presence of entrapped prey (Antón and Morales 2000). This exceptional preservation and richness provides the first opportunity to study several aspects of the palaeobiology of Carnivora, including anatomy, functional morphology, ecology, and behaviour. In addition, many species from Batallones-1 were previously known only from fragmentary remains. Until now, only the machairodontine felids (Salesa 2002; Antón *et al.* 2004; Salesa *et al.* 2005, 2006b) and the early ailurid *Simocyon batalleri* (Peigné *et al.* 2005; Salesa *et al.* 2006a, 2008) have been studied.

This study describes the remains of another well-known carnivoran from Batallones-1, an amphicyonid that was informally named *Amphicyon* aff. *castellanus* in previous faunal lists for the locality (e.g. Morales *et al.* 2004). The Amphicyonidae is an arctoid family with a well-documented fossil record. It was particularly speciose and diverse during the early and middle Miocene of the Northern Hemisphere. The late Miocene was marked by several extinctions within the family so that only a few taxa survived in the Vallesian or earliest Turolian (MN 11). The presence of a high number of individuals and the perfect preservation of the material from Batallones-1 is unique in the fossil record of the family in Europe. We have performed a phylogenetic analysis at a generic level to assess the relationships of the species from Batallones-1 relative to (1) the related species '*Amphicyon*' *castellanus* and (2) the other amphicyonines.

MATERIAL AND METHODS

Material

The species described here is based on a sample that includes a minimum of 12 individuals (five are juveniles,



TEXT-FIG. 1. Geographic map of the Iberian Peninsula showing the location of Batallones-1 and the city of Madrid. The province of Madrid is shown in grey.

two are young adults, and five are adults). This material probably represents one of the best samples for the Amphicyonidae in Europe. Most of the cranial specimens are strongly laterally or dorsoventrally flattened and crushed; hence, some features cannot be observed. The craniodental remains are supplemented by postcranial remains that represent almost the entire skeleton. Only the dental and cranial specimens are described here. These are compared to most of the other Miocene amphicyonines. The description and functional morphology of the postcranial skeleton will be presented in another paper.

Methods

Format and terminology. We use the standard dental terminology proposed by Smith and Dodson (2003): upper teeth are designated by an upper case letter, lower teeth by a lower case letter, and the prefix 'd' indicates a deciduous tooth. In placental mammals, there are two generations of incisors, canines and most premolars. In most placentals (and in all of Carnivora), dP1/dp1 are not replaced by permanent teeth (i.e. P1/p1) (Luckett 1993). Thus, the so-called permanent first premolars (commonly named P1/p1) are, in fact, the unreplaced deciduous

dP1/dp1. The material described here comprises deciduous and permanent (= secondary) teeth. Therefore, we prefer to use 'dP1' and 'dp1' and to avoid terms such as 'P1' and 'p1' to designate the tooth occupying the first premolar locus. The muscular insertions and nomenclature are based primarily on Evans (1993) and Barone (2000).

Measurements. Measurements are presented in Tables 1–2 and include many abbreviations, some of which are also mentioned in the text. Although precise definitions and illustrations of the measurements taken here can be found in Peigné and Heizmann (2003), most of the measurement abbreviations are as follows: L, maximum mesiodistal length; W, maximum buccolingual width; H, height; DHI3, distal height of I3; LLP4, lingual length of P4; HPaP4, height of the paracone of P4; LMeP4, length of the metacone of P4; DWM1, distal width of M1; TBum1, buccal length of the trigonid of m1; Hprml and Hpam1, height of the protoconid or the paraconid of m1; Wtaldp4, width of the talonid of dp4; LDc-p3, length of the diastema between c and p3; Tmp3, thickness of the mandible across p3; DMp2-3, depth of the mandible below the alveolar level between p2 and p3; MdL, hemimandibular length, between the anteriormost margin of the hemimandible and the mid point of the mediolateral axis of the condyle.

Stratigraphy. The MP (Mammal Palaeogene) levels mentioned in the text correspond to the European biochronological levels for the Palaeogene continental record; they do not represent zones (Sigé and Legendre 1997), in contrast to the MN (Mammal Neogene) biozones (Mein 1999a). Each mention of MP level or MN zone is generally accompanied by the corresponding European Land Mammal Age following Mein (1999b).

Institutional abbreviations. MNCN, Museo Nacional de Ciencias Naturales, Madrid; MNHN, Muséum national d'Histoire naturelle, Paris; NHM, Naturhistorische Museum, Basel.

SYSTEMATIC PALAEOLOGY

Order CARNIVORA Bowdich, 1821
 Suborder CANIFORMIA Kretzoi, 1943
 Family AMPHICYONIDAE Haeckel, 1866
 Subfamily AMPHICYONINAE Haeckel, 1866

Remarks. The assignment of the material to the Amphicyoninae is based on a comparison with the other amphicyonid subfamilies. We follow Hunt (1998b) in recognizing four subfamilies in this family. The European Haplocyoninae (*Haplocyon* Schlosser, 1901, *Haplocyonoides* Hürzeler,

1940, *Haplocyonopsis* de Bonis, 1973) and North American Temnocyoninae (*Temnocyon* Cope, 1878, *Mammacyon* Loomis, 1936) differ in having a totally different dental specialization, i.e. they have tall, robust p2–4 and P2–3, and an M1 with a conical, isolated protocone surrounded by a strongly enlarged cingulum (see other features in Hunt 1998b, p. 201). The Daphoeninae (*Daphoenictis* Hunt, 1974, *Daphoenodon* Peterson, 1909, *Brachyrhynchocyon* Loomis, in Scott and Jepsen 1936, *Daphoenus* Leidy, 1853, *Paradaphoenus* Wortman and Matthew, 1899, *Adilophontes* Hunt, 2002a) is regarded as a monophyletic North American endemic subfamily (Hunt 1998a). According to Hunt, a different geographic and stratigraphic distribution is one of the main supports for distinct evolutionary histories for the Daphoeninae and Amphicyoninae (including the material from Batallones-1), but amphicyonines also differ from daphoenines in having more derived features (e.g. the M2–3 are enlarged relative to M1, and the premolars are reduced in size; see also Hunt 1998b, p. 202).

Genus MAGERICYON gen. nov.

Derivation of name. After Magerit, the original name of Madrid, in reference to the location of the sites of Batallones in the Province of Madrid.

Type species. *Magericyon anceps* sp. nov.

Other referred species. *Magericyon castellanus* (Ginsburg et al., 1981).

Diagnosis. Large amphicyonine amphicyonid with reduced premolars (dP1/dp1 absent, P2/p2 absent, p3 single-rooted, P3 strongly reduced and showing a distolingual inflation, p4 strongly reduced relative to m1 and with no accessory cuspids), metaconid absent or vestigial on dp4, m1, and m2, M2/m2 reduced relative to M1/m1, a short palate that does not extend posterior to the M2s.

Differential diagnosis. *Magericyon* differs from *Amphicyon* Lartet, 1836, *Crassidia* Heizmann and Kordikova, 2000, *Ysengrinia* Ginsburg, 1965, *Pseudocyon* Lartet, 1851, *Cynelos* Jourdan, 1862, *Pseudarctos* Schlosser, 1899, and *Ictiocyon* Crusafont, De Villalta and Truyols 1955 in the absence of dP1/dp1 and P2/p2, and in having a strongly reduced and distolingually inflated P3, a single-rooted p3, a metaconid that is absent or vestigial on m1 and m2, and a reduced M2 relative to M1. It differs further from all of these taxa except *Ictiocyon* and *Pseudarctos* in the absence of a distal accessory cuspid on p4; from all except *Pseudocyon steinheimensis* in having a strongly reduced p4 relative to m1; from *Amphicyon*, *Ysengrinia*, and *Cynelos* in

the absence of a metaconid on dp4; from *Ictiocyon* and *Pseudarctos* in having taller buccal cusps of the upper molars; from *Thaumastocyon* Stehlin and Helbing, 1925 in having a more transversely elongated M1, a wider m2 relative to m1, and an m3; and from *Amphicyon*, *Cynelos*, and *Ysengrinia* in having a palate that is shortened and does not extend backwards beyond the level of the M2s.

As pointed out in the discussion of the phylogenetic analysis, some taxa were not included in our analysis because the data are incomplete. However, significant differences exist between *Magericyon* and many of these taxa, which need to be mentioned here. *Magericyon* differs from all of these Amphicyoninae in having reduced anterior premolars. It differs further from *Myacyon* Sudre and Hartenberger, 1992, most Asian *Amphicyon*, *Maemohcyon* Peigné, Chaimanee, Yamee, Tian and Jaeger, 2006b, *Pliocyon* Matthew, 1918, and *Ischyrocyon* Matthew and Gidley, 1904 (at least primitively for the latter; Hunt 1998b) in the absence of a metaconid on m1 and, if available in the material, on m2, and except for *Myacyon*, in the absence of a distal accessory cuspid on p4; from *Agnotherium* Kaup, 1832 and *Ischyrocyon* in having a centrally positioned hypoconid on m1; from *Pliocyon* in the retention of an M3; from *Ischyrocyon* in having a much smaller I3; from *Afrocyon* Arambourg, 1961, *Maemohcyon*, and *Myacyon* in its more reduced m2 (in length and in width) relative to m1; and from *Afrocyon* in its single-rooted m3. *Janvierocyon* Ginsburg, 2000 and *Meiniogale* Ginsburg, 2002 are more poorly known than other taxa; they are only represented by a few isolated teeth and include species that were much smaller than *Magericyon* spp.

Distribution and age. Known only from late Miocene (Vallesian) deposits in Spain at Los Valles de Fuentidueña (MN 9) and Batallones-1 (MN 10).

Magericyon anceps sp. nov.

Text-figures 2–6

1997 *Amphicyon castellanus*; Fraile et al., table 1.

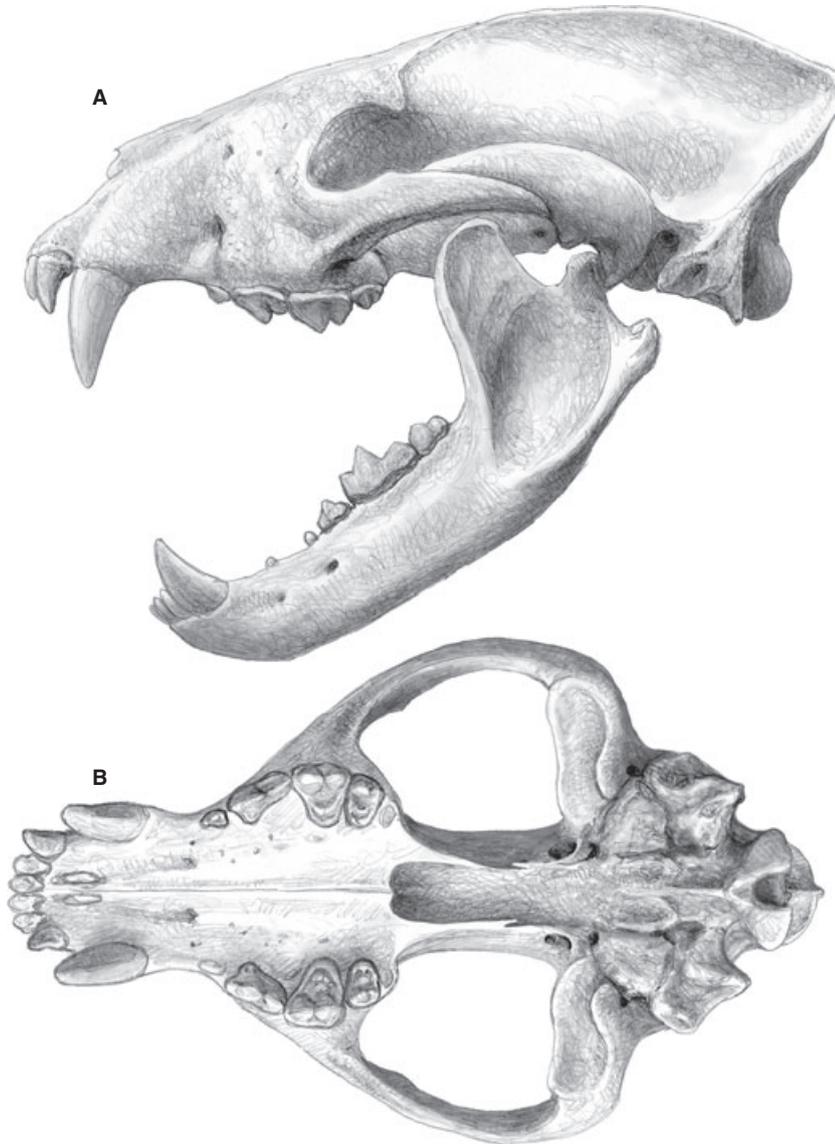
1999 *Amphicyon (Euroamphicyon) castellanus*; Ginsburg, p. 116

2004 *Amphicyon* cf. *castellanus*; Morales et al., table 1.

Derivation of name. Latin, *anceps*, trenchant, with reference to the dental morphology of this species.

Holotype. B-4071, complete skull of a young adult with I3, P4–M2, and unerupted left M3 (Text-fig. 3).

Paratypes. Juvenile specimens (only the deciduous dentition is present): BAT-1'-05-E3-31, left hemimandible with dp3–4 (Text-fig. 4C–D; Text-fig. 6F–H); B-299, fragment of right maxilla with



TEXT-FIG. 2. Idealized reconstruction of the skull and mandible of *Magericyon anceps* from Batallones-1. A, lateral view of an articulated skull and mandible. B, occlusal view of the skull (Art by M. Antón).

dP3 and B-4215(1), fragment of left maxilla with dP3–4 (Text-fig. 5A), possibly from the same individual; B-707, dorsoventrally compressed skull with unerupted (but visible) left I1–2, dP3 and right dP3 (Text-fig. 4A–B); B-2070, right dP4; B-3304, right edentulous subcomplete hemimandible and B-4174, left hemimandible with dp2, possibly from the same individual; B-3373, right dp4; B-4877, left dP4; B-4995, left dP4; B-4049, left dP4; B-5022, right hemimandible with dp3; B-5432, right hemimandible with dp2–4, erupting m1 (Text-fig. 4E–F), and B-5437, fragment of left hemimandible with erupting m1, probably from the same individual; B-5438, fragments of skull including fragment of left maxilla with dP3, unerupted P4, and erupting M1, and isolated left M2, from the same individual (Text-fig. 5C); B-5440, left dp4; B-5444, associated skull and mandible with only left dC and right dP3 visible. Young adult specimens (the dentition is slightly or not worn): B-396, left I3 (Text-fig. 5G–H); B-475, left c (Text-fig. 6A–B) and B-566, right c, probably from the same individual; B/S-678, snout with left P4–M2 (Text-fig. 5D); B-890, right m2 (Text-fig. 6L–N); B-935, left P3; B-957, left C; B-1304, left p3; B-1337, left I3; B-

2791, left C (Text-fig. 5E–F); B-3139, left hemimandible with c, dp2, m1–2 (Text-fig. 4I–J); B-3365, left p3; B-3583, left m2; B-4493, right I3; B-5433, fragment of right hemimandible with m2 and unerupted m3; B-5439, fragment of left maxilla with partial P4, M1, unerupted M3 and fragment of right maxilla with broken I3, lingual part of M1 and M2; B-5441, fragmentary left m2; B-5442, left P3; B-5443, left p4 (Text-fig. 6I–K). Sub-adult specimens (deciduous teeth may be present and the permanent dentition is erupting): BAT-1'05-D8-101, left hemimandible with erupting canine, dp2, and m1 (Text-figs 4G–H, 6O–Q); B-834/1, right hemimandible with erupting c, dp1–2, and m1, and B-834/2, left hemimandible with erupting c, dp2, m1, and erupting m2; B-834 (37), right m3 (Text-fig. 6C–E); B-936, right hemimandible with erupting c, dp2, m1; B-5434, strongly transversely compressed skull with unerupted canines, P4–M1 on both sides, unerupted M2s; B-5435, dorsoventrally flattened skull with unerupted canines, P4–M1 on both sides, and erupting M2. Adult specimens (the dentition is moderately or heavily worn): B-5436, skull with P3–M2 on both sides, right hemimandible with p3–m2, and

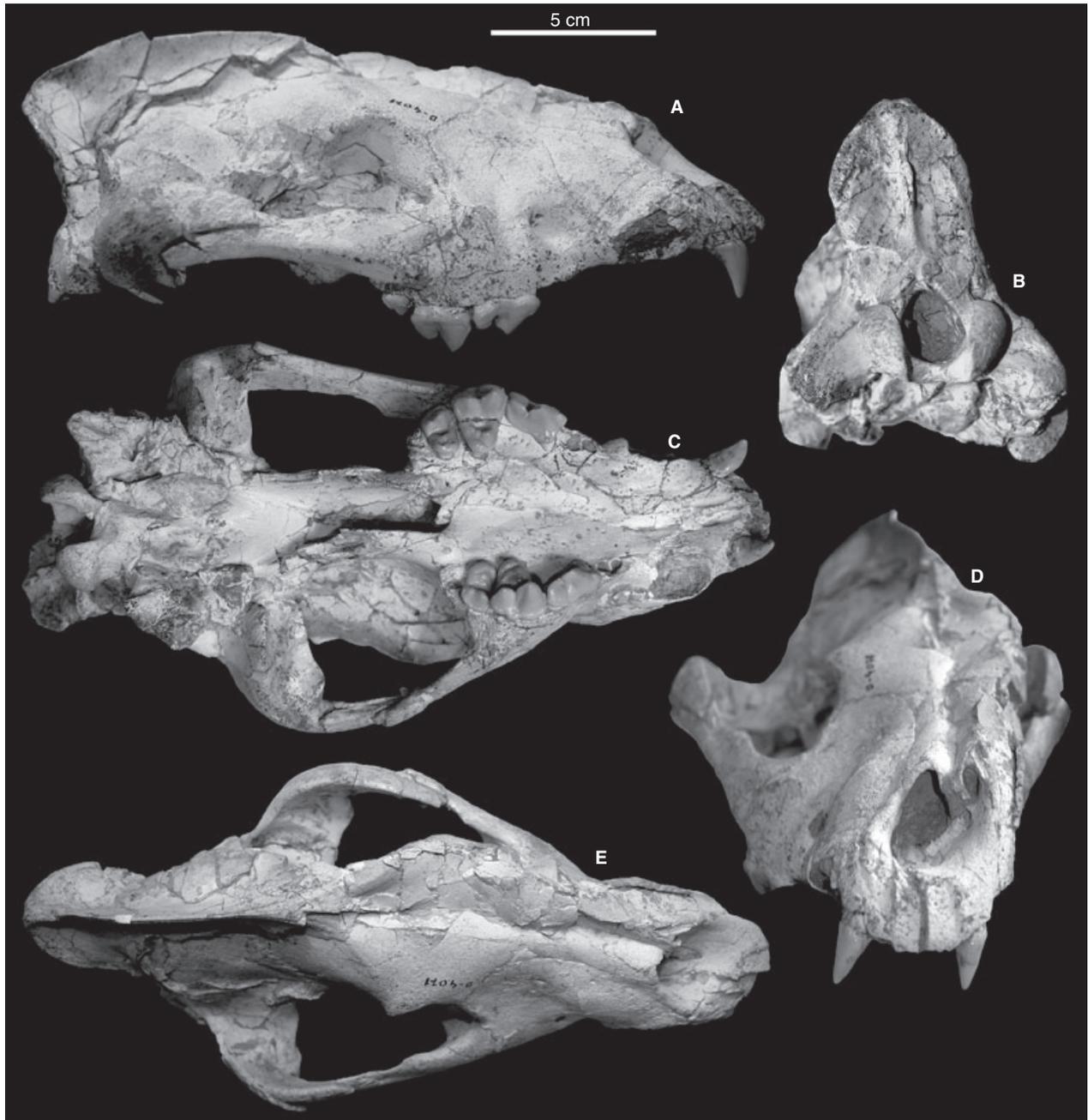
fragment of left hemimandible with dp2, p4, and subcomplete m1; BAT-1'03-E4-194, right? i2; B-287 (16), left i3; B-715, right i3; BAT-1'01-D4-98, skull with C-M2 and right I3-M2, mandible with left c-m2 and right i3-m2. All the specimens are stored in the palaeontological collections of the MNCN.

Differential diagnosis. *Magericyon anceps* differs from *M. castellanus* in having a more transversely compressed upper canine, a less transversely elongated M2, and a narrower m2.

Distribution. Known only from Batallones-1, late Miocene (Vallesian, MN 10, Spain).

Description

Skull of sub-adults and adults (Text-fig. 3). The premaxilla is narrow, short, and widely separated from the frontal by the maxilla. The nasal has a markedly concave anterior border. It is subrectangular in shape, short, and its posterior border is



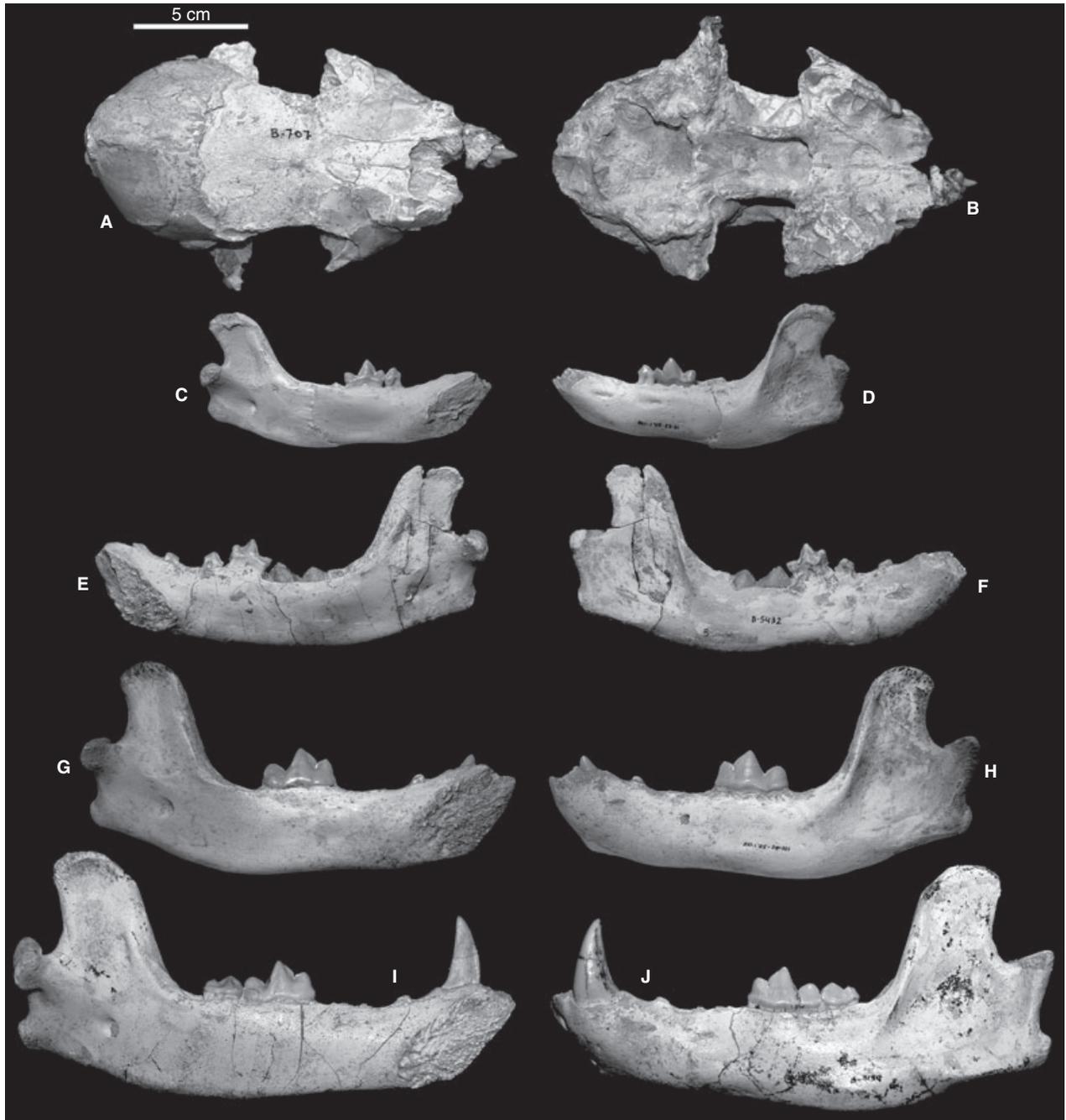
TEXT-FIG. 3. *Magericyon anceps* gen. et sp. nov. from Batallones-1. B-4071, complete skull (holotype) in A, lateral, B, caudal, C, ventral, D, cranial, and E, dorsal views.

anterior to the lacrimal. The posterior margin is rounded. The frontal extends forward up to the level of the infraorbital foramen. The postorbital process of the frontal is poorly developed, whereas that of the jugal is almost absent. The postorbital constriction is weakly marked. The frontoparietal suture is not distinct in the sub-adult and adult specimens. The zygomatic arch is softly curved. The sagittal crest, which arises from the level of the postorbital constriction, and the nuchal crests are very developed, especially in older and larger specimens (e.g. BAT-1'01-D4-98). The dorsal profile of the skull describes a soft curve. The snout is short relative to the total length of the skull, and shows a marked anterior projection at the premaxilla. The infraorbital foramen is small, rounded, and located above the mesial border of P4. The anterior margin of the orbit is at the level of the paracone of M1. The lacrimal foramen is small and lateromedially compressed; the suture of the lacrimal with the surrounding bones is not distinct. The jugal portion of the zygomatic arch is markedly shallower than its squamosal portion. The auditory region is anteroposteriorly short. The postglenoid process is lower than the mastoid process. The two processes delimit a narrow auditory notch. The mastoid process is massive, though not prominent. Its morphology is variable in the sample studied. Sub-adults and young adults have a mastoid process with a concave and rough ventrolateral surface (see e.g. B-4071, Text-fig. 3), whereas in older individuals (BAT-1'01-D4-98, B-5436) it is laterally inflated and less rugose. The snout is short and has strongly concave lateral faces just anterior to the P3s. The palatine fissures are elongated and very close to each other; their posterior border is at the level of the mesial border of the canine alveolus. The palatine foramina are immediately anterior to P3 and are extended anteriorly by a deep groove. The palate is shortened posteriorly compared to that of e.g. *Cynelos* or *Amphicyon*. Its posterior border is at the level of the distal border of M2; the caudal nasal spine is very short. The vomer crest is well developed and variable in length. The pterygopalatine wings are thin, parallel, and present a lateral groove along their posterior margin. The posterior opening of the alisphenoid canal and the foramen ovale are close to each other; they are located medial to the preglenoid process. The latter is poorly developed except for its lateralmost portion, and is much more transversely developed than the postglenoid process. A robust process, located at the suture between the squamosal and the alisphenoid, provides the medial limit of the glenoid fossa. The auditory region is compressed and damaged on most of the cranial specimens. The postglenoid foramen, which is large, is located medially on the postglenoid process (e.g. see BAT-1'01-D4-98). It is hidden by the external auditory meatus in most specimens. The basicranium is wide and laterally convex, especially in the anterior portion of the basioccipital. On the latter, there is a large, prominent, oval, and very rugose tubercle for the insertion of the terminal tendon of the *M. longus capitis*, which suggests a strong development of this flexor muscle. A low longitudinal crest is present in the posterior part of the basioccipital, and on both sides there is a marked depression for the insertion of the *M. rectus capitis ventralis*. The paroccipital process is robust and ventrally, and somewhat posteriorly, projected. It is triangular in shape and divided into two

unequal parts: the lateral, larger part consists of a concave and rugose area, to which the *M. digastricus* and the *M. rectus capitis lateralis* are attached; the medial part is also rugose and concave. The dorsal margin of the occipital region is well rounded, while its lateral margins diverge ventrally. The occipital crest is strongly marked throughout its dorsoventral height. It divides the occipital region into two equal surfaces, each of which has a dorsal portion, and a lateral portion that shows a strongly depressed and rugose surface for the attachment of neck muscles.

Skull of juveniles (Text-fig. 4). The skull of one cub is available. It is damaged and strongly dorsoventrally compressed; most of the basicranium and the auditory region are not well preserved (Text-fig. 4A–B). We will only emphasize the main features and differences from the sub-adult and adult cranial morphology here. The posterior border of the nasal is posterior to the anterior border of the orbit. There is no postorbital process. The sagittal crest is absent. The nuchal and occipital crests are present, though they are much less developed than in the sub-adults and adults. The palatine foramen is slightly posterior to the canine alveolus. The vomer crest is not developed. The postglenoid foramen is approximately the same diameter as that of sub-adult and adult individuals. The mastoid process is much smaller and has a pyramidal shape.

Mandible (Tables 1–2). Four ontogenetic stages are represented in the sample. The earliest (Stage 1) is known from at least three, possibly four, juvenile individuals that preserve only one or two deciduous teeth (B-3304, B-5022, B-4174, and BAT-1'05-E3-31, Text-fig. 4C–D). Except for its much smaller size, the mandible of these individuals differs from that of sub-adults and adults in its relatively thicker corpus owing to an inflation through the m1 locus. There are two well-separated mental foramina; one is below dp1 and the other one is below dp3. The ventral border of the mandibular body is gently convex. As in the adults, the angular process is not prominent and displays a large attachment surface for the *Musculus pterygoideus medialis*. The coronoid process is somewhat more backwardly orientated than in the adult specimens, though it has the same proportions. The dorsal border of the process is thick and rugose. The development and orientation of the mandibular condyle are as in the adults. Only one individual (B-5437 and B-5432, Text-fig. 4E–F) represents the next ontogenetic stage (Stage 2). The only significant difference from Stage 1 is the overall larger size. The anterior mental foramen is below the postcanine diastema and the posterior mental foramen is below the mesial portion of dp4. There are no significant differences between the mandibles of sub-adults (Stage 3: e.g. B-834, B-936, BAT-1'05-D8-101, Text-fig. 4G–H) and adults (Stage 4: e.g. B-3139, Text-fig. 4I–J; BAT-1'01-D4-98), except for an increase in the overall size. The adult specimens display a long and posteriorly deep corpus. Its ventral border is relatively horizontal below the premolars and m1, it is then convex below m2–3. In lateral view, the curvature of the symphysis is not regular but displays a marked angle. There are two mental foramina: the anterior one, which may be absent (e.g. B-834), is below the mid-length of the postcanine diastema;



TEXT-FIG. 4. A–J, *Magericyon anceps* from Batallones-1, ontogenetic stages. A–B, B-707, complete skull of a cub (Stage 1) in dorsal and ventral views. C–D, BAT-1'05 E3-31, left hemimandible with dp3 and dp4 (Stage 1) in lingual and buccal views. E–F, B-5432, right hemimandible with dp2, dp3, dp4, and erupting m1 (Stage 2) in lingual and buccal views. G–H, BAT-1'05 D8-101, left hemimandible with erupting lower canine, dp2, and m1 (Stage 3) in lingual and buccal views. I–J, B-3139, left hemimandible with canine, dp2, m1, and m2 (Stage 4) in lingual and buccal views.

the posterior mental foramen is below the alveolar margin between p3–p4. The masseteric fossa is deep and extends anteriorly below m3. The coronoid process is moderately developed and somewhat similar to, though anteroposteriorly shorter than, that of *Ursus arctos*. The process is orientated backwards and has a concave posterior border. Its dorsal border is well rounded.

The angular process is short, rounded, and has a rugose posterior surface. The area of attachment for the *Musculus pterygoideus medialis* is very distinct and extends forward almost to the posterior rim of the mandibular foramen. The ventral surface of the angular region is flattened and smooth, and a small ridge is present along its ventrolateral border.

Deciduous dentition (Table 1). Upper deciduous incisors, canines and dP1–2 are not represented in the material. There is one alveolus anterior to dP3 in B-707 (Text-fig. 4A–B), B-4215(1), and B-5438 (Text-fig. 5C), which is interpreted as a single-rooted dP2. There is no evidence for the presence of a dP1 in the sample studied; it is, therefore, probable that this tooth did not develop in *M. anceps*. There is a diastema between the deciduous canine and dP2, and a shorter one between dP2 and dP3. The dP3 is elongated and trenchant. There is no protocone, though the lingual root is well developed and slightly mesial to the paracone. There is a low parastylar ridge and the metacone is shorter than the paracone. The dP4 is typically triangular in occlusal view. The buccal cusps are well developed, with the paracone somewhat taller than the metacone. The trigon basin is deep. The protocone is small and crest-like. There is a buccal cingulum that is particularly developed at the level of the metacone. The lingual cingulum is vestigial. The crown is asymmetrical owing to a distal development of the metacone, which results in a concave distal face.

Lower deciduous incisors and canines are not preserved in the material. The dp1 did not develop in most of the individuals in which the corresponding part of the mandible is preserved (eight out of 10). Its alveolus is present in B-936 and is preserved in Bat-834/1. In contrast, the dp2 is present in most of these individuals. A short diastema separates the mesial alveolus of dp1 from that of dc, whilst another separates the distal alveolus of dp2 from the mesial alveolus of dp3. The dp1 and dp2 are tiny double-rooted teeth, the latter being slightly larger than the former. Both teeth have a low, elongated crown that displays a slight lingual cingulum. Their roots are divergent, especially those of dp2. The dp3 is double-rooted and much larger than dp1–2. The crown is symmetrical and has a single

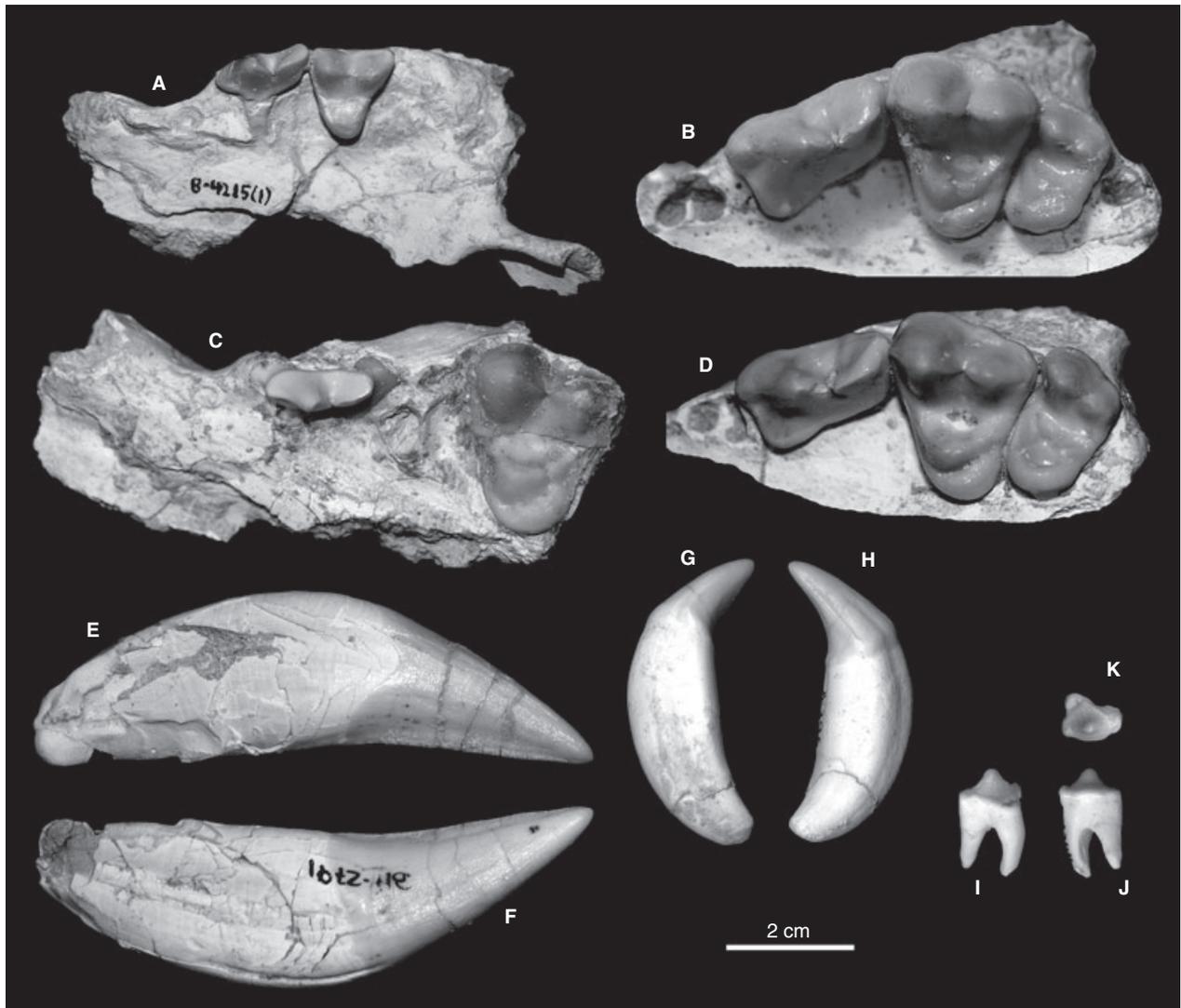
TABLE 1. *Magericyon anceps* from Batallones-1, late Miocene (Vallesian, MN 10): measurements of the deciduous dentition (in mm).

	N	Mean	Minimum–Maximum
LdP3	3	14.97	14.60–15.30
WdP3	2	8.60	8.30–8.90
HdP3	2	8.30	8.00–8.60
LdP4	5	13.06	12.70–13.50
WdP4	5	14.42	14.10–14.60
DWdP4	5	15.00	14.40–15.40
Ldp1	1	4.80	–
Wdp1	1	2.90	–
Ldp2	5	5.76	4.80–6.40
Wdp2	5	3.24	2.80–4.00
Ldp3	3	8.45	8.20–8.90
Wdp3	3	4.70	4.60–4.90
Hdp3	3	4.60	4.20–5.00
Ldp4	4	18.58	18.40–18.70
Wdp4	4	7.28	7.20–7.50
Wtaldp4	4	7.57	7.30–7.70
TBudp4	4	12.98	13.00–13.10
HPrdp4	3	9.93	9.80–10.20

cuspid; distal and distolingual low crests extend from its tip. The dp4 is elongated and much larger than dp3. The paraconid is low and reduced relative to the protoconid. The metaconid is absent and replaced by a crest in B-3373 and B-5432 (Text-fig. 4E–F); it is vestigial and basally located in B-5440. The talonid is slightly wider than the trigonid and is composed mainly of a large buccal hypoconid crest; its lingual border only displays a low ridge.

Permanent dentition (Table 2). The upper incisor arcade is curved, with I3 much larger and more distal than I1–2. The I1 is visible in its alveolus in the juvenile B-707 (Text-fig. 4A–B) because of the broken premaxilla. It is hooked, caniniform, and has an inflated lingual basis; poorly developed mesial and distal crests are present. The I2 is also present in this specimen, but only its tip is visible. The I3 is more commonly preserved, either as isolated teeth or from more complete sub-adult and adult specimens. It is large, caniniform, and has a markedly curved root and crown; the former is more inflated. The crown displays a prominent buccal vertical crest and, somewhat mesially, a discrete buccal groove on some specimens (e.g. B-396, Text-fig. 5G–H). There is a short but distinct diastema between I3 and C. The latter (Text-fig. 5E–F) is slightly larger, more transversely compressed, and less curved than the lower canine. There are prominent distal and mesiolingual crests, the rim of which is strongly wrinkled. P2 is absent. There is a short, buccally concave postcanine diastema. The double-rooted P3 is very reduced in size, markedly more than P4. The crown of P3 consists of a main, pointed cusp, with a mesial and distal, crest-like, concave rim. The distal cingulum is slightly prominent. There is a large distolingual cingulum that results in a lingual inflation of the distal root. A small depression is present in the centre of this expansion (Text-fig. 5I–K). The upper carnassial is robust. A parastylar crest is present; in some specimens (e.g. B-4071, Text-fig. 5B), it is very prominent near the enamel-dentine junction, though no cusp is present. The protocone is reduced to a smooth crest in most of the individuals or to a small style in B-4701 (Text-fig. 5B); it is distal relative to the mesial border of the parastylar region. The paracone is longer than the metastyle. The cingulum is present, though not marked. The M1 is a large triangular tooth. The paracone is much taller than the metacone and has a developed mesial ridge. The buccal cingulum is marked. The protocone, located mesially, is a low and crest-like cusp. The trigon crests are low; a vestigial metaconule may be present (e.g. B-5434). The lingual cingulum is well developed, though restricted to the distolingual border. The M2 is much more reduced and proportionally more transversely elongated than M1; it has a subrectangular shape. The paracone is larger (B/S-678, Text-fig. 5D) or much larger (B-5435) than the metacone. The trigon crests are low and blunt, with a poorly developed protocone. The lingual cingulum symmetrically surrounds the protocone. The M3 is single-rooted and is preserved solely in B-4071 in which it is unerupted. Only the occlusal surface is visible, but it is damaged and preserves no details.

The root and, especially, the crown of the lower canine are transversely compressed. The root is inflated near the cervix. The crown is curved and displays two prominent crests that are



TEXT-FIG. 5. A–K, upper dentition of *Magericyon anceps* from Batallones-1. A, B-4215(1), fragment of left maxilla with dp3 and dp4, occlusal view. B, B-4071, detailed view of left maxilla with alveolus of P3, P4, M1, M2, and unerupted M3, occlusal view. C, B-5438, fragment of left maxilla with dp3 and M1, occlusal view. D, B/S-678, fragment of left maxilla with alveolus of P3, P4, M1, and M2, occlusal view. E–F, B-2791, left upper canine in lingual and buccal views. G–H, B-396, left I3 in lingual and buccal views. I–K, B-1344, left P3 in lingual, buccal, and occlusal views.

closer to each other than in the upper canine. The p2 is absent. When dp1–2 are also absent, the c–p3 diastema is long (Table 2). The p3 is a tiny, single-rooted tooth, separated from p4 by a very short diastema. The p4 is double-rooted and relatively symmetrical. Although it is much larger than p3, its crown is very low. The mesial and distal rims of the main cuspid are crest-like and concave; there is no evidence of accessory cuspid. The m1 paraconid is short and low, and has an almost vertical mesial face. The protoconid blade is sagittally orientated, elongated, and has a distal face orientated forward. All of the specimens lack a metaconid, which may be replaced by a more (e.g. B-936) or less (e.g. B-834) prominent crest. The major portion of the talonid is occupied by a strong buccal hypoconid crest that is located distal to the protoconid, both cuspid being separated by a marked notch. The remainder of the talonid consists of a small

area in the distolingual corner with a ridge-like border. The talonid is mesiolingually open. The morphology of m2 is very variable. The paraconid is reduced to a low, mesially located transverse crest. The protoconid is the largest cuspid of the trigonid. The metaconid is reduced, either to a prominent crest (e.g. B-3139, Text-fig. 4I–J) or to a vestigial cuspid lingual to the protoconid (e.g. B-890, Text-fig. 6L–N). There is a trigonid basin, the depth of which varies with the development of the metaconid and paraconid. The talonid tapers off distally. It has a low hypoconid and a low lingual ridge, though it remains mesiolingually open. The buccal cingulum is developed and may be mesiobuccally very strong in some specimens (e.g. B-3583). The m3 is not well represented in the sample; it was single-rooted. B-5433 displays a part of the occlusal surface of an unerupted m3, which does not allow a precise description.

TABLE 2. *Magericyon anceps* from Batallones-1, late Miocene (Vallesian, MN 10): measurements of the permanent dentition (in mm).

	N	Mean	Minimum–Maximum
LI1	1	4.70	–
WI1	1	8.00	–
LI3	5	11.00	10.50–11.90
WI3	6	12.38	11.70–13.00
DHI3	4	21.76	21.00–22.60
LC	2	24.40	23.20–25.60
WC	2	13.75	13.20–14.30
LP3	5	9.22	8.30–9.70
WP3	5	7.42	6.60–8.40
LP4	5	24.66	23.55–25.85
WP4	5	14.26	13.30–15.50
LLP4	5	24.46	23.20–25.40
HPaP4	4	13.18	12.80–13.65
LMeP4	4	10.49	10.00–11.30
LM1	6	21.30	20.35–22.50
WM1	6	27.23	26.25–28.00
DWM1	7	24.42	23.15–25.80
LM2	4	12.77	11.45–13.40
WM2	5	19.79	18.10–20.70
Li3	1	7.50	–
Wi3	1	10.30	–
Lc	3	20.90	19.20–23.00
Wc	3	13.08	12.25–14.60
Hc	1	27.50	–
Lp3	1	5.10	–
Wp3	1	4.25	–
Lp4	4	12.46	12.05–13.00
Wp4	4	7.09	6.70–7.50
Lm1	5	32.85	31.20–34.70
Wm1	5	14.79	14.30–15.50
TBum1	4	22.83	21.90–23.90
HPrm1	4	19.08	18.50–19.60
HPam1	4	12.15	11.50–12.70
Lm2	6	17.77	16.20–19.20
Wm2	5	13.48	12.40–14.60
LDc–p3	4	31.25	26.00–38.25
TMp3	4	17.00	15.00–18.30
TMm1	4	18.18	17.00–19.70
DMp2–3	4	34.78	33.60–35.50
DMp3–4	4	35.08	34.10–37.00
DMp4–m1	4	36.18	34.60–39.20
DMm1–2	3	41.87	39.90–44.80
DMm2–3	2	47.55	41.60–47.50
MdL stage 1	3	130.83	128.50–132.80

PHYLOGENY OF MAGERICYON

A phylogenetic analysis was performed to determine the relationships of *Magericyon anceps* to other taxa in the Amphicyoninae. We have focused on the Amphicyoninae because our material differs markedly from taxa of the other amphicyonid subfamilies (see ‘Systematic palaeon-

tology’). Nevertheless, our analysis does not intend to be a phylogenetic analysis of the entire subfamily Amphicyoninae. The first consequence of this is that we have focused our phylogenetic analysis on the characters that distinguish *M. anceps*: some characters, used by previous authors for resolving relationships of amphicyonids (e.g. Viranta 1996), may be uninformative or included in a modified version in the present study. A second consequence is that only dental characters were used so that they could be coded in the majority of the taxa. The final consequence is that, with the exception of one species (*Pseudocyonopsis ambiguus*), we do not include in our analysis any taxa known from strata that are reputed to be Eocene or Oligocene in age (stratigraphic information for specimens from some localities, e.g. the old collections of the Phosphorites of Quercy, are imprecise; see Vianey-Liaud and Legendre 1986) such as *Goupilictis* Ginsburg, 1969, *Pseudocyonopsis* Kuss, 1965, and *Brachycyon* Filhol, 1872. *Pseudocyonopsis ambiguus* is well known from the old collections of the Phosphorites of Quercy (Oligocene, France) and was regarded as a possible ancestor for most of the Miocene Amphicyoninae (e.g. Hunt 1998b, fig. 11.3); it is included as a representative of the Palaeogene taxa. Data for this species are based on our observations of the lectotype mandible (MNHN-QU 9249) and some referred maxilla (MNHN-QU 9266, 9267), and on the literature (Springhorn 1977).

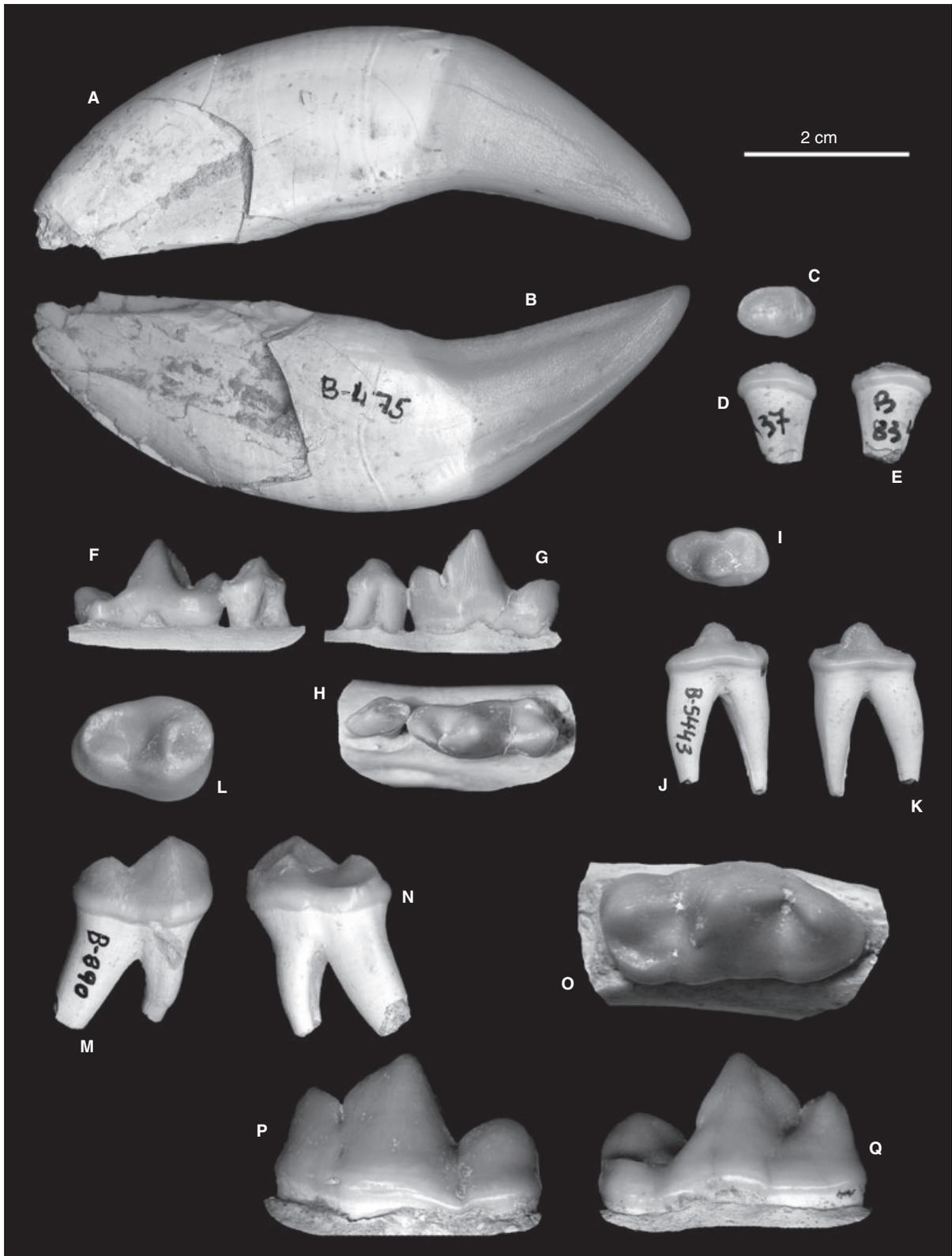
Our comparisons are mainly based on our own data; additional data come from the literature and are mentioned for each taxon (see below).

Outgroup used in the analysis

The Haplocyoninae is taken as the outgroup, and serves to root the cladograms, because it is probably the sister-subfamily of the Amphicyoninae. The definition of character states for the Haplocyoninae is based primarily on species of *Haplocyon* (*H. dombrowski*, *H. elegans*, and *H. crucians*) because they are less derived than those of *Haplocyonopsis* and *Haplocyonoides*, for example. A list of the material studied can be found in Peigné and Heizmann (2003, appendix).

Miocene Amphicyoninae included

Whilst the specific content of *Crassidia*, *Ysengrinia*, *Ictiocyon*, and *Pseudarctos* is relatively clear, that of *Amphicyon*, *Pseudocyon*, and *Cynelos* is much less so, at least in Eurasia. For this reason, we propose a definition of each genus as used in our analysis. The North American taxa are relatively well defined (Hunt 1998b), although pub-



TEXT-FIG. 6. A–Q, lower dentition of *Magericyon anceps* from Batallones-1. A–B, B-475, left lower canine in buccal and lingual views. C–E, B-834 (37), right m3 in occlusal, buccal, and lingual views. F–H, BAT-1'05 E3-31, detailed view of dp3 and dp4 in lingual, buccal, and occlusal views. I–K, B-5443, left p4 in occlusal, buccal, and lingual views. L–N, B-890, right m2 in occlusal, buccal, and lingual views. O–Q, BAT-1'05 D8-101, detailed view of left m1 in occlusal, buccal, and lingual views.

lished data are not available for some of them (e.g. *Pseudocyon* spp. and some species of *Cynelos*).

Ysengrinia. This genus is known from six species that range from late Oligocene (MP 30) to early Miocene (MN 4) in North America (one species), Europe (four species) and Africa (one species). Here, we consider that *Ysengrinia* includes the following species: *Y. gerandiana* (the type species), *Y. tolosana*, *Y. depereti*, *Y. valentiana*, *Y. ginsburgi*, and *Y. americana*. Data for the North American *Y. americana* are based on Hunt (2002b) and those for the European and African species are based essentially on a direct study by at least one of us (Morales *et al.* 1998, 2003; Peigné and Heizmann 2003). The isolated M1 from the Miocene of Japan assigned to *Ysengrinia* (Kohno 1997) may be rather close to *Cynelos* (Hunt 2002b).

Cynelos (= *Heizmannocyon* Ginsburg, 1999 = *Hecubides* Savage, 1965). This is the most diverse genus in the Amphicyoninae, with probably six species in North America (of which three remain undescribed and unnamed) from the early and middle Miocene (c. 19.2–14.5 Ma; Hunt 1998b), up to nine European species known from the Oligocene–middle Miocene, and two African species (see Peigné and Heizmann 2003). Some authors refer the species *bohemicus* and *steinheimensis* to this genus (Ginsburg 1989; Hunt, 1998b); Kuss (1965) also regarded these two species as closely related. It is important to note that there is no consensus among previous authors regarding the assignment of the species *steinheimensis*: it is *Pseudocyon steinheimensis* according to Viranta (1996), *Cynelos steinheimensis* according to Hunt (1998b), and *Amphicyon steinheimensis* according to, e.g. Heizmann (1973) and Ginsburg (1999). At least the general morphology of the teeth (e.g. reduction of M2/m2) indicates that it cannot be assigned to *Amphicyon*. Given the possible close relationships between *Cynelos* and *Pseudocyon* (Hunt 1998b), its assignment to either of these genera may be subjective and/or arbitrary. It is arbitrarily included in our phylogenetic analysis as *Pseudocyon steinheimensis*. We thus consider the genus to include *Cynelos crassidens*, *C. piveteaui*, *C. quercensis*, *C. lemanensis*, *C. schlosseri*, *C. rugosidens*, *C. helbingi*, *C. bohemicus* (= *Cynelos dietrichi*), *C. caroniavorus*, *C. sinapius*, and *C. idoneus*. In Africa, the genus is represented by the species *C. euryodon* and *C. macrodon* from the lower and middle Miocene of Kenya and Uganda (these species were originally assigned to *Hecubides*), and by isolated teeth assigned to *Cynelos* sp. from the early Miocene of Egypt (Morlo *et al.* 2007). Our data are mainly first hand; additional data for *C. bohemicus* and *C. caroniavorus* are from White (1942, 1947), Thenius (1949), Olsen (1958), and Kuss (1965).

Cynelos sinapius, *C. idoneus*, and *C. macrodon* were not included in our analysis because the data on them are incomplete.

Amphicyon (*Arctamphicyon* Pilgrim, 1932 = *Hubacyon* Kretzoi, 1985 = *Megamphicyon* Kuss, 1965 = *Euroamphicyon* Viranta, 1996). This genus is represented by three species in North America ranging from c. 18 to 14 Ma (Hunt 1998b, 2003). They are, from the earliest to the latest: *Amphicyon galushai*, *A. frendens*, and *A. ingens*. There is less of a consensus over the specific content of *Amphicyon* in Europe, except for the recognition of *A. major* and *A. giganteus*. Ginsburg *et al.* (2000) recognized two earlier species, *A. laugnacensis* and *A. lathanicus* that, except for some details, are similar to *A. giganteus*. Hunt (2003) recognized three species in Europe (*A. aurelianensis*, *A. giganteus*, and *A. major*), in addition to which Viranta (1996) recognized *A. pannonicus* and *A. guttmani*, but these two species are poorly known and are not included in our analysis. *Amphicyon eibiswaldensis* and *A. eppelsheimensis*, which were sometimes regarded as synonyms of *A. giganteus* and *A. major*, respectively, were also recognized. Finally, *A. olisiponensis* was assigned to its own genus *Euroamphicyon* (Viranta 1996), on the basis of the distobuccal extension on m1 and the mesio-buccal extension on m2. However, our observations indicate that this feature does not support a generic distinction. In *Amphicyon*, it is variable in presence and size; hence, it may be poorly developed or absent, or present and large, in particular in m2, as in *A. major* (e.g. MNHN Sa 36, Sa 844), *A. lathanicus* (e.g. MNHN FP 208), and *A. giganteus* (e.g. MNHN Chi 259; see also Kuss 1965, figs 49–51). For this reason, we consider that *Euroamphicyon* is a junior synonym of *Amphicyon*; Ginsburg (1999) regarded it as a subgenus of *Amphicyon*.

In Africa, only one species, *A. giganteus*, is known. This is from Arrisdrift, Namibia (MN 4, early Miocene; Morales *et al.* 1998, 2003). The genus is also known from fragmentary remains from early Miocene deposits in As-Sarrar, Saudi Arabia (Thomas *et al.* 1982) and Gebel Zelten in Libya (Ginsburg 1979; Ginsburg and Welcomme 2002).

Endemic species from Asia assigned to *Amphicyon* are not included in our analysis because of their uncertain generic assignment and/or incomplete data (but see Peigné *et al.* 2006b, and below). In our work, *Amphicyon* includes the following species: *A. galushai*, *A. frendens*, *A. ingens*, *A. major*, *A. giganteus*, *A. laugnacensis*, *A. lathanicus*, and *A. olisiponensis*.

Data for the North American species are based on Hunt (1998b, 2003). Those for the European species are mainly ours; additional information and measurements were taken from Kuss (1965), Ginsburg and Antunes

(1968), Beaumont (1984), and Ginsburg (1989, 2000, 2003).

Crassidia. This genus is only represented by its type species, *C. intermedia*. Data are from our observations and from the literature (Heizmann and Kordikova 2000).

Pseudocyon. This genus is represented by a single, unnamed lineage in North America (Hunt 1998b) for which the published data are incomplete. In Europe, 1–5 species are recognized (Viranta 1996; Hunt 1998b; Ginsburg 1999; Ginsburg *et al.* 2000). Our definition of *Pseudocyon* is based mainly on *P. sansaniensis* and *P. steinheimensis*; *P. styriacus* and *P. caucasicus* are not included in the analysis because the data on them are incomplete. The data used are based on Hunt (1998b) for the North American material and on our own observations for the European taxa.

Pseudarctos. This genus is endemic to Europe. The only species known, *P. bavaricus*, is middle Miocene–early late Miocene in age (MN 5–MN 9). The data come from a direct study by at least one of us and from the literature (Helbing 1937; Kuss 1965; Ginsburg 1992, 1999; Viranta 1996).

Ictiocyon. This European endemic genus is represented by only one species, *I. socialis*, known from early Miocene (MN 3–MN 4) deposits. The data come from a direct study by at least one of us and from the literature (Dehm 1950; Crusafont *et al.* 1955; Kuss 1965; Ginsburg 1992, 1999; Viranta 1996).

Thaumastocyon. This genus is sometimes grouped with *Agnotherium* Kaup, 1832 in the endemic European subfamily Thaumastocyoninae (e.g. Ginsburg 1999). It is known from two species: *Thaumastocyon bourgeoisi* (MN 5, middle Miocene) and *T. dirus* (MN 9, late Miocene). *Thaumastocyon* is more derived than *Agnotherium*, e.g. in having an m1 and an m2 without a metaconid, and in lacking an m3. Only *T. bourgeoisi* is included in our analysis.

Miocene Amphicyoninae not included

The genera *Pliocyon* and *Ischyrocyon* are not included in our study mainly because of their endemic status, since they are only known from North America (Hunt 1998b). The following genera that are monospecific and/or poorly known are also excluded: *Afrocyon*, *Agnotherium*, *Askazansoria* Kordikova, 2001, *Janvierocyon*, *Maemohcyon*, *Meiniogale*, *Myacyon*, *Vishnucyon* Pilgrim, 1932, and *Aktaucyon* Kordikova *et al.*, 2000. The last of these is possibly related to the Daphoeninae (Kordikova *et al.* 2000).

Some other species are not included for similar reasons and/or because of uncertainty regarding their generic assignment. These are the Asian species referred to *Amphicyon* (see Peigné *et al.* 2006b), and two European species *A. gutmanni* and *A. pannonicus* (erroneously called *A. hubacyon* by Viranta 1996, p. 12), which are assigned to *Hubacyon* Kretzoi, 1985.

The most important differences between most of the taxa not included in the analysis and *Magericyon* are mentioned above in the differential diagnosis of the genus.

Character analysis

For the definition of characters and their states, see the Appendix. The polarity of the character states is based on an outgroup comparison.

Cladistic analysis

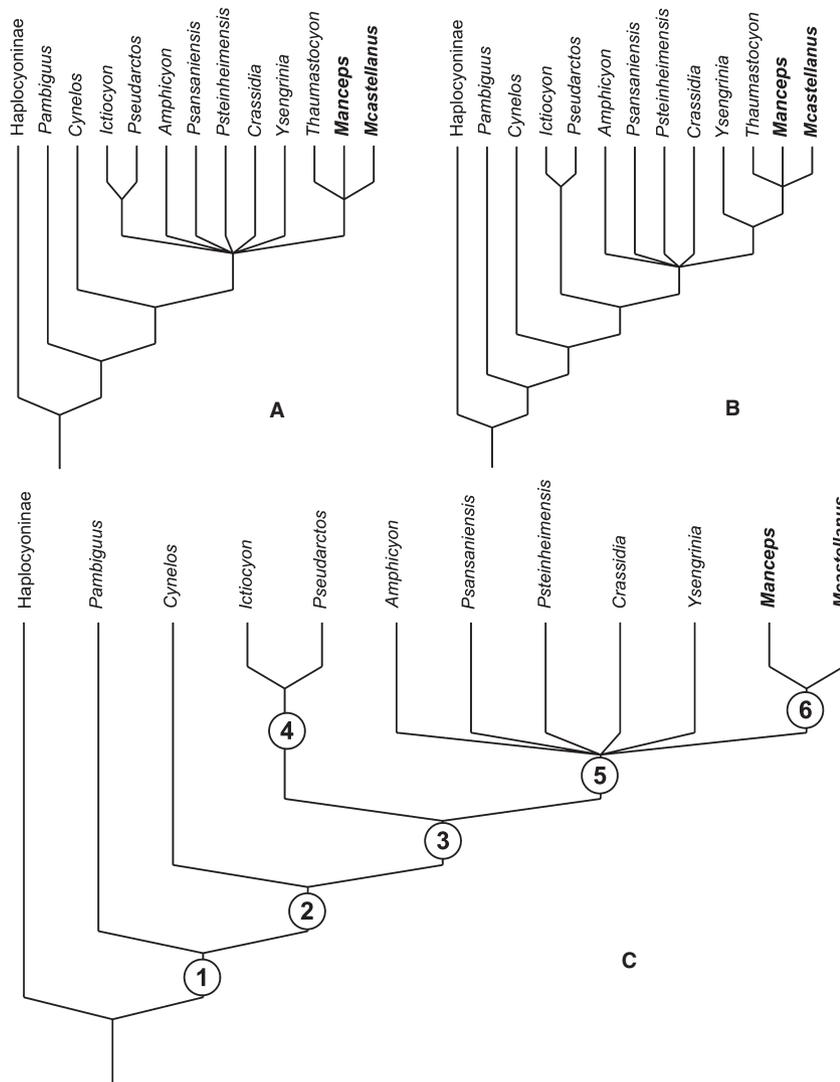
The data matrix included 13 taxa and 18 unweighted and unordered dental characters (Table 3). It was compiled in MacClade 4 and run in PAUP 4.0b10 (Swofford 2002) using a branch-and-bound search. This analysis produced 190 most parsimonious trees (MPTs) of 29 steps (CI = 0.793; RI = 0.806; rescaled CI = 0.640). As expected from using dental characters only, the relationships of the large Amphicyoninae are poorly resolved in the strict consensus tree (Text-fig. 7A). However, five clades are recovered in all trees. The clade comprising *Pseudarctos* and *Ictiocyon*, and, more interestingly for the present study, that comprising the two species of *Magericyon* and *Thaumastocyon*, are of particular importance. The 50 per cent majority-rule consensus (Text-fig. 7B) reveals two additional clades. One is recovered in 92 per cent of the MPTs and supports the dichotomy between the large amphicyonines (*Magericyon*, *Thaumastocyon*, *Amphicyon*, *Pseudocyon*, *Crassidia*, and *Ysengrinia*) and the *Pseudarctos*–*Ictiocyon* clade. The second clade, recovered in only 51 per cent of the MPTs, supports the distinction of a clade grouping *Ysengrinia* with *Magericyon*–*Thaumastocyon*. In addition, the placement of the species *Pseudocyon steinheimensis* within large Amphicyoninae (*Amphicyon*–*Pseudocyon sansaniensis*–*Crassidia*–*Ysengrinia*) is recovered in all of the MPTs. As expected from its derived dentition, *Thaumastocyon* is closely related to *Magericyon*. *Thaumastocyon* differs from the latter in its more derived and trenchant dentition, reduced upper molars, a more reduced m2, and the loss of m3, but this genus remains poorly known; the data matrix shows more than 50 per cent of the data are missing, including character 7, and this may obscure the resolution of the analysis. Removing *Thaumastocyon* and this character from the analysis decreases the

numbers of MPTs to 83 (27 steps, CI = 0.778, RI = 0.778, rescaled CI = 0.605). These changes in topology are not visible in the strict consensus, which does not differ from the phylogeny obtained using the complete matrix. The majority-rule consensus tree (Text-fig. 7C) gives less support to the clade *Ysengrinia*–*Magericyon* (present in less than 40 per cent of the MPTs), but the same strong support for the clade grouping all of the large amphicyonines. Our discussion below is based on the 50 per cent majority-rule consensus tree in Text-fig. 7C.

DISCUSSION

Phylogenetic analysis

Given the differences of character treatment and their taxonomic content, the results of our analysis can hardly be compared to those obtained by Viranta (1996). In addition, as pointed out above, our main goal was to determine the relationships of *Magericyon*, not to resolve the relationships of all of the amphicyonine genera.



TEXT-FIG. 7. Phylogeny of *Magericyon*: strict and 50 per cent majority-rule consensus trees found by the branch-and-bound option of the PAUP program. A, strict consensus tree obtained from the analysis of the complete matrix. B, 50 per cent majority-rule consensus tree obtained from the analysis of the complete matrix. C, 50 per cent majority-rule consensus tree obtained from the analysis excluding *Thaumastocyon* and character 7 (see character analysis). Characters supporting each node are presented in Table 4 and discussed in the text. Abbreviations: *Pambiguus*: *Pseudocyonopsis ambiguus*; *Psansaniensis*: *Pseudocyon sansaniensis*; *Psteinheimensis*: *Pseudocyon steinheimensis*; *Manceps*: *Magericyon anceps*; *Mcastellanus*: *Magericyon castellanus*.

TABLE 3. Data matrix used in the PAUP program.

Taxa	Character																	
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8
Haplocyoninae	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0
<i>Psambiguus</i>	?	0	0	1	0	0	?	0	0	?	1	0	0	?	0	?	?	?
Manceps	1	1	1	2	1	1	1	2	1	0	1	0	2	1	0	0	0	1
Mcastellanus	0	?	?	?	1	1	?	2	1	0	1	0	2	1	1	0	1	1
<i>Amphicyon</i>	0	0	0	1	0	0	0	1	0	1	1	0	1	1	2	0	1	0
<i>Psansaniensis</i>	?	0	0	1	0	0	?	1	0	?	1	0	1	1	2	0	1	0
<i>Psteinheimensis</i>	?	?	0	1	0	0	?	2	0	0	1	0	1	1	2	0	1	0
<i>Cynelos</i>	0	0	0	1	0	0	0	0	0	0	1	0	0	0	2	0	0	0
<i>Ysengrinia</i>	0	0	0	1	0	0	0	1	0	0	1	0	2	1	2	0	0	0
<i>Pseudarctos</i>	?	0	0	1	?	0	?	1	1	0	1	1	0	0	2	1	1	0
<i>Ictiocyon</i>	0	0	0	1	0	0	?	1	1	0	1	1	0	0	2	1	1	0
<i>Thaumastocyon</i>	?	0	1	?	?	?	?	?	?	?	1	0	2	1	?	2	0	1
<i>Crassidia</i>	?	0	0	1	0	0	?	1	0	1	1	0	1	1	?	0	0	0

Abbreviations: *Pambiguus*, *Pseudocyonopsis ambiguus*; *Psansaniensis*, *Pseudocyon sansaniensis*; *Psteinheimensis*, *Pseudocyon steinheimensis*; *Manceps*, *Magericyon anceps*; *Mcastellanus*, *Magericyon castellanus*.

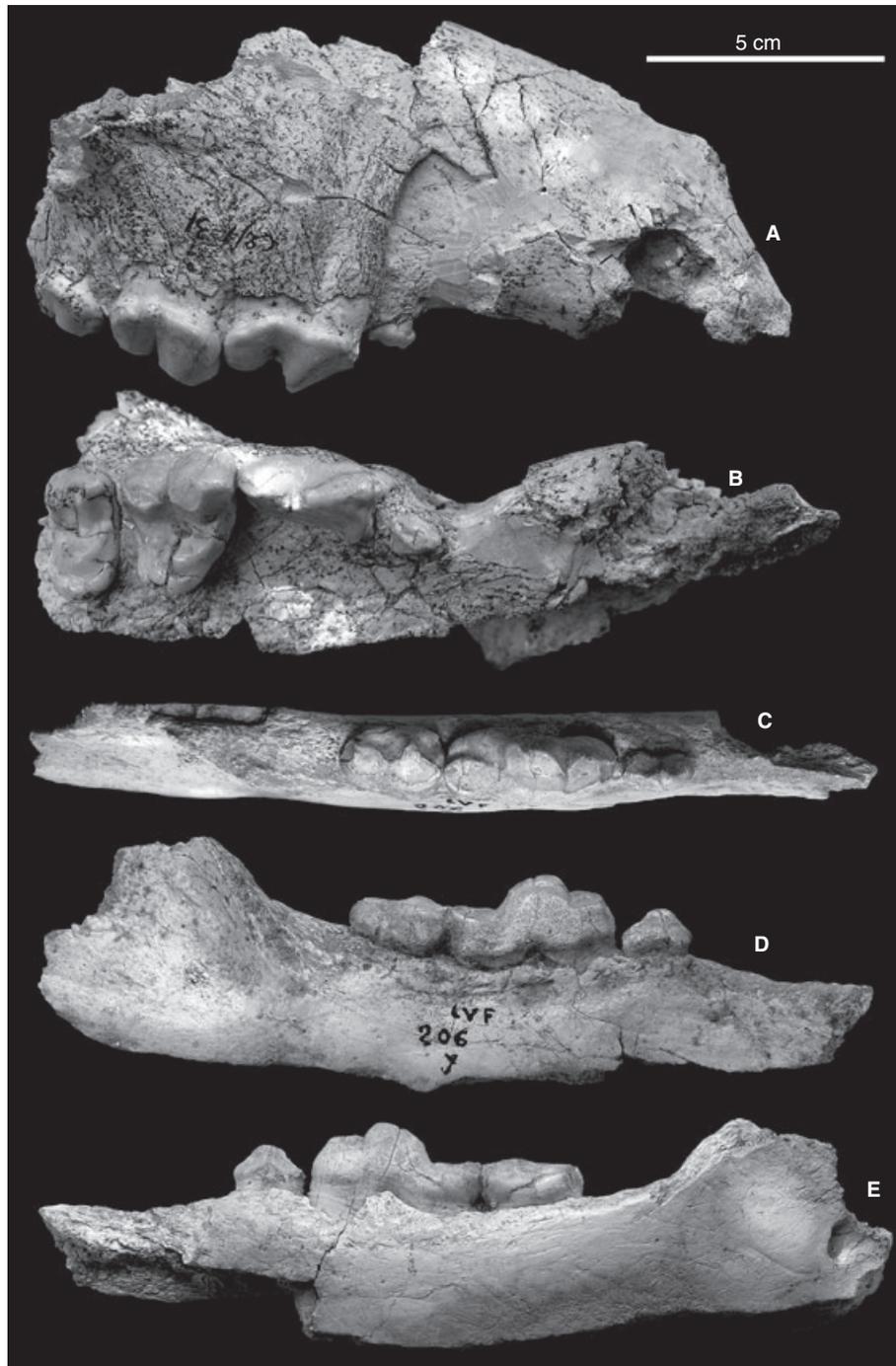
The basal relationships within the Amphicyoninae are relatively well resolved, with *Pseudocyonopsis ambiguus* and *Cynelos* being successive sister-taxa of the other Amphicyoninae. In contrast, the clade including the latter is not well resolved and shows a basal polytomy, although it includes two relatively well-supported clades. Table 4 presents the distribution of character states for internal nodes and terminal taxa of the 50 per cent majority-rule consensus tree (see Text-fig. 7C). Because our analysis did not intend to resolve the basal relationships within the Amphicyoninae, only a few apomorphies support nodes 1, 2, and 3, but these nodes are recovered in all of the MPTs. The phylogenetic analysis confirms the hypothesis that ‘*Amphicyon*’ *castellanus* from Los Valles de Fuentidueña and ‘A.’ cf. *castellanus* from Batallones-1 are closely related and markedly different from the other genera included: consequently the erection of a new genus for these taxa is well justified. *Magericyon* differs from other genera (whether included in the cladistic analysis or not) by autapomorphies such as the transverse compression of the upper canine and the reduction of the premolars. However, it is worth noting that data for *M. castellanus* are fragmentary (the anterior dentition is not known) (Text-fig. 8). Nevertheless, given the similarity between the two species of *Magericyon*, the absence of the first premolars (i.e. dP1/dp1 and P2/p2) and the strong reduction of p3 in *M. castellanus* are highly probable. Additional apomorphies of *Magericyon* include the shortening of M2 (which remains transversely elongated) and the absence of the metaconid on m2 (as in *Thaumastocyon*, not included in the final analysis), which, together with the reduction of premolars and the transverse com-

TABLE 4. Phylogeny of *Magericyon*: distribution of character states for internal nodes in the 50 per cent majority-rule consensus tree of the MPTs (see Text-fig. 2; italics indicate homoplastic characters).

Node/taxa	Character:state
Node 1	4:1, 11:1
Node 2	15:2
Node 3	8:1, 17:1
Node 4	9:1, 12:1, 16:1
Node 5	13:1, 14:1
Node 6	2:1, 3:1, 4:2, 5:1, 8:2, 9:1, 13:2, 15:1, 17:0, 18:1
<i>Amphicyon</i>	10:1
<i>Crassidia</i>	10:1, 17:0
<i>Ysengrinia</i>	13:2, 17:0
<i>Manceps</i>	1:1, 15:0

pression of upper canines, indicates a general trend towards hypercarnivory. This trend is further strengthened by additional derived characters observed in *Magericyon*, although they are homoplastic: reduction in length of p4 (convergence with *Pseudocyon steinheimensis*), absence of distal accessory cuspid on p4 (convergence with the clade *Pseudarctos-Ictiocyon*), metaconid absent or vestigial on m1 (as in *Thaumastocyon*, not included in the final analysis: possible convergence with *Ysengrinia*, since this genus may be not closely related to *Magericyon*; see Text-fig. 7C).

It is clear that the systematic position of *Magericyon* results from the general trend towards hypercarnivory observed in this genus, which is particularly obvious in the dentition. However, a detailed analysis of the distribu-



TEXT-FIG. 8. A–E, upper and lower dentition of *Magericyon castellanus* from Los Valles de Fuentidueña. A–B, MNCN 3836, fragment of right maxilla with P3, P4, M1, and M2 (holotype) in lateral and occlusal views. C–E, MNCN 3836, fragment of right hemimandible with p4, m1, and m2 (paratype) in occlusal, buccal, and lingual views.

tion of the character states indicates that the characters that may represent hypercarnivorous traits (loss or reduction of teeth or cusps, more trenchant teeth) may not be correlated with each other, that the degree to which they are developed may vary between taxa or that the changes in these character states may prove eventually to be unre-

lated to this trend. Although *Magericyon* and *Thaumastocyon* share a few common features (absence of P2/p2, absence of a metaconid on m1 and m2), they are distinguished from each other by a large number of features. *Magericyon* possesses a more compressed upper canine and has lost dP1/dp1, whereas *Thaumastocyon* has a more

trenchant dentition, upper molars that are more reduced in size, an m2 that is more reduced relative to m1, and no m3. There are also several examples of characters that may not be related to hypercarnivory. Thus, the strong reduction in the length of p4 and the absence of the distal accessory cuspid of this tooth, observed in *Magericyon*, also characterize *Ictiocyon* and *Pseudarctos*, both of which have a much less trenchant dentition than the other taxa included in the ingroup. The m2 is small in *Ictiocyon* and *Pseudarctos*, extremely reduced in *Thaumastocyon*, but much larger in *Amphicyon* and *Magericyon*. The P4 parastyle is absent in *Magericyon* but present in *Amphicyon*.

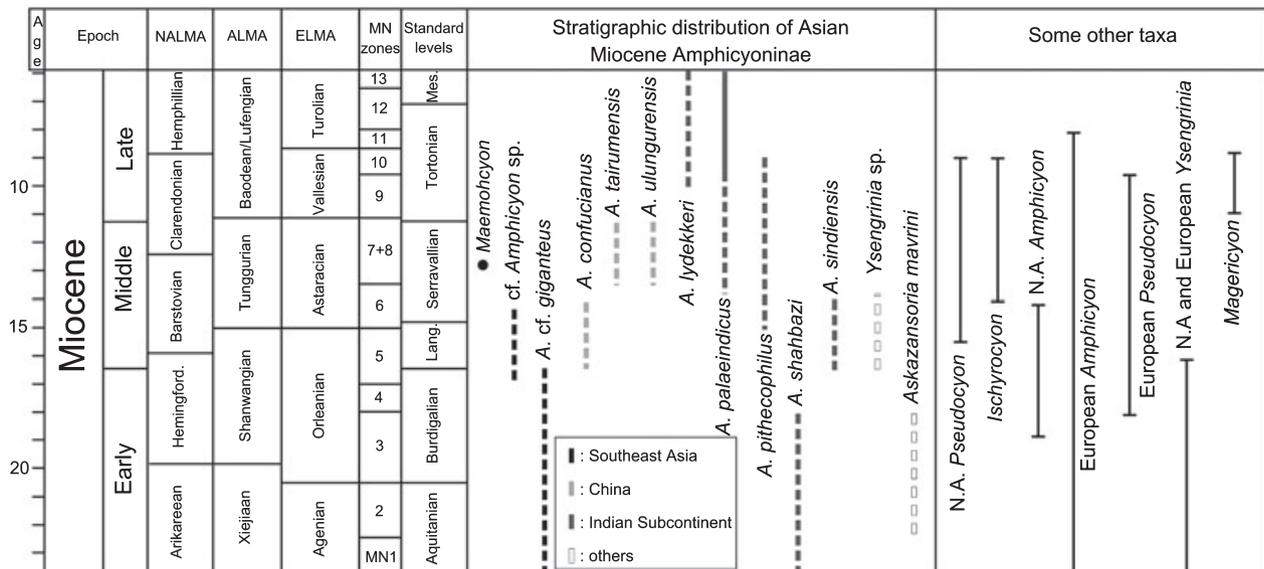
If the clade including the large taxa (node 5 in Text-fig. 7C) is presented in its stratigraphic context (Text-fig. 9), it is notable that there is a marked gap between the end of the temporal distribution of *Ysengrinia* (biozone MN 4, early Miocene) and *Crassidia* (biozone MN 2, early Miocene) and the first occurrence of *Magericyon* (biozone MN 9, late Miocene). The probability of a sister-group relationship between either of these genera and *Magericyon* is, therefore, reduced. Given that the last appearance of *Pseudocyon* and *Amphicyon* is in the upper Miocene, it seems likely that the sister-group of *Magericyon* may be found among members of these genera. Nevertheless, our initial phylogenetic analysis (Text-fig. 7A–B) indicated a close relationship between *Magericyon* and *Thaumastocyon*, as both taxa show a trend towards hypercarnivory. However, shared characters for these taxa are few, and *Thaumastocyon* has hypercarnivorous traits that are more strongly developed than those in *Magericyon* (see above). Thus, a divergence of one species of *Magericyon* from a species of *Thaumastocyon* is unlikely, especially if we consider the middle Miocene age (MN 5) of

T. bourgeisi included here. The relationship of *Thaumastocyon* to other amphicyonines will remain uncertain until this genus is better known.

Palaeobiology and evolution of Magericyon anceps

The trend towards hypercarnivory displayed by *Magericyon anceps* is unique among the Amphicyonidae, but comparable developments have been observed in some other lineages of arctoids, such as the specialized ursid genus *Agriotherium* Wagner, 1837. The species *A. africanum* in particular displays a reduction of the metaconid of the lower molars as part of a set of hypercarnivorous traits (Hendey, 1980). These functional similarities led this author to suggest that *Agriotherium* and large amphicyonines were ‘ecological twins’.

The trend observed in *M. anceps* probably supports a marked difference in its palaeoecology relative to other amphicyonines. The study of the postcranial material will provide more detailed data on locomotor adaptations of this species. Nevertheless, the overall morphology of the dentition of *M. anceps* points towards a more specialized hunting technique than that of other amphicyonines. One of the most striking characters is the presence in *M. anceps* of strongly flattened upper canines with crenulation-like margins, which is an autapomorphy of this species. This compression increases the risk of breakage owing to lateral forces, especially when subduing prey. Although inferring the killing techniques of *M. anceps* is difficult, it would be expected that this animal used its canines within a biomechanical situation that was somewhat different from that experienced by more plesiomorphic amphicyo-



TEXT-FIG. 9. European stratigraphic ranges of the genera of Amphicyoninae comprising the clade supported by node 5 in Text-figure 7.

nines. At the very least it implies that *M. anceps* would be more likely to avoid having its teeth come into contact with bone. Even though the wear pattern observed in the carnassials of *M. anceps* is quite similar to that of other large amphicyonines, implying a similar occlusal mechanism, the absence of dP1/dp1 and P2/p2, and the strong reduction of M2–3/m2–3 and P3/p3–4 indicate a lesser importance for the crushing function of the dentition (Text-fig. 2). Thus, the dental morphology of *M. anceps* suggests that the diet of this animal included a greater proportion of meat compared to that of the other amphicyonine species included in our analysis.

Preliminary observations on the demographic structure of the sample of *M. anceps* described here indicate a high proportion of juveniles (c. 40 per cent of the sample). This contrasts with the absence or scarcity of juveniles in the sample of the other carnivorans frequently found in Batallones-1, such as *Machairodus aphanistus*, *Paramachairodus ogygia*, and *Protictitherium crassum* (Antón and Morales 2000; Salesa *et al.* 2006b). The high percentage of juveniles can only be explained if they followed the adults during foraging activities and, thus, became trapped at Batallones-1 at the same time. This close bond between cubs and adults, presumably the females, may be compared to that observed in extant ursids.

CONCLUSIONS

Our study confirms the close relationships between the species from Batallones-1 and ‘*Amphicyon*’ *castellanus*. Based on a phylogenetic analysis including well-known European genera of Amphicyoninae and their North American relatives, we also demonstrate that these two highly specialized species display marked differences not only when compared to *Amphicyon* (their previous generic assignment) but also to all known genera of Amphicyoninae. This supports the erection of a new genus, *Magericyon*, for these Spanish taxa. Many of the morphological features distinguishing *Magericyon* from other Amphicyoninae appear to be related to adaptations for hypercarnivory.

Acknowledgements. This study is part of the research projects CGL2005-03900/BTE and CGL2004-02094/BTE (Secretaría de Estado de Universidades e Investigación, Ministerio de Educación y Ciencia). We thank the Comunidad Autónoma de Madrid (Dirección General de Patrimonio Histórico) for continuous support, provided in the form of funding (Research Group UCM-CAM 910607) and permission to excavate. Additional support was provided by the National Geographic Society (Grant 6964-01), and by the Fondation Singer-Polignac (Paris) and the Alexander von Humboldt Stiftung (Bonn) to SP. MJS holds a CSIC contract within the ‘Juan de la Cierva’ programme, linked to the project CGL2004-02094/BTE. We also thank two anonymous reviewers for suggestions that improved the clarity of the

paper, Stefan Gabriel (Queen Mary, University of London) for language revision, and those individuals who gave us access to the comparative material: B. Sánchez (MNCN), P. Tassy and C. Sagne (MNHN), B. Engesser (NHM), E. P. J. Heizmann (SMNS), K. Heissig (BSP). We are grateful to P. Tassy and P. Richir for providing various casts of Oligocene *Cynelos* spp. and *Pseudocyonopsis ambiguus*, and to O. Fejfar for providing a cast of the type of *Cynelos bohemicus*.

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APPENDIX

Character analysis

1. C1 crown. One of the striking features of *Magericyon anceps* is its compressed upper canines (L/W ratio is 1.76–1.79; N = 2). The upper canine of the other taxa is much less transversely compressed: e.g. L/W is 1.37–1.57 in *Amphicyon* (N = 6), 1.49 in *Magericyon castellanus*, 1.33–1.53 in *Cynelos* (N = 11), and 1.34 in *Ysengrinia* (N = 1). The upper canine of *Haplocyon* is not known, but that of the species of *Haplocyonoides*, which are more derived and have a more trenchant dentition than those of *Haplocyon*, has an L/W ratio of 1.36–1.49 (N = 7).
- 0, upper canine poorly compressed; 1, upper canine very compressed.
2. dp1/dP1: presence/absence. The first premolar locus is occupied in most placental mammals by a tooth of the first generation (= deciduous teeth) that is not replaced by a tooth of the second generation (= permanent teeth) (Luckett 1993). This is always the case among the Carnivora. While typically the first premolars are very reduced in amphicyonines, they are rarely absent. In *Magericyon anceps*, the dP1 is always absent and the dp1 is frequently absent (80 per cent of the total number of individuals; absent in all subadults and adults). We have coded dp1/dP1 as present in *Cynelos* (only *Cynelos helbingi* lacks the first premolar).
- 0, dp1/dP1 present; 1, dp1/dP1 absent.
3. p2/P2: presence/absence. As dP1/dp1, p2/P2 are generally reduced in size in Miocene amphicyonines. The deciduous

second premolars are usually present in the juveniles of *M. anceps*. P2/p2 are present in the taxa for which data are available, with the exception of Batallones material and of the holotype of *Thaumastocyon bourgeoisi*.

- 0, P2/p2 present; 1, P2/p2 absent.
4. p3 size. The reduction in size of the premolars in *Magericyon anceps* is also illustrated by the presence of a single-rooted p3 (state 2). In the other amphicyonines, p3 is much more reduced than p4, but it is double-rooted (state 1). The p3 is much larger in the Haplocyoninae (state 0). That tooth is also absent in the holotype mandible of *Thaumastocyon bourgeoisi*. However, this specimen presents an abnormal anterior dentition with a dp1 but no evidence for p2 and p3, and resorbed alveoli of p4, which is, therefore, absent. Therefore, this species is coded as '?' for this character.
 - 0, p3 tall and slightly reduced relative to p4; 1, p3 markedly reduced relative to p4 but still double-rooted; 2, extreme reduction of p3, single-rooted.
 5. P3. The reduction of P3 is based only on an LP4/LP3 ratio. We measured the height of P3 and P4 paracone, but these measurements are not generally provided in the literature, which prevents us from making a useful comparison. In addition, a tooth row with both P3 and P4 is not known from each taxon. In *Magericyon*, the P3 is greatly reduced. LP3 is more than 2.5 times smaller than LP4, whereas in the other taxa, LP4 is, at most, twice the length of P3.
 - 0, P3 is at least half the length of P4; 1, P3 is more than 2.5 times shorter than P4.
 6. Distolingual inflation of P3. A striking feature of the P3 of *Magericyon* is the presence of a distolingual inflation.
 - 0, no distolingual or lingual inflation on P3; 1, strong distolingual inflation on P3.
 7. dp4. Unfortunately, this tooth is not known from all of the Amphicyoninae. The metaconid is vestigial or absent on the dp4 of *M. anceps*, whereas this cuspid is still present and much more developed in *Amphicyon* (known for *A. major* only), *Ysengrinia* (*Y. ginsburgi*), and *Cynelos* (*C. helbingi*, *C. schlosseri*).
 - 0, metaconid present on dp4; 1, metaconid vestigial or absent on dp4.
 8. p4 size. The size of p4 is estimated here by the ratio of the length of p4 to the length of m1. A better estimate would be also to take into account the height of p4, because it is not strictly correlated to the length. However, the height of p4 is not usually provided in the literature. The p4 is very reduced in *Magericyon anceps* and *Pseudocyon steinheimensis* (Lp4/Lm1 is much less than 0.50) (state 2). The shortening of p4 is similar in all of the species of *Amphicyon*: *A. galushai* (0.58–0.61; N = 3), *A. frendens* (0.50–0.60; N = 11), *A. ingens* (0.52–0.61; N = 14), *A. lathanicus* (0.58; N = 1), *A. giganteus* (0.51–0.60; N = 3), and *A. major* (0.48–0.54; N = 4). It is interesting to note that the proportion of p4 relative to m1 does not change through time in the European and North American lineages of the genus. A similar ratio is found in *Ysengrinia* spp. (0.53–0.71; N = 8), *Ictiocyon socialis* (0.60–0.62; N = 3), *Pseudarctos bavaricus* (0.56–0.61; N = 2), *Pseudocyon sansaniensis* (0.51 for the holotype), and

Crassidia intermedia (0.62–0.67; N = 2) (state 1). In the majority of the species of *Cynelos*, this ratio is also markedly distinct from that of the Batallones material, and it is slightly greater than in e.g. *Amphicyon* spp. In the Oligocene species *C. crassidens* (0.79 in the type) the p4 is even less reduced, as in *P. ambiguus* and in the Haplocyoninae (state 0), which indicates that a poorly reduced p4 is primitive for *Cynelos*.

- 0, p4 poorly reduced relative to m1, its length being more than three-quarters of the length of m1; 1, p4 moderately reduced, as in the majority of the taxa included here; 2, p4 strongly reduced, its length being markedly less than half of the length of m1.
9. p4 distal accessory cuspid. The presence of a distal accessory cuspid in the p4 is a primitive character known from both the Haplocyoninae and *P. ambiguus*. This cuspid is also generally present in the other Amphicyoninae. It is absent or vestigial in *Magericyon*, *Pseudarctos* and *Ictiocyon*.
 - 0, well-developed accessory cuspid present in p4; 1, distal accessory cuspid of p4 vestigial or absent.
 10. P4 parastyle. Among Caniformia, the presence of a parastyle in P4, which is derived, characterizes many clades, families, or subfamilies like the Canidae (Wang *et al.* 1999), the Mustelidae (Wang *et al.* 2005), and the Ursidae (Hunt 1998a). In the Amphicyonidae a parastyle may also occur in P4, as in e.g. *Crassidia* and *Amphicyon*. The parastyle is absent in the Haplocyoninae. The presence of a parastylar cusp is not strictly correlated to the hypercarnivorous adaptation. Thus, the species of *Magericyon* have a more or less prominent ridge instead of a true parastylar cusp. In his diagnosis of the North American *Amphicyon*, Hunt (2003) mentioned the presence of a small parastyle. In Europe, the type of *A. laugnacensis*, and some specimens of *A. lathanicus* and *A. giganteus* do have a parastyle. *Amphicyon major* is polymorphic for this character. The majority of the specimens of *A. major* only present a parastylar ridge. This is particularly the case in the sample from Sansan (MN 6, middle Miocene, France), which includes a single individual with a true parastylar cusp. The other specimens of *A. major* studied here include one P4 from Çandır (MN 6, middle Miocene, Turkey). The recent description of this specimen mentions a strong parastyle (Nagel 2003) whereas the illustration of this tooth clearly shows that there is no cusp, but a parastylar crest (Gürbüz 1974, figs 1–3). Some additional specimens from La Grive-Saint-Alban (middle Miocene, France), Ravensburg (middle Miocene, Germany), Oberkirchberg (middle Miocene, Germany), Melchingen (MN 9, late Miocene, Germany), and those from the early late Miocene assigned to *Amphicyon major eppelsheimensis* also have a true parastylar cusp. We have coded *Amphicyon* as possessing a parastylar cusp (state 1). The European species of *Cynelos* do not possess a parastylar cusp. We lack published data on the North American *Cynelos*, but they resemble their European counterparts (Hunt 1998b), which suggests that they do not possess this cusp either. In contrast to our work, Viranta (1996) coded the presence of a parastyle as primitive; this is not supported by our outgroup comparison.
 - 0, true parastylar cusp absent, parastylar ridge may or may not be present; 1, true parastylar cusp present.

11. Position of P4 protocone. In contrast with e.g. haplocyonines (state 0), amphicyonines do not display a mesiolingually projected, large protocone. This cusp is reduced in almost all of the taxa of the subfamily, in which it is generally crest-like. We disagree with Viranta (1996), who considered that the presence of a protocone is correlated with the presence of a parastyle. Our study of the amphicyonines supports the opposite view, that taxa showing a strong parastylar cusp display a variable development of the protocone in P4. The morphological variation of the development and position of the protocone may be great, as in *Amphicyon giganteus* (see Ginsburg and Antunes 1968, pl. 1; Peigné *et al.* 2006a). Therefore, we do not distinguish more than two discrete states for the position of the protocone. The majority of the Amphicyoninae included here show state 1.
 - 0, protocone large, mesiolingually projected; 1, protocone retracted, with its mesial border across or distal to the mesial border of the paracone.
12. Protocone development in width. The lingual extension of the protocone in amphicyonines varies independently of the shape of the cusp itself (e.g. cusp-like or crest-like). The development in width of the protocone is measured by the WP4/LP4 ratio. In the Haplocyoninae (outgroup) and in the majority of the amphicyonines, the protocone is poorly extended lingually and the ratio WP4/LP4 is, therefore, small (c. 0.57) (state 0). In contrast, *Pseudarctos bavaricus* and *Ictiocyon socialis* can be distinguished by a low but lingually extended protocone (WP4/LP4 \geq 0.7) (state 1).
 - 0, protocone poorly extended lingually; 1, protocone greatly extended lingually.
13. m1 metaconid. Within Amphicyonidae, the metaconid of m1 is always reduced and its tip generally reaches the level of the paraconid tip in lingual view. In some taxa the metaconid is further reduced, applied to the protoconid (state 1), whereas in a few species only (e.g. *Magericyon* spp.), the metaconid is vestigial or absent (state 2). We have coded the metaconid as vestigial in *M. castellanus*; the carnassial of the holotype is very worn, but another m1 from the same locality (MNCN 35876; Ginsburg *et al.* 1981, pl. 1, fig. 10) supports our statement.
 - 0, metaconid reduced; 1, metaconid very reduced and applied to the protoconid; 2, metaconid vestigial or absent.
14. M1 cusps. In the Haplocyoninae and in many amphicyonines, the paracone and metacone of M1 are poorly elevated, with the paracone only slightly taller than the metacone (state 0). A tall paracone and a tall metacone, the former being much taller than the latter, characterizes genera such as *Magericyon*, *Amphicyon*, *Pseudocyon*, and *Ysengrinia*.
 - 0, paracone and metacone of M1 low, with paracone only slightly taller than the metacone; 1, paracone and metacone tall, with the paracone much taller than the metacone.
15. M2 size. Primitively, M2 is more reduced than M1 in both length and width, as in the Haplocyoninae. A same degree of reduction of M2 is found in *Magericyon anceps*. A single species, *M. castellanus*, has an M2 as short as in state 0, but it is transversely much more elongated (state 1). The other taxa have an M2 that is either wider or longer, or longer and wider than in the taxa displaying states 0 and 1.
 - 0, M2 reduced relative to M1; 1, M2 as short as in state 0, but transversely more elongated; 2, M2 enlarged relative to states 0 and 1.
16. m2 length. Primitively, the length of m2 is slightly greater than the half-length of m1 (state 0): this is the case in *Haplocyon* spp. and in most of the taxa included in the analysis. In some taxa, the crushing function is developed by elongating the m2 relative to the m1 (state 1). The primitive condition observed in *A. galushai* indicates that this character evolved within the *Amphicyon* lineage. In *Thaumastocyon bourgeoisi*, m2 evolved in the opposite way and became strongly reduced (state 2). *Magericyon* probably secondary reduced its m2, but this tooth remains relatively longer than in *Thaumastocyon*.
 - 0, m2 length slightly greater than the half-length of m1; 1, m2 much enlarged compared to state 0; 2, m2 much more reduced compared to state 0.
17. m2 width. An outgroup comparison shows that an m2 distinctly narrower than m1 is the primitive state. This is observed in Batallones-1 material, *Crassidia*, *Cynelos* (especially in the Oligocene species), *Ysengrinia* (*Y. gerandiana*, *Y. americana*), and *Thaumastocyon*. In the other taxa, m2 equals or surpasses m1 in width (state 1).
 - 0, m2 distinctly narrower than m1; 1, m2 width similar or greater than m1 width.
18. m2 metaconid. It is present but reduced and cusp-like in haplocyonines, *Pseudocyon*, *Amphicyon*, *Ysengrinia*, *Ictiocyon*, and *Pseudarctos* (state 0); the metaconid is absent or vestigial, and then replaced by a low crest, in *Magericyon* and *Thaumastocyon*.
 - 0, metaconid present and reduced; 1, metaconid absent or vestigial.