FOSSIL IMPRINT • vol. 77 • 2021 • no. 1 • pp. 126–144

NATIONAL MUSEUM

THE AMPHICYONINAE (AMPHICYONIDAE, CARNIVORA, MAMMALIA) OF THE EARLY MIOCENE FROM TUCHOŘICE, THE CZECH REPUBLIC

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Morales, J., Fejfar, O., Heizmann, E., Wagner, J., Valenciano, A., Abella, J. (2021): The Amphicyoninae (Amphicyonidae, Carnivora, Mammalia) of the early Miocene from Tuchořice, the Czech Republic. – Fossil Imprint, 77(1): 126–144, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Abstract: The Amphicyoninae of the early Miocene from the locality of Tuchořice, the Czech Republic, are represented by three species. Two of them are classified within the tribe Amphicyonini: *Paludocyon bohemicus* (Schlosser, 1899) as the type species of *Paludocyon* n. gen., and a large-sized amphicyonid determined as *Megamphicyon carnutense* (Antunes et Ginsburg, 1977). *Dehmicyon* n. gen. aff. *schlosseri* is determined by two small teeth. This new genus has been proposed for the species *Amphicyon schlosseri* Dehm, 1950 from Wintershof-West and is tentatively included in the tribe Pseudarctini nov. together with the genera *Ictiocyon* and *Pseudarctos*. This association of Amphicyoninae provides valuable information on the taxonomy and systematics of this subfamily during the early Miocene, at which time important environmental changes were taking place in Europe, which undoubtedly affected the evolution of Amphicyonidae.

Key words: Amphicyonidae, Amphicyoninae, systematics, early Miocene, Europe

Received: April 20, 2021 | Accepted: July 21, 2021 | Issued: December 9, 2021

Zoobank: http://zoobank.org/urn:lsid:zoobank.org:pub:8C73FDF8-9155-4700-B53A-185CF3394B6B

Introduction

The early Miocene (MN 3) Amphicyonidae of Tuchořice (the Czech Republic) are represented by two subfamilies; Thaumastocyoninae Hürzeler, 1940, which contains a unique species (Morales et al. 2019), and Amphicyoninae Trouessart, 1885, with three species varying greatly in size from almost the smallest to the biggest species of this subfamily; they represent the first morphological stages of two different evolutionary lineages. Tuchořice is the type locality of *Pseudocyon bohemicus* Schlosser, 1899, a species with a controversial systematic status. However, remains obtained in a relatively recent field campaign (Fejfar et al. 2003) enabled us to perform a more accurate taxonomic assignation. As a result of this study, this species is now determined as *Paludocyon* n. gen. *bohemicus*, which is relatively similar to *Heizmannocyon*, a taxon proposed by Ginsburg (1999) as a subgenus of *Amphicyon*, which is considered herein as possessing a generic status. The Amphicyoninae of Tuchořice are also represented by a small sized species, *Dehmicyon* aff. *schlosseri* (Dehm, 1950), which is related to the *Ictiocyon-Pseudarcto*s group, and by the giant-size *Megamphicyon carnutense* (Antunes et Ginsburg, 1977). The present paper attempts to conduct a systematic study of these Amphicyoninae which should make a significant contribution to the knowledge of the early stage of European Miocene Amphicyoninae radiation.

DOI 10.37520/fi.2021.011

Tuchořice locality

The fossiliferous locality of Tuchořice is located in North Bohemia, the Czech Republic, close to the southern margin of the Chomutov-Most brown coal basin near the villages of Tuchořice and Lipno (Fejfar and Heizmann 2016 and references herein). Tuchořice mammal remains are found associated with freshwater travertine sediments, the site has been known since the nineteenth century (Reuss and Meyer 1851, Suess 1861) and is considered one of the classical European Miocene mammal localities. It is characterized by the abundance of carnivoran mammals, with a predominance of amphicyonid species (Fejfar et al. 2003, Fejfar and Heizmann 2016, Morales et al. 2019).

Material and methods

Nomenclature and measurements

Dental nomenclature follows Ginsburg (1999). Measurements were made to the nearest 0.1 mm using Mitutoyo Absolute digital callipers. The material studied is displayed in Tables 1 and 2. A bivariate diagram of Width/Length of P4, M1, M2, m1 and m2, and also of Length P4/Length M1, Length M1/Length M2, Length m1/Length m2 and Length p4/Length m1 of the small and middle-sized species studied in the present research can be seen in Text-figs 1 and 2 respectively.

In the past, the material from Tuchořice was published under several provisional numbers (see e.g., Fejfar and Heizmann 2016). At present, all the material is housed in the Department of Palaeontology, National Museum, Prague under the inventory numbers beginning with Pv (except the specimens housed in Naturhistorisches Museum Wien).

Institutional abbreviations

BSP	Bavarian State Collections of Palaeontology and Geology, Munich, Germany
FS	Faluns d'Anjou, France; casts stored at the MNCN, Madrid, Spain
MNHN	Muséum national d'Histoire naturelle, Paris, France
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain
NMB	Naturhistorisches Museum Basel, Basel, Switzerland
NM	National Museum, Prague, the Czech Republic (inv. no. Pv)
TU	Provisional numbers used by O. Fejfar for Tuchořice specimens

Systematic palaeontology

Order Carnivora Bowdich, 1821
Suborder Caniformia Kretzoi, 1943
Infraorder Arctoidea Flower, 1869
Family Amphicyonidae Trouessart, 1885
Subfamily Amphicyoninae Trouessart, 1885

Emended diagnosis. Amphicyonidae with robust carnassials (m1/P4), P4 tends to have a reduced protocone and crushing molars (m2, M1 and M2) with a highly developed occlusal surface.

Included tribes. Amphicyonini, Pseudarctini n. tribe, Magericyonini n. tribe.

Remarks. The taxonomy and systematics of the Miocene Amphicyonidae is highly complex (e.g., Kuss 1965, Viranta 1996, Hunt 1998, Ginsburg 1999, Peigné et al. 2008, Morales et al. 2016), and the reasons for this are well known: 1) proliferation of taxa, often with descriptions and definitions based on scarce and sometimes uncharacteristic fossils; 2) a dental morphology displaying very limited variability, associated with a wide size range and the presence of different species in the same locality.

According to Ginsburg (1999), the subfamily Amphicyoninae is represented by 6 genera in Europe: *Amphicyon* Lartet, 1836, *Cynelos* Jourdan, 1862, *Pseudocyon* Lartet, 1851, *Ysengrinia* Ginsburg, 1966, *Pseudarctos* Schlosser, 1899 and *Ictiocyon* Crusafont, Villalta et Truyols, 1955. Moreover, he recognized three additional subgenera for *Amphicyon*: *Megamphicyon* Kuss, 1965, *Euroamphicyon* Viranta, 1996 and *Heizmannocyon* Ginsburg, 1999. These subgenera are considered to have been included in a generic rank in the present research. With the exception of *Ysengrinia*, which has been transferred to the Thaumastocyoninae (Heizmann and Kordikova 2000, Morales et al. 2019), the remaining genera of the subfamily, with the addition of the two new genera defined herein, can be classified into three groups, for which we propose the taxonomic rank of a tribe.

Amphicyonini Trouessart, 1885, comprising *Amphicyon*, *Cynelos*, *Paludocyon* n. gen., *Heizmannocyon*, *Megamphicyon* and *Euroamphicyon*. This group included the most typical Amphicyoninae; its molar dentition tends to present an increased surface area, the carnassials are robust and the premolar dentition progressively decreases in size and complexity.

Pseudarctini tribe nov. comprising the genera *Pseudarctos* and *Ictiocyon*. As in the previous group, the molars tend to present a larger crushing surface, albeit displaying a different pattern with a greater mesiodistal length in the upper molars and buccolingual length in the lower molars. This is associated with a significant reduction of the carnassial teeth, and loss of the p4 distal accessory cuspid. *Dehmicyon* n. gen. is provisionally included as a basal form of this tribe.

Magericyonini tribe nov. comprising genus *Magericyon* and with some doubt also *Pseudcyon*. Magericyonini represents a new attempt to develop an advanced hypercarnivore adaptation in the Amphicyonidae, while remaining closely related to the amphicyonines, but differing from the Thaumastocyoninae in the slightly reduced crushing dentition and in the morphology of the upper and lower carnassials, which retain an Amphicyonini pattern.

Tribe Amphicyonini Trouessart, 1885

Type genus. *Amphicyon* Lartet, 1836.

Emended diagnosis. Amphicyoninae with molar dentition tending to increase the molar surface area, the carnassial teeth are robust and the premolar dentition progressively decreases in size and complexity.

European genera included. *Amphicyon*, *Megamphicyon*, *Euroamphicyon*, *Cynelos*, *Heizmannocyon* and *Paludocyon* n. gen.

Genus *Paludocyon* n. gen.

Type and only species. *Pseudocyon bohemicus* Schlosser, 1899.

Etymology. From the Latin paludes, which means swampy areas, in relation to the marshy/ lacustrine sediments from the locality of Tuchořice.

Diagnosis. Medium sized Amphicyonini, lower premolar row without diastemas, p4 small, with wide talonid. The m1 is robust, trigonid with low paraconid and large metaconid. The talonid is wider than the trigonid; it comprises a strong, high hypoconid, the lingual base is thickened apically, and has a subdivided entoconid. The m2 is short in comparison with the m1, and presents a reduced entoconid. P4 slender, with mesially elongated paracone and weak parastyle; the protocone is relatively strong and mesially located. The M1 shows two morphotypes, one subtriangular due to the narrowed lingual area, and the second with a subquadrangular lingual area. The paracone is high compared to the metacone. The metaconule is broad and clearly differentiated from the protocone. The M2 has a quadrangular occlusal shape, with a short buccal wall and a wide transversal diameter; metacone reduced. M3 and m3 reduced, with simple morphology.

Differential diagnosis. *Paludocyon* n. gen. differs from *Pseudocyon sansaniensis* Lartet, 1851 (type species of *Pseudocyon*) in the greater robustness of its m1 and m2; the greater width of the m1 talonid and in its strong hypoconid which occupies almost the entire area of the talonid; additionally, the p4 and m2 exhibit a smaller reduction compared to the m1. It differs from *Cynelos* in the limited development of the distal molars (M2/M3 and m2/m3) compared with the first molars; it also differs in the significant reduction of the lower premolars, including p4; the greater width of the m1 talonid in relation to the trigonid and the greater height and size of its hypoconid, together with the reduction of the entoconid. The P4 of *Paludocyon* n. gen. has an elongated paracone mesial crista, whereas in *Cynelos* it is short and more vertical. The metacone of the M2 is smaller than the paracone, while in *Cynelos lemanensis* both are similar in size. Differences when compared to *Amphicyon major* Blainville, 1841 are also evident. Apart from the larger size, its dentition is characterized by the great width of the crushing dentition. Additionally, the *A. major* m1 trigonid is better developed than that in the *Paludocyon* species. *Paludocyon* also differs from *Amphicyon* in the reduced development of the distal molars relative to the first molars. This relatively small size of the distal molars in *Paludocyon* also enables it to be differentiated from *Megamphicyon*, which has large distal molars. *Paludocyon* differs from *Heizmannocyon* as the latter shows more specialized characters, such as: 1) the presence of more developed diastemas between the lower premolars; 2) the strong reduction of the lower premolars, including p4; 3) a higher m1 with a stronger hypoconid, placed in a central position; 4) a short robust P4, with the protocone distally displaced and reduced; 5) M1 showing a trapezoidal occlusal shape, enlarged trigone and reduced lingual area ; 6) M2 with a longer buccal wall and a shortened buccolingual diameter.

Paludocyon bohemicus (Schlosser, 1899)

Text-figs 1–4, Tabs 1a, 2a

1861 *Amphicyon intermedius* Mey.; Suess, p. 224, pl. II.
1868 *Amphicyon intermedius* H. v. Meyer; Peters, p. 190.
1899 *Pseudocyon bohemicus* n. sp.; Schlosser, p. 124, pl. XIV, figs 3, 4, 9.
1901 *Amphicyon bohemicus* Schlosser; Schlosser, p. 62, pl. I, figs 18, 23–26, 29, 30.
1929 *Amphicyon bohemicus* Schloss.; Viret, p. 113.
1965 *Amphicyon steinheimensis bohemicus* (Schlosser) 1899; Kuss, pp. 40–46, figs 16–23.
1973 *Amphicyon bohemicus*; Heizmann, pp. 17–20.
1977 "*Amphicyon*" *bohemicus*; Ginsburg, pp. 94–95.
1999 *Cynelos* (*Heizmannocyon*) *bohemicus* (Schlosser, 1899); Ginsburg, p. 116.
2000a *Cynelos* (*Heizmannocyon*) *bohemicus* (Schlosser) 1899; Ginsburg, p. 11.
2003 *Amphicyon bohemicus*; Hunt, p. 105.
2008 *C*[*ynelos*] *bohemicus*; Peigné et al., p. 954.
2015 *Cynelos bohemicus*; Hunt and Stepleton, p. 2.
2016 *Amphicyon bohemicus* (Schlosser 1899); Fejfar and Heizmann, p. 320, figs 9, 10, 11.1–5+11–17.
2020 *Cynelos* cf. *bohemicus* (Schlosser 1899); Jiangzuo et al., p. 23, fig. 4.4–6.

Lectotype. NM-Pv 11677, left m1, figured by Schlosser (1899: pl. 14, fig. 4; Text-fig. 4a herein). Lectotype designated by Kuss (1965: 41; he listed it under the old number 4330).

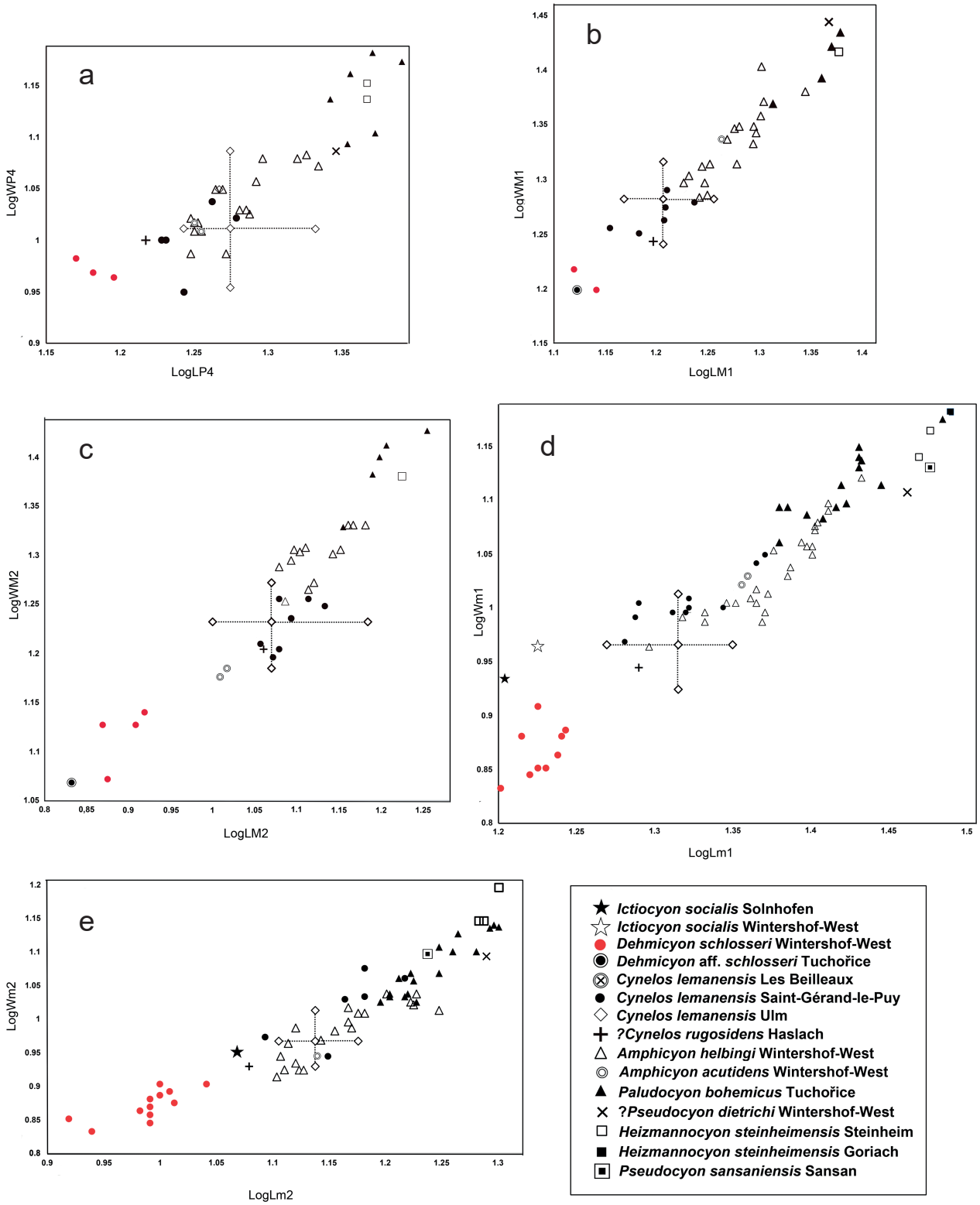
Paralectotypes. NM-Pv 11678 (old no. 4329), left P4, figured by Schlosser (1899: pl. 14, fig. 3); NM-Pv 11679 right incomplete M2, and NM-Pv 11731 right complete M3 (both old no. 205/1), figured by Schlosser (1899: pl. 14, fig. 3); and NM-Pv 11680 (old no. 4310) left m3, figured by Schlosser (1899: pl. 14, figs 4 and 9).

Type locality. Tuchořice, the Czech Republic.

Age. Early Miocene, MN 3.

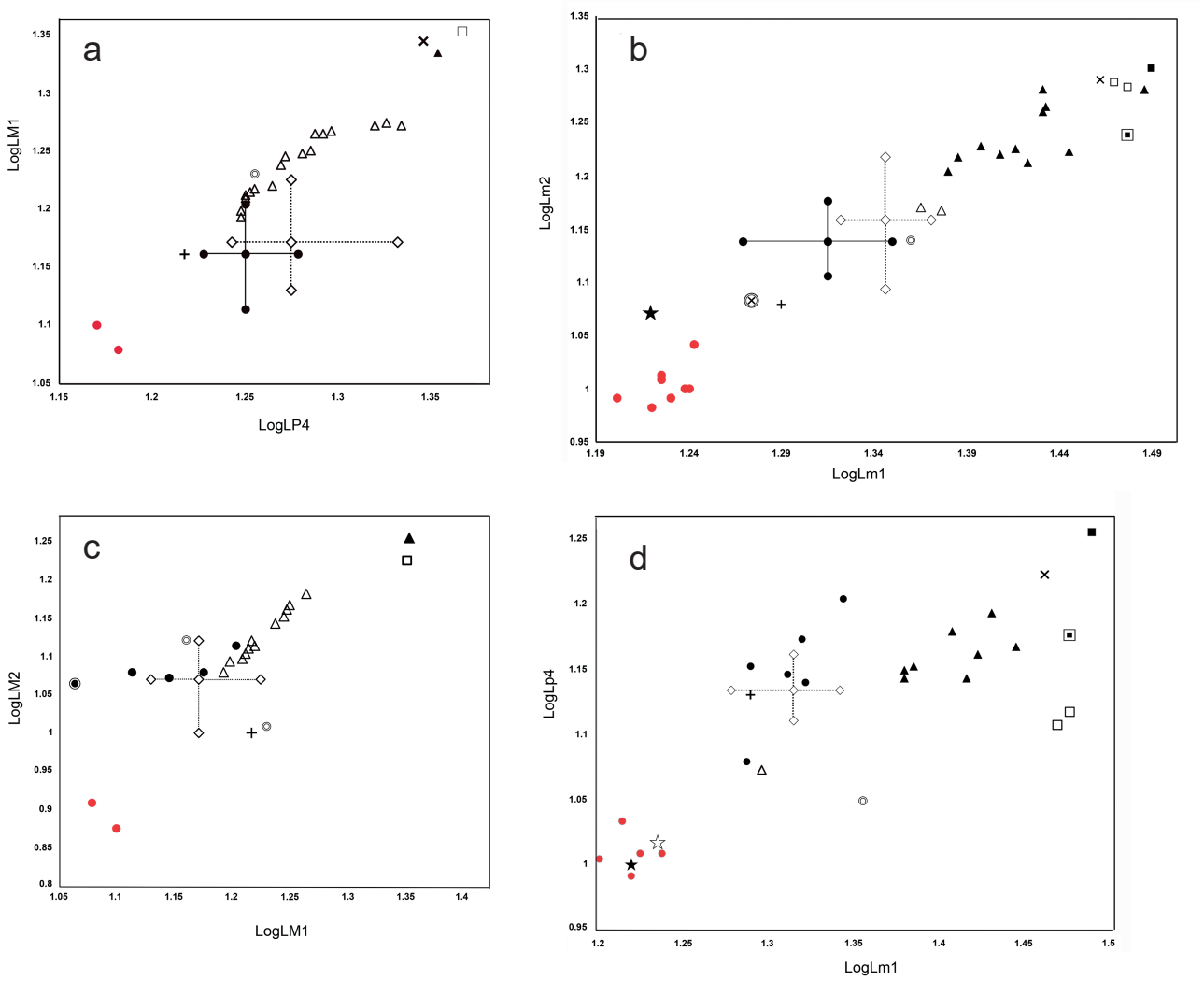
Diagnosis. Same as genus.

Additional material from type locality. NM-Pv 11681 (TU 7391149), left P4; NM-Pv 11682 (TU 7391150), left P4; NM-Pv 11683 (TU 739113), right P4; NM-Pv 11684 (TU 739155), left P4; NM-Pv 11685 (TU 739176), right M1; NM-Pv 11686 (TU 7391150), left M1; NM-Pv 11687 (TU 739185), M2 right; NM-Pv 11688 (TU 739149), left M2; NM-Pv 11689 (TU 739122), right M2; NM-Pv 11690 (TU 7391150), left M2; NM-Pv 11691 (TU 739165), right M3; NM-Pv 11692 (TU 739185), left M3; NM-Pv 11695 (TU-739157), right mandible with p2–m2; NM-Pv 11697 (TU 739135), right mandible with p3–m3; NM-Pv 11698 (TU 739142), association of right p4, m1 and m2; NM-Pv 11699 (TU 739141), left mandible with p3–m3; NM-Pv 11700 (TU 739177), left mandible with canine, p1–p2 alveolus and p3–m2; MN-Pv 11722, association of left p4–m3.



Text-fig. 1. Bivariate diagram of length and width of the upper dentition of selected European small and middle size Amphicyoninae compared with the Tuchořice specimens. a: P4; b: M1; c: M2; d: m1; e: m2. Data from Schlosser (1899, 1904), Thenius (1949), Dehm (1950), Heizmann (1973), Ginsburg (1977, 1989), Peigné (2012). Dotted line – ranges of maximum and minimum values from the average of teeth of *Cynelos lemanensis* from Ulm (Peigné and Heizmann 2003). Abbreviations: L – length; W – width.

D e s c r i p t i o n . NM-Pv 11678, left P4 (paralectotype, Text-fig. 3a). Well-developed basal cingulum, especially in the lingual wall. The protocone is located in a mesial position; it is wide but not very prominent or clearly differentiated from the cingulum. The union with the base of the paracone is not rectilinear, marking a clearly pronounced inflection. There is no isolated parastyle, although the mesial crista of the paracone bifurcates before reaching the base of the tooth.



Text-fig. 2. Bivariate diagram of length and width of the lower dentition of selected European small and middle size Amphicyoninae compared with the Tuchořice specimens. a: length P4 and M1; b: length m1 and m2; c: length M1 and M2; d: length m1 and p4. Symbols the same as in Text-fig. 1. Data from Schlosser (1899, 1904), Thenius (1949), Dehm (1950), Heizmann (1973), Ginsburg (1989), Peigné (2012). Dotted line – ranges of maximum and minimum values from the average of teeth of *Cynelos lemanensis* from Ulm (Peigné and Heizmann 2003); solid line – ranges of maximum and minimum values from the average of teeth of *Cynelos lemanensis* from Saint Gérand (Ginsburg 1977). Abbreviations: L – length.

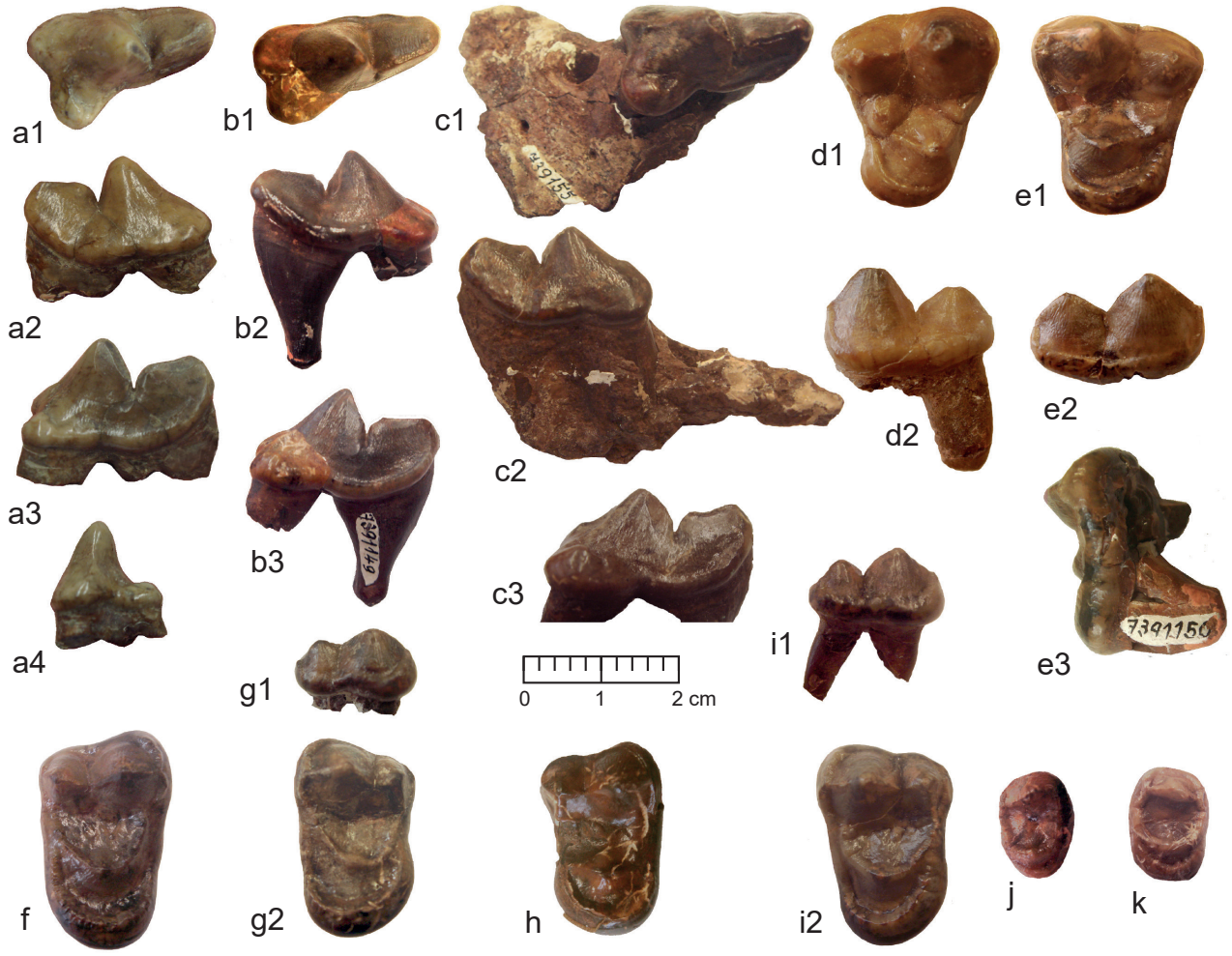
One of the branches is directed towards the protocone and the other mesiobuccally. The paracone is tall and pyramidal and the metastyle is relatively long. Both paracone and metastyle display vertical wear facets on the lingual side.

NM-Pv 11681, left P4 (Text-fig. 3b). Differs from the former P4 in which the paracone mesial crista is more pronounced before reaching the basal cingulum. The protocone is somewhat smaller and the mesial inflection between the base of the protocone and the paracone is less marked. NM-Pv 11682, right P4, is similar in morphology to the previous specimen, with a more reduced protocone and without the inflexion at the junction between the bases of the paracone and the protocone. NM-Pv 11683, right P4, has the same morphology to that of the paralectotype (NM-Pv 11678). NM-Pv 11684, left P4 (Text-fig. 3c), is somewhat larger than the other P4s and possesses a particularly wide protocone.

NM-Pv 11685, right M1 (Text-fig. 3d). Molar with subtriangular occlusal shape; it is relatively short, with a distally projected narrowed lingual area, moderately developed and with a mesiolingually strong basal cingulum. The paracone is high compared to the metacone. Small parastyle and metastyle. Paraconule and metaconule differentiated from the protocone cristae, almost symmetrical in comparison to the transversal axis of the molar; metaconule larger than paraconule. Very large but low dune-form protocone. Trigone valley sub-rounded.

NM-Pv 11686, left M1 (Text-fig. 3e). Differing from the previous M1 in the greater development of the lingual cingulum, which completely surrounds the protocone, from the base of the paraconule to the base of the metaconule, and also a wider lingual area.

NM-Pv 11687, M2 right (Text-fig. 3f). Sub-quadrangular in shape, with a short buccal wall and a wide transverse diameter in comparison with the M1. Moderately high buccal cusps. Strong buccal cingulum, especially at the base of the paracone. Low protocone forming a single semicircular crista which reaches the base of both the paracone and the metacone. Very strong lingual cingulum, which is semicircular and completely surrounds the protocone.



Text-fig. 3. ***Paludocyon bohemicus*** **(Schlosser, 1899), from Tuchořice, the Czech Republic, upper teeth. a: NM-Pv 11678, left P4 (paralectotype), a1 – occlusal view, a2 – buccal view, a3 – lingual view, a4 – mesial view; b: NM-Pv 11681, left P4, b1 – occlusal view, b2 – buccal view, b3 – lingual view; c: NM-Pv 11684, left P4, c1 – occlusal view, c2 – buccal view, c3 – lingual view; d: NM-Pv 11685, right M1, d1 – occlusal view, d2 – buccal view; e: NM-Pv 11686, left M1; e1 – occlusal view, e2 – buccal view, e3 – distal view; f: NM-Pv 11687, right M2 in occlusal view; g: NM-Pv 11688, left M2, g1 – buccal view, g2 – occlusal view; h: NM-Pv 11689, right M2 in occlusal view; i: NM-Pv 11690, left M2, i1 – buccal view, i2 – occlusal view; j: NM-Pv 11692, left M3 in occlusal view; k: NM-Pv 11691, right M3 in occlusal view.**

Other M2s such as Pv 11688 (Text-fig. 3g), NM-Pv 11689 (Text-fig. 3h) and NM-Pv 11690 (Text-fig. 3i) are similar in morphology to the previously described M2.

NM-Pv 11691, right M3 (Text-fig. 3j), small molar with reduced metacone. Central protocone opposite to the paracone, both are joined by a circular serrated crista. Strong buccal and lingual cingula. The left M3 NM-Pv 11692 (Text-fig. 3k) is somewhat smaller than the previous specimen, differing in the complete loss of the metacone.

NM-Pv 11677, left m1 (lectotype, Text-fig. 4a). Very robust molar, with a short paraconid presenting a vertical mesial cristid. High and very bulky protoconid. Metaconid quite strong, slightly displaced distally and with the lingual wall somewhat rounded. Short talonid, almost completely occupied by the hypoconid, the buccal wall of which is almost vertical. Low and crestiform entoconid. Small hypoconulid. Lingually weak basal cingulum, much stronger buccally, particularly at the base of the hypoconid, which is thickened apically.

NM-Pv 11700, left mandible with canine, p1–2 alveolus and complete p3–m2 (Text-fig. 4b). It corresponds to a small specimen, but the dentition is morphologically similar to that of other specimens. The p1 and p2 alveoli are uniradiculated and reduced, a large diastema is developed between canine–p1 and p1–p2.

NM-Pv 11695, right mandible with p2–m2 (Text-fig. 4c), mesial premolars practically unicuspidated; the p3 is unicuspid; the p4 is quite well developed, as is the main cuspid, which is higher than the m1 paraconid; a clearly separated and relatively acute distal cuspid is present. The m1 is very robust, with a short paraconid, mesial cristid somewhat inclined distally, and very pronounced. High and very bulky protoconid, with sharp mesial and distal cuspids. Quite strong metaconid, slightly displaced distally and with the lingual wall somewhat swollen. Short talonid, almost completely occupied by the hypoconid, the buccal wall of which is vertical. Low crestiform subdivided entoconid. Very weak basal cingulids. As in the m1 NM-Pv 11677,

Table 1. Measurements in mm of the upper teeth. a: *Paludocyon bohemicus* (Schlosser, 1899); b: *Megamphicyon carnutense* (Antunes et Ginsburg, 1977); c: *Dehmicyon* aff. *schlosseri* (Dehm, 1950). Abbreviations: TU – Tuchořice; L – mesio-distal diameter; W – width buccal-lingual.

Paludocyon bohemicus	LP2	WP2	LP3	WP3	LP4	WP4	LM1	WM1	LM2	WM2	LM3	WM3
NM-Pv 11678					22.0	13.7						
NM-Pv 11731											9.5	13.2
NM-Pv 11681					23.6	12.7						
NM-Pv 11683					22.7	14.5						
NM-Pv 11684					24.6	14.9						
NM-Pv 11685							22.6	27.2				
NM Pv 11682 NM-Pv 11686/NM-Pv 11690					22.6	12.4	21.6	24.7	14.3	21.3		
NM-Pv 11687/NM-Pv 11692									16.1	25.8	10.0	15.0
NM-Pv 11688									15.8	25.1		
NM-Pv 11689									15.5	24.1		
NM-Pv 11691											10.6	16.4
NM-Pv 11739					23.5	15.2						
NM-Pv 11741							22.1	26.4				
NM-Pv 11742							19.3	23.4				

a

Megamphicyon carnutense	LP2	WP2	LP3	WP3	LP4	WP4	LM1	WM1	LM2	WM2	LM3	WM3
NM-Pv 11701					29.9	17.3						
NM-Pv 11703					26.8	16.5						
NM-Pv 11704							27.0	34.6				
NM-Pv 11705									21.0	33.4		
NM-Pv 11706											18.0	26.7
NM-Pv 11707											14.3	21.9
NM-Pv 11749							24.4	31.2				

b

Dehmicyon aff. *schlosseri*	LP2	WP2	LP3	WP3	LP4	WP4	LM1	WM1	LM2	WM2	LM3	WM3
NM-Pv 11675							12.0	15.8				
NM-Pv 11676									6.8	11.7		

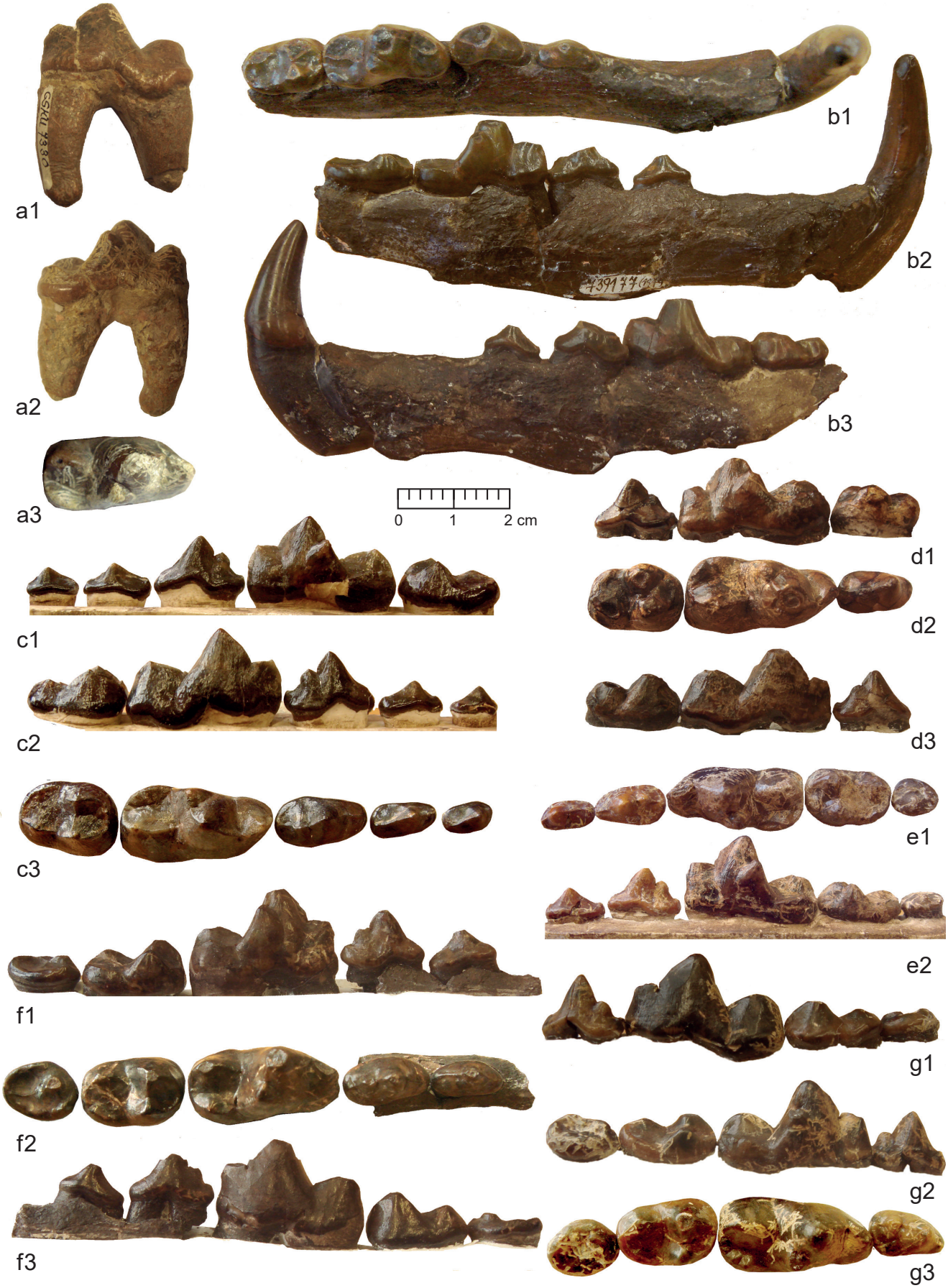
c

the buccal base of the hypoconid is thickened apically. The m2 has a moderately high trigonid, with the protoconid and metaconid almost the same height, although the protoconid is better developed. The protoconid presents a weak buccal widening. Very small paraconid, barely separated from the anterior cristids of the protoconid and metaconid; both join together, closing mesially the trigonid valley. Wide talonid, with a buccal hypoconid, clearly separated from the protoconid. A low, peripheral and crestiform entoconid is connected with the distal cristid of the hypoconid, clearly delimiting the talonid valley, which is flat and very wide. Basal cingulid very weak.

NM-Pv 11698, association of a right p4, m1 and m2 (Text-fig. 4d1–3). Neither the p4 nor the m1 show any differences from those described above. The m2 has a shortened talonid dominated by a very broad hypoconid. The cuspids are somewhat bunodont although they exhibit the same morphological arrangement as the previously described m2.

NM-Pv 11697, right mandible with p3–m3 (Text-fig. 4e1–2). It differs from NM-Pv 11695 in the greater gracility of the dentition, especially evident in m1 and m2, additionally the m2 has a relatively longer talonid. The m3 is sub-rounded and very small in size with respect to the m2.

NM-Pv 11699, left mandible with p3–m3 (Text-fig. 4f1–3), in which the mandibular bone is only partially preserved in the mesial section (alveolus for p2 and p3–p4 in situ), p3 unicuspid, p4 with a well-developed posterior cusp, and a thickened mesial cristid which does not form a distinct cusp. m1 robust and short, the trigonid is relatively high with



Text-fig. 4. ***Paludocyon bohemicus*** **(Schlosser, 1899), from Tuchořice, the Czech Republic, lower teeth. a: NM-Pv 11677, left m1 (lectotype), a1 – buccal view, a2 – lingual view, a3 – occlusal view; b: NM-Pv 11700, left mandible with c, alveoli for p1–p2, and p3–m2, b1 – occlusal view, b2 – lingual view, b3 – buccal view; c: NM-Pv 11695, right mandible with p2–m2, c1 – lingual view, c2 – buccal view, c3 – occlusal view; d: NM-Pv 11698, right p4–m2, d1 – lingual view, d2 – occlusal view, d3 – buccal view; e: NM-Pv 11697, right p3–m3, e1 – occlusal view, e2 – lingual view; f: NM-Pv 11699, left mandible with p3–m3, f1 – lingual view, f2 – occlusal view, f3 – buccal view; g: NM-Pv 11722, left p4–m3, g1 – buccal view, g2 – lingual view, g3 – occlusal view.**

Table 2. Measurements in mm of the lower teeth. a: *Paludocyon bohemicus* (Schlosser, 1899); b: *Megamphicyon carnutense* (Antunes et Ginsburg, 1977). Abbreviations: TU – Tuchořice; L – mesio-distal diameter; W – width buccal-lingual.

Paludocyon bohemicus	**Lci**	**Wci**	**Lp2**	**Wp2**	**Lp3**	**Wp3**	**Lp4**	**Wp4**	**Lm1**	**Wm1**	**Lm2**	**Wm2**	**Lm3**	**Wm3**
NM-Pv 11677									27.5	14.1				
NM-Pv 11695			9.7	5.1	12.7	6.4	16.4	9.1	27.1	13.7	18.4	13.4		
NM-Pv 11697					11.0	5.7	13.9	8.0	26.1	12.4	16.8	11.4	8.7	7.4
NM-Pv 11698							14.7	7.1	27.9	13.0	16.7	11.7		
NM-Pv 11699					12.5	6.3	15.6	8.0	27.0	13.5	18.2	12.6	13.8	10.9
NM-Pv 11700					10.4	5.0	13.9	6.8	24.0	11.5	15.7	10.6		
NM-Pv 11726									25.0	12.2	16.9	10.6	9.5	7.7
NM-Pv 11732									26.3	13.0				
NM-Pv 11723			10.9	5.6	12.5	6.9	15.1	7.7	25.6	12.1	16.6	10.9	9.5	7.2
NM-Pv 11722							14.5	8.4	26.5	12.5	16.3	11.5	12.0	9.6
NM-Pv 11724							14.1	8.1	24.0	12.4	16.0	10.9	8.7	7.1
NM-Pv 11725									27.0	13.8	19.1	12.6	13.2	10.3
NM-Pv 11728							14.2	7.8	24.3	12.4	16.5	10.8		
NM-Pv 11736 / NM-Pv 11737											19.8	13.8	13.2	9.7
NM-Pv 11733											17.7	12.8		
NM-Pv 11734											16.0	10.8		
NM-Pv 11735											17.7	11.7		
NM-Pv 11748													12.8	11.6

a

Megamphicyon carnutense	**Lci**	**Wci**	**Lp2**	**Wp2**	**Lp3**	**Wp3**	**Lp4**	**Wp4**	**Lm1**	**Wm1**	**Lm2**	**Wm2**	**Lm3**	**Wm3**
NM-Pv 11708							18.0	9.8						
NM-Pv 11709							15.7	10.0						
NM-Pv 11745									34.2	17.8				
NM-Pv 11710									35.8	18.5				
NM-Pv 11746									35.7	18.4				
NM-Pv 11711									33.3	16.9				
NM-Pv 11747									30.6	13.5	19.6	13.5	14.0	11.0
NM-Pv 11712									31.4	16.1	23.0	17.2		
NM-Pv 11713											26.2	19.2		
NM-Pv 11714											24.6	18.9		
NM-Pv 11717											23.8	16.9		
NM-Pv 11696											19.9	13.7	14.3	11.5
NM-Pv 11718											21.3	16.2		
NM-Pv 11716											21.7	16.6		
NM-Pv 11719													16.5	13.6

b

respect to the talonid, the metaconid is strong. Talonid with well-developed entoconid, separated by the narrow valley of the hypoconid. The m2 is narrow with a highly developed protoconid; the talonid is short with well-developed cusps. The m3 is sub-rounded, simple, with only the protoconid clearly pronounced, a cingulum almost surrounding the entire molar.

MN-Pv 11722, association of left p4–m3 (Text-fig. 4g1–3). The p4 is tall, with the distal part widened. m1 with reduced metaconid, and talonid dominated by a strong hypoconid, the entoconid is subdivided. m2 with a narrow talonid dominated by a strong hypoconid. m3 is more compressed buccolingually than in other specimens

Discussion. *Paludocyon bohemicus* was originally included by Schlosser (1899) in *Pseudocyon*, but its systematic position has since aroused controversy (Schlosser 1891, Kuss 1965). Ginsburg (1999), in his review of the

Miocene carnivorans of Europe, included it in the clade comprising *Amphicyon* (*Heizmannocyon*) *bohemicus-steinheimensis* with *Amphicyon steinheimensis* Fraas, 1885, choosing the latter as the type species of the new subgenus. Peigné et al. (2008) considered this subgenus as a synonym of *Cynelos*, and even pointed out the difficulties involved in relating these two species. Hunt (2003), without establishing its validity, points out that *Heizmannocyon* would be closer to *Cynelos* than to *Amphicyon*, an observation most likely influenced by the retention of primitive dental characters in *Cynelos*, as is also the case in *P. bohemicus*.

As we have pointed out in the differential diagnosis of *Paludocyon*, it differs from *Cynelos* sufficiently to separate both genera. *Cynelos lemanensis* represents a lineage of Amphicyoninae that presents greater development of the crushing teeth, but has maintained slightly modified premolars and carnassials. *Paludocyon* shows a somewhat contrasting trend, characterized by a moderate increase in the size of the crushing teeth, widening of the m1 talonid, and a reduction in the size of the lower premolars. Some of these characters are found in *Heizmannocyon steinheimensis* but the morphology of the upper and lower molars of both genera differ to a large extent. The differences between *Paludocyon* and *Pseudocyon sansaniensis* are significant, as can be seen in our differential diagnosis. However, this comparison is limited due to the lack of well-preserved upper dentition of *Pseudocyon sansaniensis*, as recognized by Ginsburg (1961) and more recently by Peigné (2012). Morphologically, *Heizmannocyon steinheimensis* and *Pseudocyon sansaniensis* are similar; both share a significant reduction of the p4 as well as a narrow talonid in both the m1 and m2, but *H. steinheimensis* retains a large m2.

Paludocyon bohemicus is morphologically quite different from *Amphicyon major* from Sansan (Ginsburg 1961); indeed, the latter shares many derived characters with *Cynelos lemanensis*, particularly those related to the high degree of development in the crushing dentition. Additionally, the m1 of *A. major* presents better development of the trigonid compared with the *Paludocyon* and *Cynelo*s species (Ginsburg 1961). This mixture of crushing molar dentition and the high degree of development of carnassial teeth characterizes the *Amphicyon* species and would appear to culminate in *Megamphicyon*.

Paludocyon bohemicus is absent in the Wintersoft-West Amphicyonidae association, although some authors considered *Amphicyon dietrichi* Dehm, 1950 as a very similar species, and have even proposed to synonymize both species (Kuss 1965, Peigné et al. 2008, Hunt and Stepleton 2015). However, the revision of *P. bohemicus* makes it possible to discard such a close relationship. The m1 morphology suggests a greater proximity between *A. dietrichi* and *Pseudocyon sansaniensis* than with *Paludocyon bohemicus*. A different case could occur with the mandible from the Thenay site determined as *Cynelos bohemicus* by Gagnaison et al. (2012). The excellent preservation of this mandible shows that the m1 has a very wide talonid, dominated by a powerful hypoconid, morphologically the dentition is very close to that of *Heizmannocyon steinheimensis*, being more derived than that of *Paludocyon bohemicus*. Finally, Jiangzuo et al. (2020) pointed out that the first record of *Cynelos* cf. *bohemicus*, together with *Cynelos* cf. *helbingi*, is in the middle Miocene Halamagai Formation from Northwestern China. The material is scarce and alternatively to its determination as two different forms, the three specimens (M1, M2 and m2) could correspond to a single species, clearly determined by these authors as *Cynelos* cf. *helbingi*.

Genus *Megamphicyon* Kuss, 1965

1965 *Megamphicyon*; Kuss, p. 66.

Type species. *Canis giganteus* Schinz, 1825 (assigned to genus *Amphicyon* as *Amphicyon giganteus* by Laurillard (1843: 567)).

Diagnosis. In Kuss (1965: 66).

Megamphicyon carnutense (Antunes et Ginsburg, 1977)

Text-figs 5, 6 Tabs 1b, 2b

1965 *Pseudocyon sansaniensis* aff. *sansaniensis* Lartet 1851; Kuss, pp. 119–122, fig. 77.
1977 *Amphicyon giganteus carnutense*; Antunes and Ginsburg, p. 341.
1989 *Amphicyon giganteus carnutense* Antunes et Ginsburg, 1977; Ginsburg, p. 102, figs 1–4.
2000b *Amphicyon* (*Megamphicyon*) *lathanicus* n. sp.; Ginsburg et al., p. 607, fig. 6.
2003 *Megamphicyon giganteus*; Fejfar et al., p. 167.
2016 *Megamphicyon* '*major – giganteus*'; Fejfar and Heizmann, p. 320, figs 7.2, 12.
2019 *Amphicyon carnutense*; Jiangzuo et al., p. 2.

Holotype. NMB S.O. 6531, left mandible with canine and p4–m2.

Type locality. Chilleurs, France.

Age. Early Miocene, MN 3.

Diagnosis. In Antunes and Ginsburg (1977).

Studied material from Tuchořice. NM-Pv 11701 (TU 738911), right P4; NM-Pv 11703 (TU 738910), P4 left; NM-Pv 11704 (TU 73892), left M1; NM-Pv 11705 (TU 738912), left M2; NM-Pv 11706 (TU 738916), left M3; NM-Pv 11707 (TU 738920), left M3; NM-Pv 11708 (TU 73898), left p4; NM-Pv 11709 (TU 738919b), left p4; NM-Pv 11747 (TU 739152), left m1–m3; NM-Pv 11710 (TU 738918), left m1; NM-Pv 11711 (TU 73896), left m1; NM-Pv 11712 (TU 739154), left m1–m2; NM-Pv 11713 (TU 73914), left m2; NM-Pv 11714 (TU 73893), left m2; NM-Pv 11716 (TU 73897), left m2; NM-Pv 11717 (TU 73899), left m2; NM-Pv 11718 (TU 738913), right m2; NM-Pv 11696 (TU 739120/21), association of right m2 and m3; NM-Pv 11719 (TU 738914a), left m3.

Remarks. The large-sized Miocene amphicyonids of Western Europe have frequently been determined as *Amphicyon giganteus* (Schinz, 1825) or *Megamphicyon giganteus* (Schinz, 1825), depending on the authors (Kuss 1965, Ginsburg and Antunes 1968, Ginsburg 1999, Peigné et al. 2006). Some of the large species from the early Miocene have been classified in other amphicyonid genera such as *Ysengrinia* and *Crassidia* (Heizmann and Kordikova 2000) and even in *Pseudocyon* (Ginsburg 1967, 1999, Heizmann and Kordikova 2000). These three genera exhibit different degrees of hypercarnivorous dental adaptation (Morales et

al. 2019), which serves to separate them from the *Amphicyon major* group, which reveals a tendency to enlarge the crushing molar surface.

From at least the late Oligocene to the middle Miocene, a set of large forms is recorded in Europe, which are close in size and morphology to *Amphicyon major*, but show some differences which are very difficult to evaluate (Kuss 1965). Increased dental size can be recognised when comparing from the oldest form to the most modern ones, but due to the great variability in size and morphology, there are real difficulties involved in assigning these fossil assemblages to different taxa. Some of the older forms from the early Miocene (MN 2–3) have received different determinations, including *Amphicyon giganteus carnutense* Antunes et Ginsburg 1977, *Amphicyon giganteus laugnacensis* Ginsburg, 1989 and *Amphicyon* (*Megamphicyon*) *lathanicus* Ginsburg, Cheneval, Janvier, Pouit et Sen, 2000 (see Ginsburg 2000b, 2002). However, the type species, *Megamphicyon giganteus* (Schinz, 1825), would be reserved for the largest species with molars similar in size to those from the type locality of Averay (France), also found in some European localities of MN 4–6 age (Artenay, Baigneaux, La Romieu, Pont Levoy and Arroyo del Val among others), where molar sizes can greatly exceed that of *Amphicyon major* (Ginsburg 1989, 1999, Peigné et al. 2006). However, there is a need for an in-depth review of this group, a task that lies beyond the scope of the present research.

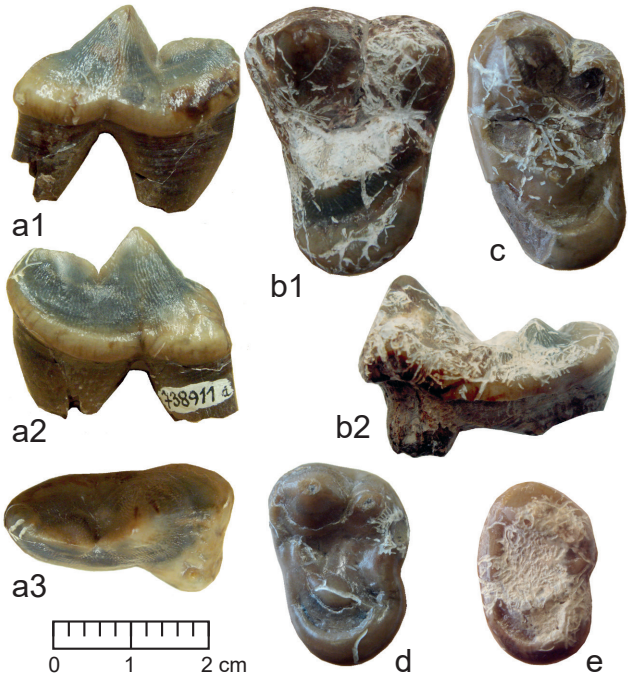
Description. NM-Pv 11701, right P4 (Text-fig. 5a1–3). Quite elongated, with a relatively long metastyle, and a narrow mesially widened paracone, although without developing an authentic parastyle. The mesial crista of the paracone is strogly pronounced, with a small incision near the base, which changes its inclination, tending to become more horizontal and displaced buccally. Consequently, the base of the paracone is continued mesially. The protocone is moderate in size, placed in the mesial position, with a poorly separated cusp. Highly developed basal cingulum.

NM-Pv 11703, P4 left. This tooth presents an intermediate size, somewhere between the two previous specimens; the buccal part of the metastyle is broken. The anterior crista of the paracone is clearly more vertical than in the other two specimens.

NM-Pv 11704, left M1 (Text-fig. 5b1–2). Molar with a subtriangular occlusal shape, the base of the lingual wall is somewhat broken; whether a basal cingulum existed is not evident. The paracone is robust and large, the metacone is low and somewhat smaller. Buccal styles scarcely developed. The large pyramidal protocone does not reveal the presence of a paraconule, but a rather large metaconule can be observed. Cingulum buccal very strong.

NM-Pv 11705, left M2 (Text-fig. 5c). Molar quite wide, but narrow. Paracone very pronounced in relation to the metacone, which is somewhat displaced lingually. The protocone and the lingual cingulum are well developed.

NM-Pv 11706, left M3 (Text-fig. 5d), compared to the previous molar it is smaller, but the height and strength of its buccal cones rule out any possible interpretation as an M3, although there is a strong constriction in the distal wall, which is similar to that observed in the specimen NM-Pv 11707, which is considered as an M3.



Text-fig. 5. ***Megamphicyon carnutense*** **(Antunes et Ginsburg, 1977), from Tuchořice, the Czech Republic, upper teeth. a: NM-Pv 11701, right P4, a1 – buccal view, a2 – lingual view, a3 – occlusal view; b: NM-Pv 11704, left M1, b1 – occlusal view, b2 – mesial view; c: NM-Pv 11705, left M2 in occlusal view; d: NM-Pv 11706, left M3 in occlusal view; e: NM-Pv 11707, left M3 in occlusal view.**

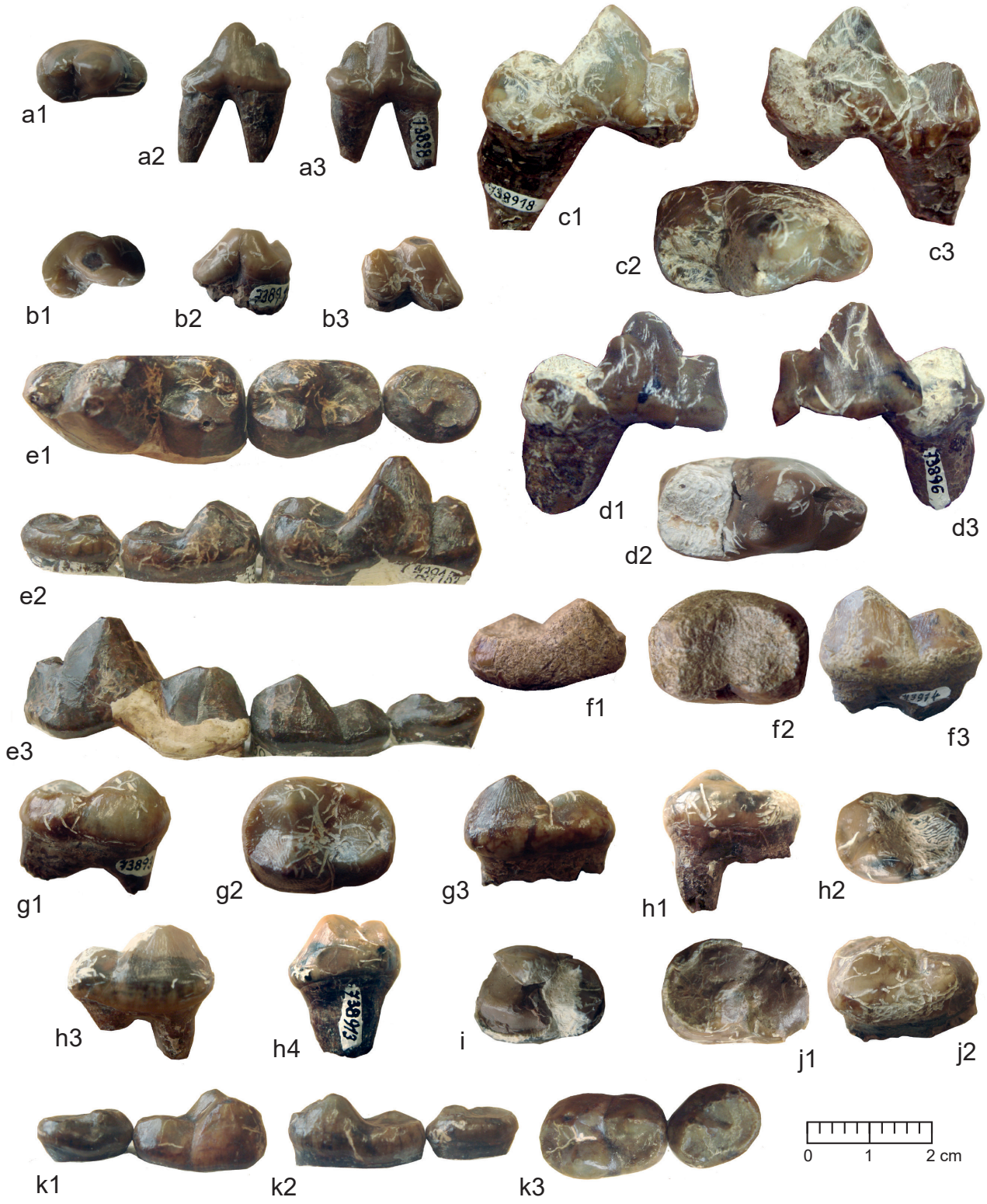
NM-Pv 11707, left M3 (Text-fig. 5e). Similar in morphology to the M3 described above, but with very poorly developed cusps. The metacone is very small, almost lost. Occlusal kidney-shaped form. Very strong buccal cingulum, which represents almost the most developed element of the molar.

NM-Pv 11708, left p4 (Text-fig. 6a1–3). Premolar with strong and high distal cuspid. Distolingual cingulid well developed and talonid moderately expanded.

NM-Pv 11709, left p4 (Text-fig. 6b1–3), smaller than the previous specimen and differs from it in the strong constriction of the lingual wall.

NM-Pv 11710, left m1 (Text-fig. 6c1–3). Very robust molar, with a short paraconid and the mesial cristid distally inclined. High and very robust protoconid. Metaconid quite reduced, slightly displaced distally and with a somewhat swollen buccal wall. Short talonid, almost completely occupied by the hypoconid whose buccal base is somewhat widened apically. Entoconid low and elongated and joined to the distal hypoconid cristid. Weak basal cingulum. NM-Pv 11711, left m1 (Text-fig. 6d1–3) more slender but with similar morphology to that described above. NM-Pv 11712, left m1–m2, the m1 is somewhat smaller than the other carnassial teeth; the associated m2 is similar to the morphotype of NM-Pv 11713 described below.

NM-Pv 11747, left m1–m3 (Text-fig. 6e1–3); slightly smaller size compared to the rest of the specimens attributed to this species, m1 very robust, with a short paraconid, and a mesial cristid distally inclined. High and very robust protoconid. Metaconid still strong. Short talonid, almost



Text-fig. 6. ***Megamphicyon carnutense*** **(Antunes et Ginsburg, 1977), from Tuchořice, the Czech Republic, lower teeth. a: NM-Pv 11708, left p4, a1 – occlusal view, a2 – buccal view, a3 – lingual view; b: NM-Pv 11709, left p4, b1 – occlusal view, b2 – buccal view, b3 – lingual view; c: NM-Pv 11710, left m1, c1 – lingual view, c2 – occlusal view, c3 – buccal view; d: NM-Pv 11711, left m1, d1 – lingual view, d2 – occlusal view, d3 – buccal view; e: NM-Pv 11747, left m1–m3, e1 – occlusal view, e2 – lingual view, e3 – buccal view; f: NM-Pv 11713, left m2, f1 – lingual view, f2 – occlusal view, f3 – buccal view; g: NM-Pv 11714, left m2, g1 – lingual view, g2 – occlusal view, g3 – buccal view; h: NM-Pv 11718, right m2, h1 – lingual view, h2 – occlusal view, h3 – buccal view, h4 – distal view; i: NM-Pv 11716, left m2 in occlusal view; j: NM-Pv 11717, left m2, j1 – occlusal view, j2 – buccal view; k: NM-Pv 11696, right m2–m3, k1 – lingual view, k2 – buccal view, k3 – occlusal view.**

completely occupied by the hypoconid, entoconid low and elongated and joined to the distal hypoconid cristid. The buccal basal wall is broken. The m2 is relatively large with respect to m1, trigonid with high protoconid somewhat larger than the metaconid, small mesiocentral paraconid. Talonid large with strong hypoconid attached to a peripherical

entoconid. The m3 is well developed with a dominant protoconid, and vestigial metaconid and hypoconid. The talonid is robust.

NM-Pv 11713, left m2 (Text-fig. 6f1–3). It has a relatively high trigonid, dominated by the protoconid, although the metaconid is also quite well developed. The protoconid base is buccally widened. Very small paraconid, poorly differentiated from the anterior cristids of the protoconid and metaconid, which are joined together, closing mesially the trigonid valley. Talonid wide, with a high buccal hypoconid, clearly separated from the protoconid. The crestiform entoconid, low and peripheral, is joined distally to the distal hypoconid cristid, thus strongly delimiting the talonid valley, which is flat and very wide. Moderate basal cingulum, only strong in the mesiobuccal area. Another two m2, NM-Pv 11714 (Text-fig. 6g1–3) and NM-Pv 11712, display a similar morphology. NM-Pv 11718, right m2 (Text-fig. 6h1–4), NM-Pv 11716, left m2 (Text-fig. 6i) and Pv 11717, left m2 (Text-fig. 6j1–2) present a morphological pattern somewhat different from that of the teeth described above, in particular as a result of the narrow form of the talonid, which seems relatively more reduced.

NM-Pv 11696, is an association of a right m2 and m3 (Text-fig. 6k1–3). The m2 has a slightly better-developed paraconid than in the previously described specimens. The mesial wear facet with the m1 talonid is very clear. The m3 is oval in shape with a strong mesiobuccal protoconid, from which a mesial cristid extends to the lingual position, marking a small cuspid (paraconid). The talonid is poorly differentiated from the trigonid, and the hypoconid is very low and extends into a peripheral cristid that completely surrounds the talonid.

D i s c u s s i o n . *Megamphicyon carnutense* was defined by Antunes and Ginsburg (1977) as a new subspecies *Amphicyon giganteus carnutense*, in the same paper where they defined a new species *Amphicyon olisiponensis*, from the locality of Quinta do Narigao, Lisbon Basin, Portugal. According to these authors, *Amphicyon olisiponensis* appears to show affinities with both the mandible classified by Kuss (1965) as *Pseudocyon sansaniensis* aff. *sansaniensis* from Chilleurs, France, and the primitive forms of *Amphicyon giganteus*. Antunes and Ginsburg (1977) highlighted the difficulties involved in distinguishing between the Chilleurs form and *Amphicyon olisiponensis*. However, the small morphological differences between these two forms, together with the more modern age of the Lisbon site, lead them to maintain a specific distinction between the two. Therefore, according to these authors the Chilleurs form should be classified as *Amphicyon giganteus*, but differences in size lead them to propose a new subspecies *A. giganteus carnutense*.

Ginsburg (1989) added a third subspecies, *Amphicyon giganteus laugnacensis*, to distinguish the maxilla from Laugnac, determined by de Bonis (1973) as *Amphicyon* cf. *astrei* Kuss, 1962 from the other subspecies. He concluded that the *Amphicyon giganteus* species would comprise three successive stratigraphic subspecies; *Amphicyon giganteus laugnacensis*: MN 2; *Amphicyon giganteus carnutense*: MN 3; *Amphicyon giganteus giganteus*: MN 4a (Artenay), MN 4b (Baigneaux-en-Beauce), MN 5 (Pontlevoy, Falun d'Anjou). However, Ginsburg et al. (2000) subsequently reconsidered the taxonomic attribution of the Chilleurs mandible (type of *Amphicyon giganteus carnutense*), considering the determination by Kuss to be correct (1965). Hence, the validity of *Amphicyon giganteus carnutense* was discarded. Therefore, the materials from Les Beilleaux attributed by Ginsburg (1989) to this taxon remained unnamed, and he proposed the new species *Amphicyon* (*Megamphicyon*) *lathanicus* for this fossil considering *Megamphicyon* Kuss, 1965 as a valid subgenus.

Nonetheless, we recognised many problems in the use of the denomination of *Pseudocyon sansaniensis* for the mandible from Chilleurs (Kuss 1965: fig. 77). The Chilleurs species possesses a more robust m1 than that of the mandible type of *P. sansaniensis* (Ginsburg 1961) but above all, it presents a significantly larger m2 relative to m1, in contrast with the small size of the m2 of the Sansan species. Thus, the decision of Antunes and Ginsburg (1977) remains valid; that the Chilleurs form and *Amphicyon olisiponensis* are very similar. Likewise, Ginsburg (1989) considered that *A. olisiponensis* could belong to the same group as *Amphicyon giganteus*. We think that the least confusing taxonomic hypothesis is that of Antunes and Ginsburg (1977), considering that the large Chilleurs form determined by Kuss (1965) as *Pseudocyon sansaniensis* should be called *Megamphicyon carnutense*, whilst *Amphicyon* (*Megamphicyon*) *lathanicus* should currently be considered as a synonym for the previous species, an opinion already expressed by Jiangzuo et al. (2019).

The dentition from Tuchořice is similar to that of *Megamphicyon carnutense*, but some teeth manifest morphological variations that may suggest the presence of a second species; as is the case of three m2 (specimens NM-Pv 11718, NM-Pv 11716 and NM-Pv 11717), which possess a narrow talonid, and are slightly smaller than the specimens with a subquadrate talonid. However, similar differences are found in the m2 of the Falun d'Anjou described as *Amphicyon lathanicus* by Ginsburg (2000b), in which morphotypes with a wide and subquadrate talonid (m2, FS 6953) coexist with others possessing a narrower talonid (FS 6965). We therefore regard all described specimens as belonging to a single species, *Megamphicyon carnutense*.

Tribe Pseudarctini nov.

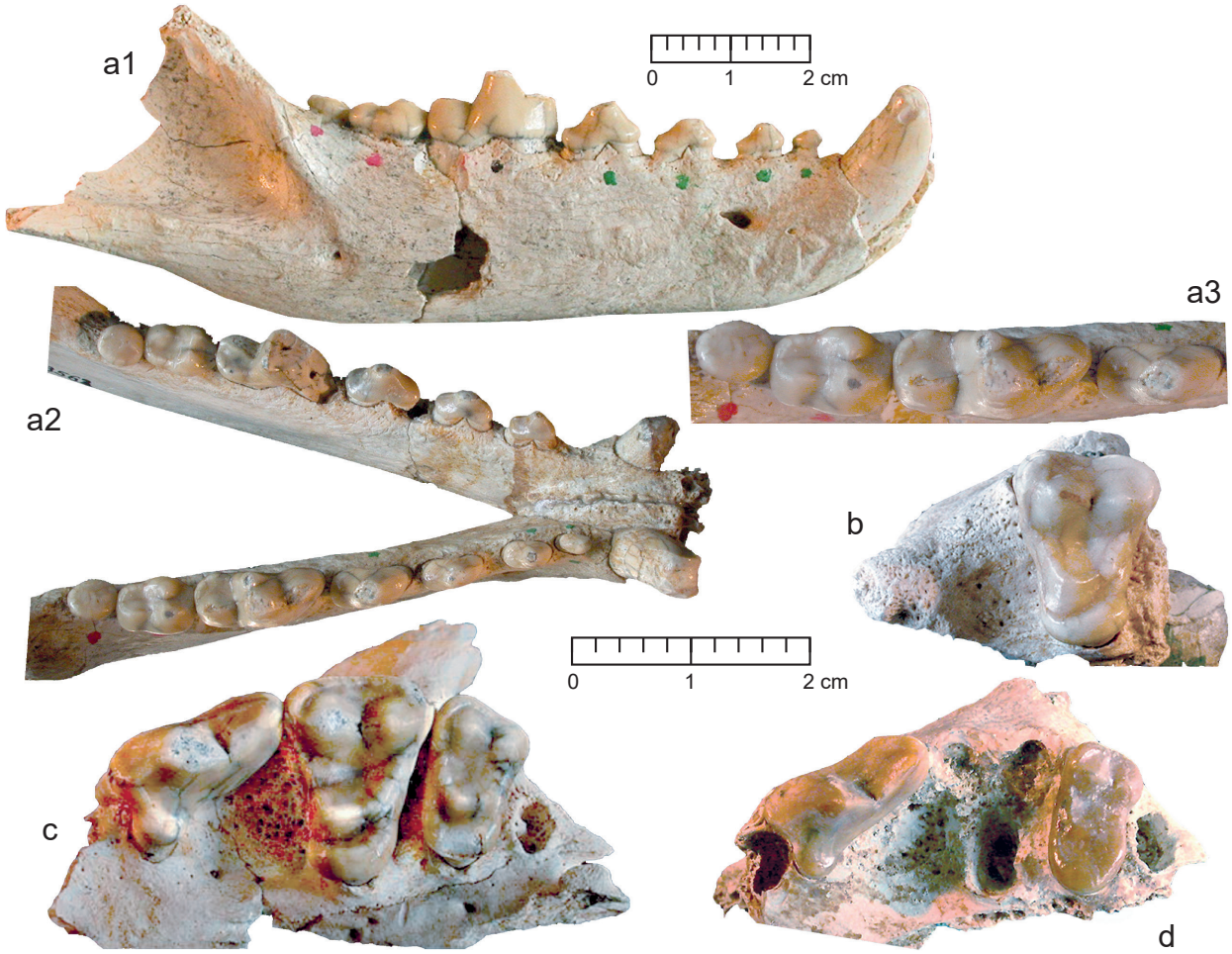
T y p e g e n u s . *Pseudarctos* Schlosser, 1899.

D i a g n o s i s . As in the Amphicyonini tribe, the molars tend to present a larger crushing surface, albeit displaying a different pattern with a greater mesiodistal length of the upper molars and buccolingual length in the lower molars, associated with a significant reduction of the carnassial teeth, and loss of the p4 distal accessory cuspid. *Dehmicyon* n. gen. is included as a basal form of this tribe.

I n c l u d e d g e n e r a . *Pseudarctos* Schlosser, 1899, *Ictiocyon* Crusafont, Villalta et Truyols, 1955 and *Dehmicyon* n. gen.

Genus *Dehmicyon* n. gen.

T y p e s p e c i e s . *Amphicyon schlosseri* Dehm, 1950 (Wintershof- West, Germany; early Miocene, MN 3).



Text-fig. 7. *Dehmicyon* n. gen. *schlosseri* (Dehm, 1950), from Wintershof-West, Germany. a: BSP 13562, mandible (holotype), a1 – right hemimandible in buccal view, a2 – occlusal view, a3 – left p4–m2 in occlusal view; b: BSP 12365, left maxilla fragment with M1 in occlusal view; c: BSP 13562, left maxilla fragment with P3 broken, P4–M2 and M3 alveolus (holotype) in occlusal view; d: BSP 12343 left maxilla fragment with P4, alveolus for M1, M2 and M3 alveolus in occlusal view.

Etymology. In honour of Dr. Richard Dehm.

Diagnosis. Pseudarctini with robust mandible, small mesial premolars (p1–p3), p4 unicuspidated. High m1 trigonid with strong metaconid; short and narrow talonid. m2 remaining long compared with m1. P4 robust with strong protocone. Slender M1 with subtriangular occlusal shape. M2 small compared to M1.

Dehmicyon schlosseri (Dehm, 1950)

Text-figs 7, 8

1950 *Amphicyon schlosseri* n. sp.; Dehm, p. 20, figs 9–17.
1965 *Cynelos rugosidens schlosseri* (Dehm) 1950; Kuss, p. 63–66.
1981 ?*Cynelos schlosseri* (Dehm), 1951; Ginsburg et al., p. 185, fig. 2.
1989 *Cynelos schlosseri*; Ginsburg, p. 107.
1996 *Cynelos schlosseri* (Dehm, 1950); Viranta, p. 22, fig. 7.
1999 *Cynelos schlosseri* (Dehm, 1950); Ginsburg, p. 116.
2003 *Cynelos schlosseri*; Peigné and Heizmann, p. 14.
2008 *C*[*ynelos*] *schlosseri*; Peigné et al., p. 954.
2015 *Cynelos schlosseri*; Hunt and Stepleton, p. 4

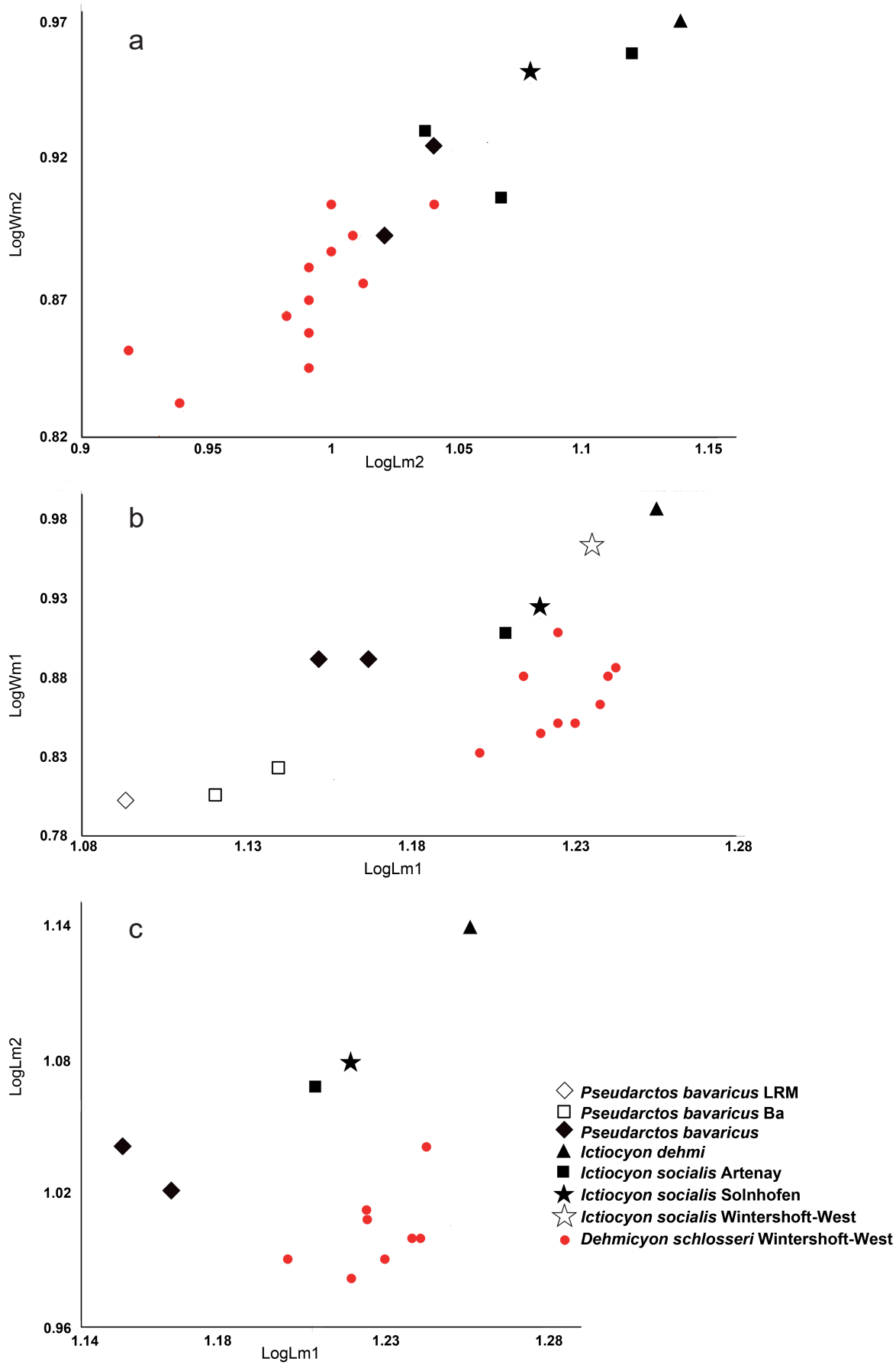
Holotype. BSP 1937 II 13562, mandible and maxilla (Dehm 1950: figs 9–11). See Kuss (1965: 63).

Type locality. Wintershof-West, Germany.

Age. Early Miocene, MN 3.

Emended diagnosis. Same as genus.

Remarks. *Dehmicyon schlosseri* presents an interesting combination of morphological features, which enable it to be differentiated from *Cynelos lemanensis* (Pomel, 1846) and from the *Ictiocyon-Pseudarctos* group. Their separation from *C. lemanensis* and related species is unequivocal, as evidenced by Peigné and Heizmann (2003), in particular due to the poor development of the crushing molars, which suggests a more primitive morphological stage than the *Cynelos-Amphicyon* group species, typical representatives of the Amphicyoninae clade. Together with the *Ictiocyon-Pseudarctos* group, it shares the robustness of the jaw and the morphology of the lower p4 lacking a distal accessory cuspid (residual in some specimens). Other morphological characters that it shares, in particular with *Ictiocyon*, involve the strong development of the buccal wall of the M1 in relation to the lingual area, the large size of the buccal cingulum and the robust development of the styles. However, in *Ictiocyon* the M1 is wide, especially on its occlusal surface, similar to that of the other molars



Text-fig. 8. Bivariate diagram of length and width of the lower dentition (m1 and m2) of *Pseudarctos*, *Ictiocyon* and *Dehmicyon* species. a: m2; b: m1; c: length m1 and m2. Data from Schlosser (1904), Helbing (1937), Thenius (1949), Dehm (1950), Crusafont et al. (1950), Ginsburg (1992). Abbreviations: L – length; W – width; Ba – Baigneaux; LRM – Pellecahus.

(Crusafont et al. 1955). This tendency towards a larger crushing surface in the molar dentition is shared with the *Cynelos-Amphicyon* group, but in the *Ictiocyon-Pseudarctos* group the carnassials are significantly reduced (P4/m1), whereas in *Cynelos* and *Amphicyon* they tend to show an increase in size. In the latter genus, the upper molars maintain a strong buccal-lingual development, while in *Ictiocyon* they tend to present a sub-square occlusal shape.

Ginsburg (1992) reviewed the species included in *Pseudarctos*, rejecting the proposal of Kuss (1965) that supported the existence of an anagenetic line formed by a single species *Pseudarctos bavaricus* with different temporal subespecies. The French author, proposing the existence of two genera; *Ictiocyon* Crusafont, Villalta et Truyols, 1955 new rank and *Pseudarctos* Schlosser, 1899, but without accepting the validity of *Ictiocyon dehmi* the type species of *Ictiocyon*, which he considered as synonymous with *Ictiocyon socialis*. However, *Ictiocyon dehmi* shows more derived characteristics than *Ictiocyon socialis*. This is seen especially in the greater robustness of the premolars and the morphology of the m1–m2 talonid, which are wider and more developed than the trigonid. This tendency to increase the surface of the talonid relative to the trigonid became a significant feature in *Pseudarctos*. The morphology of m1 suggest that the mandible of Wintersoft-West BSP 1937 II 12301 determined as *Ictiocyon socialis* by Dehm (1950) could be closer to *Ictiocyon dehmi* than to *I. socialis*, so we suggest it be reclassified as *Ictiocyon* cf. *dehmi*.

Dehmicyon can be interpreted as a similar form to *Ictiocyon* genus with which it appears to share derived characters such as mandibular robustness and loss of the posterior accessory cuspid on the p4; other features shared by both groups can be considered as primitive; e.g., the strong development of the styles and the buccal cingulum and the narrow morphology of the lingual area of the M1 or the small size of the second and third molars. Unfortunately, the absence of upper dentition in *Ictiocyon socialis* prevents direct comparison with the new genus. However, the morphology of the lower dentition supports the proposal that *D. schlosseri* is closer to *I. socialis* than *I. dehmi*.

D. schlosseri has simultaneously a less specialized dental morphology than *I. socialis* (in particular seen in the reduced robustness of the m1) and greater size of the m2 with compared to the m1 (Text-fig. 8). These differences are sufficiently important to separate both species at a generic level. *Dehmicyon schlosseri* can be interpreted as a basal form of Pseudarctini, already far removed from the primitive Amphicyonini represented by *Cynelos* species.

Dehmicyon aff. *schlosseri* (Dehm, 1950)

Text-figs 1, 9, Tab. 1c

Locality. Tuchořice, the Czech Republic.

Age. Early Miocene, MN 3.

Studied material. NM-Pv 11675 (TU 738922), right M1; NM-Pv 11676 (TU 738923), right M2.

Description. NM-Pv 11675, right M1 (Text-fig. 9a1–4). Molar with elongated buccal wall and narrow lingual wall. Well-developed metastyle, separated by a notch from the mesial crista of the metacone. Strong parastyle. Large buccal cingulum. Paracone and metacone subequal in size. Strong pyramidal protocone, surrounded by a prominent cingulum that reaches the bases of both the paracone and the metacone. Reduced paraconule and metaconule, almost completely included in the cingulum.

Text-fig. 9. ***Dehmicyon*** **aff.** ***schlosseri*** **(Dehm, 1950), from Tuchořice, the Czech Republic. a: NM-Pv 11675, right M1, a1 – buccal view, a2 – mesial view, a3 – distal view, a4 – occlusal view; b: NM-Pv 11676, right M2 in occlusal view.**

NM-Pv 11676, right M2 (Text-fig. 9b). Small size compared with the M1. Developed parastylar area. Medium-sized parastyle and metastyle. Weak buccal cingulum. Metacone much smaller than the paracone. Protocone in central position which, together with the paraconule and the metaconule, form a semicircle. Strong, wide lingual cingulum.

Discussion. The size of these two molars is similar to that of the homologous teeth of *Dehmicyon schlosseri* from Wintershof-West described by Dehm (1950) (Text-fig. 7). Features shared with this species: 1) the greater buccal length with respect to the lingual length; 2) the strong development of the buccal cingulum and the buccal styles; 3) the similar paracone-metacone size ratio in the M1; 4) the small size of the M2 compared with the M1. Some of these characters were already pointed out by Peigné and Heizmann (2003) as being typical of *D. schlosseri*. However, in the morphology of the M1 from Tuchořice there are some differences in relation to this species; in particular, the greater development of the buccal cingulum and the mestastyle are striking; the protocone is placed in a central position, it is robust and surrounded by a very prominent cingulum which reaches the bases of the paracone and metacone, and in which the very reduced paraconule and metaconule are included. The differences in the morphology of the M2 are minor. Taking into account the highly variable dental morphology of most of the amphicyonid species, we classify these two molars from Tuchořice as *Dehmicyon* aff. *schlosseri*.

Tribe Magericyonini nov.

Type genus. *Magericyon* Peigne, Salesa, Anton et Morales, 2008

Diagnosis. Amphicyoninae with hypercarnivorous dentition; premolars strongly reduced; metaconid reduced or absent in m1 and m2; robust P4; M1 with high buccal cusps; M2⁄m2 reduced relative to M1⁄ m1, M3/m3 vestigial.

Included genera. *Magericyon* Peigne, Salesa, Anton et Morales, 2008 and ?*Pseudocyon* Lartet, 1851

Remarks. Two species are recognized within genus *Magericyon* – *M. anceps* Peigné, Salesa, Antón et Morales, 2008 and *M. castellanus* (Ginsburg, Morales et Soria, 1981). Genus *Pseudocyon* is assigned to this tribe with some doubt.

Conclusions

The early Miocene (MN 3) Amphicyonidae of Tuchořice (the Czech Republic) are represented by two subfamilies; Thaumastocyoninae Hürzeler, 1940, which contains a unique species *Peignecyon felinoides* (see Morales et al. 2019), and Amphicyoninae Trouessart, 1885, with three species.

The two more abundant species belong to the genera included in the tribe Amphicyonini; *Paludocyon* n. gen. and *Megamphicyon* Kuss, 1965. *Paludocyon bohemicus* (Schlosser, 1899) from Tuchořice was originally determined as *Pseudocyon bohemicus* by Schlosser (1899). *Paludocyon* could have diverged from *Cynelos*, maintaining smaller crushing molars and modifying the remaining dentition. Ginsburg (1999) proposed a close relationship between *Paludocyon bohemicus* and *Heizmannocyon steinheimensis*, including both species in *Heizmannocyon*. Whatever the case may be, the dental morphological differences between these species are sufficiently evident for them to be separated into two genera. The large sized amphicyonid from Tuchořice is tentatively determined as *Megamphicyon carnutense* (Antunes et Ginsburg, 1977), although the species included in the genus *Megamphicyon* require an in-depth review.

Two small teeth are classified as *Dehmicyon* n. gen. aff. *schlosseri* (Dehm, 1950). This new genus has been proposed for the species *Amphicyon schlosseri* from Wintershof-West (Dehm 1950) and is tentatively included in the tribe Pseudarctini nov. with *Ictiocyon* and *Pseudarctos* genera.

Acknowledgements

Spanish Research Projects GC2018-094122-B100 and PID2020-116220GB-I00 (AEI/ FEDER, UE) and CGL2016-76431-P (AEI/ FEDER, UE), Government of Aragon (Group ref. E33_17R), Research Groups CSIC 64 1538 and UCM 910607, and the Generalitat de Catalunya (CERCA Programme, and Beatriu de Pinós contract 2017 BP 00223 from AGAUR to J.A.) are all greatly acknowledged. This study was also funded by the Government of Aragon (Group ref. E33_20R). The "Juan de la Cierva Formación" program (FJC2018-036669-I), from the Spanish Ministry of Science, Innovation, and Universities also funded AV. Additionally, the present research received support from the SYNTHESYS Project http://www.synthesys.info/, funded by a European Community Research Infrastructure Action within the FP7 "Capacities" Program under the grant agreement (SYNTHESYS; CZ-TAF-3329) of J.A. O.F. and J.W. were granted funding by the Ministry of Culture of the Czech Republic (DKRVO 2019–2023/2.V.c, National Museum, 00023272). We also thank Dr. Serdar Mayda and Dr. Michael Morlo for helpful reviews of the manuscript.

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