

Paläontol Z (2009) 83:151–174
DOI 10.1007/s12542-009-0008-6

RESEARCH PAPER

The carnivoran community from the Miocene of Sandelzhausen (Germany)

Doris Nagel · Clara Stefen · Michael Morlo

Received: 23 May 2007 / Accepted: 10 January 2008 / Published online: 13 February 2009
© Springer-Verlag 2009

Abstract From the Bavarian Early/Middle Miocene (MN5) site Sandelzhausen, nine species of carnivoran mammals are identified including the hemicyonine ursid *Hemicyon stehlini*, the amphicyonids *Amphicyon* cf. *major* and *Pseudarctos bavaricus*, the mustelids *Ischyriactis zibethoides* and *Martes* cf. *munki*, the mephitid *Proputorius pusillus*, the viverrid *Leptoplesictis* cf. *aurelianensis*, the felid *Pseudaelurus romieviensis*, and finally the recently described barbourofelid *Prosansanosmilus eggeri*. With these taxa present, Sandelzhausen shows a carnivoran community typical, though deprived, for the Lower to Middle Miocene of Europe, but different from roughly contemporary Mediterranean faunas such as those from Çandır or Paşalar in Turkey.

Keywords Europe · Germany · Early/Middle Miocene · Carnivora · Systematics · Palaeobiogeography

Kurzfassung In der bayerischen unter-/mittelmiozänen (MN5) Fundstelle Sandelzhausen konnten 9 Raubtierarten identifiziert werden. Dazu gehören der bärenartige

Hemicyonide *Hemicyon stehlini*, die Amphicyoniden *Amphicyon* cf. *major* und *Pseudarctos bavaricus*, die Musteliden *Ischyriactis zibethoides* und *Martes* cf. *munki*, der Mephitine *Proputorius pusillus*, die viverride Form *Leptoplesictis* cf. *aurelianensis*, der felide *Pseudaelurus romieviensis* und der kürzlich beschriebene Barbourofelide *Prosansanosmilus eggeri*. Die carnivore Vergesellschaftung in Sandelzhausen ist damit typisch, wenn auch ein wenig verarmt, für das untere bis mittlere Miozän in Europa, aber doch verschieden von den ungefähr gleich alten mediterranen Faunen wie zum Beispiel Çandır und Paşalar in der Türkei.

Schlüsselwörter Europa · Deutschland · Unter-/Mittelmiozän · Carnivora · Systematik · Paläobiogeographie

Abbreviations

BSPG Bayerische Staatssammlung für Paläontologie und Geologie, München
MNHNP Muséum National d'Histoire Naturelle, Paris
NOW Neogene of the Old World. Database of fossil mammals (<http://www.helsinki.fi/science/now>)

D. Nagel (✉)

Department of Palaeontology, Universität Wien,
Althanstrasse 14, 1090 Wien, Germany
e-mail: doris.nagel@univie.ac.at

C. Stefen

Staatliche Naturhistorische Sammlungen Dresden,
Museum für Tierkunde, Königsbrücker Landstraße 159,
01109 Dresden, Germany
e-mail: clara.stefen@snsd.smwk.sachsen.de

M. Morlo

Forschungsinstitut Senckenberg, Abt. Messelforschung,
Senckenberganlage 25, 60325 Frankfurt, Germany
e-mail: Michael.Morlo@senckenberg.de

Introduction

The fossil locality Sandelzhausen in the Northalpine Molasse Basin is known since 1959 and was excavated in several campaigns by the University of Munich together with the Bayerische Staatssammlung für Paläontologie und Geologie (Fahlbusch 1974a, b; Fahlbusch and Gall 1970; Fahlbusch et al. 1972, 1974; Fahlbusch and Liebreich 1999; Fahlbusch 2003). The locality yielded abundant

material of a diverse vertebrate fauna with more than 50,000 objects. Sandelzhausen is late Early or early Middle Miocene in age and belongs to the middle part of Neogene Mammal Biozone MN5 (Daxner-Höck 2003).

More details on the geology and stratigraphy of the locality are given in Moser et al. (2009). Some carnivoran specimens were already published, but partly were wrongly identified. This is indicated in the different sections.

Materials and methods

The carnivores described herein all come from layers B and C of the section (see Moser et al. 2009 this volume for more stratigraphic/geological details), between 25 and 100 cm above the base of the section. All material is housed in the Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany (BSPG). The collection numbers of all specimens start with “BSPG 1959 II,” which is omitted in the following text. Lower teeth are referred to by lower letters, as in “m1”, uppers by capitals, as in “P4”, lower canines as “c inf.” and upper canines as “C sup.”. Measurements were taken with callipers to the closest 0.1 mm. Description of tooth morphology of *Amphicyon* follows Peigné and Heizmann (2003); all others follow Thenius (1989).

The following description focuses on the dental material. Postcranial material is evaluated if the taxonomic assignment was clear. The remaining postcranial material needs further investigation.

Systematic palaeontology

Order Carnivora Bowdich, 1821.

Family Amphicyonidae Trouessart, 1885.

Subfamily Amphicyoninae Trouessart, 1885.

Genus *Amphicyon* Lartet, 1836.

Type species: *Amphicyon major* Blainville, 1841.

Amphicyonidae is a carnivorous family that originated in the Late Eocene and vanished in the Late Miocene. It consists of a diverse group of species with different food preferences from omnivory to hypercarnivory (Viranta 1996). Within the subfamily Amphicyoninae a regular and steady increase in size is noticeable (Ginsburg 1999). Although Lartet mentioned the name “*Amphicyon*” for the first time in 1836, it took a while until a diagnosis was added (for complete history see Kuss 1965). The genus *Amphicyon* is characterized by spacings between their premolars, a single rooted p2, p4 with posterior cusp, a retention of the entoconid on m1, protocone on P4 can be reduced, and an enlarged M2 (Ginsburg 1961; Kuss 1965; Viranta 1996). It was widespread throughout Europe in the Early and Middle Miocene (see NOW) but is also cited from the early Middle Miocene of Africa (Morales et al. 1998).

Amphicyon cf. major Blainville, 1841.

Synonymy list: for complete list see Kuss (1965) and Viranta (1996).

*1841 *Amphicyon major* Blainville: pl. 14.

Material: 8106: right maxillar fragment with alveoli of M1-M2; 8241: upper incisor; 8100: left C sup.; 2222: right C sup.; 2198: right C sup.; 8101: left C sup., strongly worn; 9012: left C sup., strongly worn and crown broken; 2202: right P4 with fourth root below metacone blade (Figs. 1a, 11f–h); 2224: left P4; 2225: right P4, strongly worn; 8099: left M1 (Fig. 1c); 2213: right M1, buccal-posterior root missing, worn (Fig. 11i); 8097: right M1, strongly worn; 8102: right M1, buccal part broken; 16202: left M1; 2226: right M1 (Fig. 1b); 8103: right M1 fragment; 88: right M2; 8220: right M2, buccal root broken; 8098: right M2 (Fig. 11j); 8222: right M3. 8095: right lower jaw fragment with m1 and m2 in place, p4 attached (Fig. 11d); 8096: right lower jaw fragment with alveoli for p2-m3, c inf.

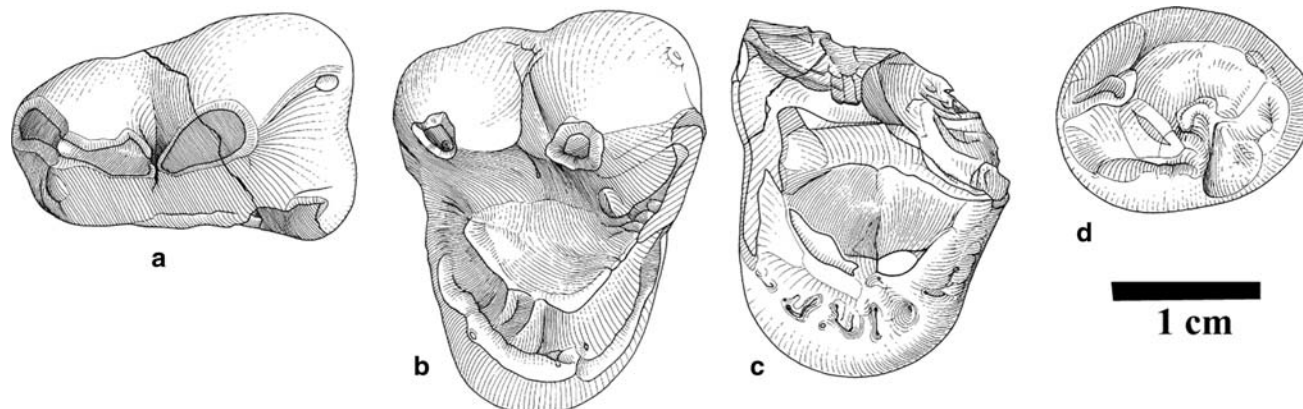


Fig. 1 *Amphicyon cf. major* Blainville, 1841. **a** 2202, right P4; **b** 2226, right M1; **c** 8099, left M1; **d** 2235, left m3; all occlusal views

alveolus is broken; 2200: left lower jaw fragment with m1 and m2 in place (Fig. 11a–c); 2199: right c inf.; 2231: right c inf., crown broken; 8223: left p4; 2227: right m1 with metaconid and talonid; 2236: right m1, only metaconid and talonid preserved; 8224: right m1 fragment; 2214: left m2; 2233: right m2; 8082: left m3 (Fig. 11E); 2235: right m3; 2229: left m3; 2244: right m3; 3938: left m3 fragment; 3717: right femur; 2201: left femur (Fig. 2t–u); 8247: right radius (Fig. 2r, s); 2204: right calcaneus (Fig. 2p, q); 2223: left calcaneus; 8249: right calcaneus; 2203: left astragalus (Fig. 2n, o); 8107: left astragalus (Fig. 2l, m); 8256: right Mc1; 2242: left Mc2; 8258: right Mc4; 2240: left Mc5; 2241: right Mc5; 8159: right Mt1 (Fig. 2d, h); 8169: right Mt2 (Fig. 2c, g, k); 2228: left Mt2; 2243: right Mt3 (Fig. 2b, f, j); 8173: right Mt4 (Fig. 2a, e, i); 8340: right Mt4 fragment; 16218: right Mt4 fragment; 2215: right Mt5; 8257: left tarsale 3; 2205, 2238, 8104, 8152, 8157, 8177, 2239, 8264, 8265, 8266 and 8342: phalange 1; 8163, 8164, 2218, 2245, 2248, 2249, 8349 and 8370: phalange 2; 2220 and 2232: last digit.

Description: From the upper jaw, only single teeth are present. The protocone of P4 is very weakly developed. Especially in 2225 and on 2202 (Fig. 1a) a swelling on the buccal-exterior part indicates a parastyle. The metastyle blade is approximately of the same length as the paracone. 2202 carries a fourth root close to the one under the metastyle root (Fig. 11f, g). The paracone of M1 is more strongly developed than the metacone and the conule show different variations. In 2213 (Fig. 11i), paraconule and metaconule are very small. In 2226 the metaconule is crest-like and the paraconule is closely attached to the paracone (Fig. 1b). The lingual border can be triangular in shape without differentiation (2213) or can be surrounded by numerous enamel folds, which lead to the protocone and give the tooth a more rounded shape (8099, Fig. 1c). In M1, the cingulum on the anterior rim of the paracone does not form a knob at the basal part of the tooth, but extends upwards along the paracone and merges with the antero-posterior crest along the paracone and metacone (2226). 8099 shows an elongated protocone and directly adjacent a nearly equally well-developed metaconule similar to *A. major* from Sansan.

The length-to-width ratio of the M2 (8098) is only slightly wider than the M1. The paracone is larger than the metacone, the protocone is rather weakly developed, and the lingual part is again marked with small enamel folds (Fig. 11j). The M3 is double-rooted (8222) and the anterior-buccal part, the position of the paracone, is a bit larger. In general, the tooth is surrounded by a thick rim with a depression in the middle.

The lower jaw (2200, Fig. 11a–c) still retains an alveolus for a single rooted p1. Unfortunately, the second lower jaw 8095 (Fig. 11d) is damaged at the front and gives no

information about the presence of a p1. Both mandibles show alveoli for p2 and p3, with at most a very small diasteme between the premolars. The p4 (2200) has no anterior cusp and a posterior cusp is close to the main cusp. The whole tooth is asymmetrical and broader at its posterior end. The m1 consists of a paraconid lower than the protoconid and a metaconid which is very close to the protoconid, but does not lean further back than the main cusp; therefore, it is not visible in buccal view. The talonid carries a prominent hypoconid, which is separated from the entoconid by a narrow groove. Paraconid, protoconid, and hypoconid are more or less in line for trenching. In 8095, the enamel of m1 is slightly rugose. The double-rooted m2 has no paraconid; the protoconid and the metaconid are equal in size with the protoconid being placed further forward than the metaconid. The talonid of the m2 is about the same size as the front part of the tooth with a hypoconid on its buccal side and no entoconid in the lingual part. The single-rooted m3 carries a protoconid with a crest leading from the anterior part of the tooth to the posterior end with no indication of a hypoconid. The talonid is basined and may carry two very small cusplets in the middle (8082) or a very small s-like crest (2235). The whole tooth is surrounded by the crest, which extends anteriorly and posteriorly from the protoconid, by a crest coming from the antero-lingual part, extending over the small metaconid and closing the circle through a cingulid on the postero-lingual part of the tooth.

Comparison and distribution: This amphicyonid of Sandelzhausen differs from other contemporary amphicyonid genera of Europe as follows:

Pseudocyon sansaniensis Filhol, 1881 (pl. 10 Figs. 1, 3, 4) has an m1 with the metaconid, which is isolated and placed in a more posterior position. Its m2 is developed in a more sectorial way, with a strong protoconid, a reduced, very lingually placed metaconid, and a trenchant talonid with the hypoconid almost centrally situated.

Ictiocyon was erected on the basis of a single species, *Ictiocyon socialis*, by Ginsburg (1992). It differs from *Amphicyon* and *Pseudocyon* in having the talonids of m1 and m2 larger than the respective trigonids, and paracone and metacone higher in M1.

Pseudarctos was defined by Schlosser (1899). The genus is characterized by the absence of p1, an asymmetrical talonid in which the entoconid is as well developed as the hypoconid, and an enlargement in the m2.

Euroamphicyon was erected by Viranta (1996) as genus, but listed as a subgenus by Ginsburg (1999). According to Viranta (1996) the taxon is characterized by a M2, which is shorter than in *Amphicyon*. Moreover, m1 and m2 are reduced in the inner part (Viranta 1996).

We thus assign the Sandelzhausen amphicyonid to *Amphicyon*.



◀ **Fig. 2** *Amphicyon* cf. *major* Blainville, 1841. **a, e, i** 8173, right Mt4; **b, f, j** 2243, right Mt3; **c, g, k** 8169, right Mt2; **d, h** 8159, right Mt1 (a–d medial; e–h lateral); **l–m** 8107, left astragalus; **l** proximal view, **m** distal view; **n, o** 2203, left astragalus; **n** proximal view; **o** distal view; **p, q** 2204, right calcaneus; **p** proximal view; **q** distal view; **r, s** 8247, right radius; **r** anterior view; **s** posterior view; **t, u** 2201, left femur; **t** anterior view; **u** posterior view

Concerning size, the measurements of the Sandelzhausen material place it between *Amphicyon major* and *A. steinheimensis* (Fraas 1885) (Fig. 3), but still in the lower size range of *A. major* from Sansan (France, MN6). The *Amphicyon* from Sandelzhausen differs morphologically from *A. steinheimensis* and other contemporary *Amphicyon* species of Europe by the following characters: in P4 from Sandelzhausen the protocone is not as strongly isolated as in *A. steinheimensis* or *A. bohemicus* (Schlosser 1899) (Figs. 1a, 11h, 2202); in M1, the paracone is larger than the metacone, the metaconule is more strongly developed than the paraconule, and the buccal border is slightly convex instead of being concave (Fig. 1b, 2226 and Fig. 11i, 2213); the M3 is double-rooted (8222) and not single-rooted as in *A. steinheimensis* and also most specimens of *A. major*. However, the M3 is as reduced as in *A. bohemicus* and *A. steinheimensis*. The p2 and p3 are double-rooted and not single-rooted as in *A. steinheimensis*, the m1 is low crowned, the metaconid is less posterior placed, and the entoconid is smaller.

The lower dentition differs from *A. gutmanni* Kittl, 1891 in having the m1 metaconid not placed more posterior than the protoconid. The hypoconid of *A. gutmanni* is larger and in addition an entoconid is present in that species which is missing in the Sandelzhausen *Amphicyon*. Furthermore, in *A. gutmanni* the lingual margin of the talonid is serrated. *A. bohemicus* is clearly smaller than *Amphicyon* from

Sandelzhausen. *A. giganteus* Schinz, 1825 is defined as different from *A. major* only by its larger size (Ginsburg 1999; Viranta 1996) and thus the material of Sandelzhausen cannot be referred to this species as it is smaller than *A. major*.

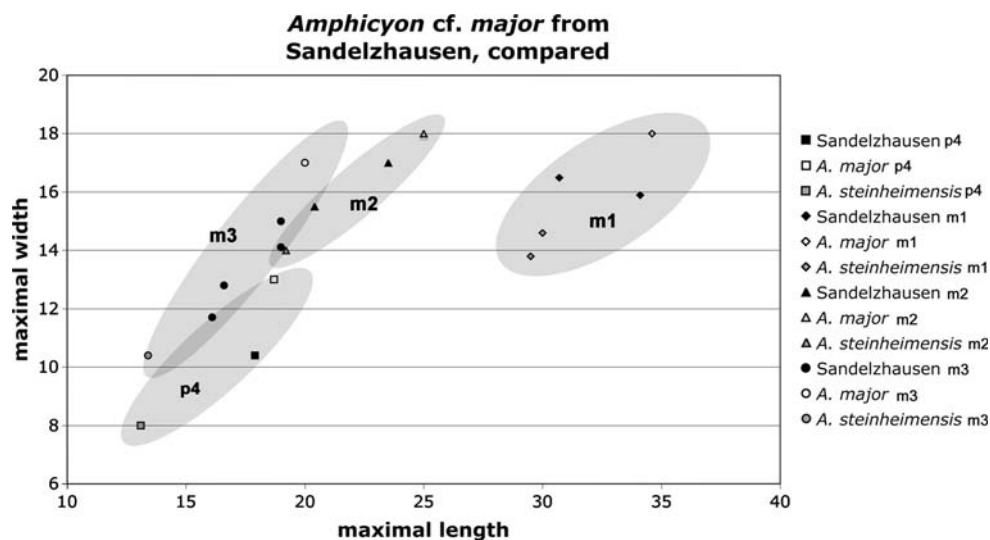
A. major is the best-known *Amphicyon* species in Europe and has a rather large variation in size as well as in morphology. *A. major* Blainville, 1841 ranges in Western Europe from MN4 to MN8 (Ginsburg 1999). The Sandelzhausen material may serve as an example of how the ancestral morphology of *A. major* from Sansan and maybe even *A. steinheimensis* may have looked like. Plesiomorphic characters are (1) the retention of a small and single rooted p1, (2) a double-rooted p2, (3) the lack of diastemes between the premolar alveoli, (4) the small m1 metaconid is not posterior to the protoconid, (5) the lack of a entoconid on the m1 talonid, (6) the poorly differentiated P4 protocone, maybe because the paraconid on m1 is not as developed as in *A. major* or *A. steinheimensis*, and (7) a double-rooted M3, a character not described in *A. major* so far. In these characters the material supports the proposed (Ginsburg 1999) origin of *Amphicyon* from *Cynelos* (Jourdan 1848). It is of course too large to belong to any known *Cynelos*, but the presence of these plesiomorphic characters sheds some doubt on the proposed direct descent of *A. major* from *A. giganteus* (Tables 1, 2).

Genus Pseudarctos Schlosser, 1899.

Type species: *Pseudarctos bavaricus* Schlosser, 1899.

Pseudarctos is a small amphicyonid, lacking p1 and with a very bunodont dentition. The p2–p4 show no accessory cusps. There is a tendency to enlarge the asymmetric talonid in m1 and m2 and to enforce the entoconid while the hypoconid remains low.

Fig. 3 Scatter diagram of p4, m1, m2, and m3 of *Amphicyon* cf. *major* from Sandelzhausen in comparison with *A. steinheimensis* from Steinheim and *A. major* from Sansan. Comparative measurements taken from Heizmann (1973) and Roth (1989). Each point represents an individual specimen



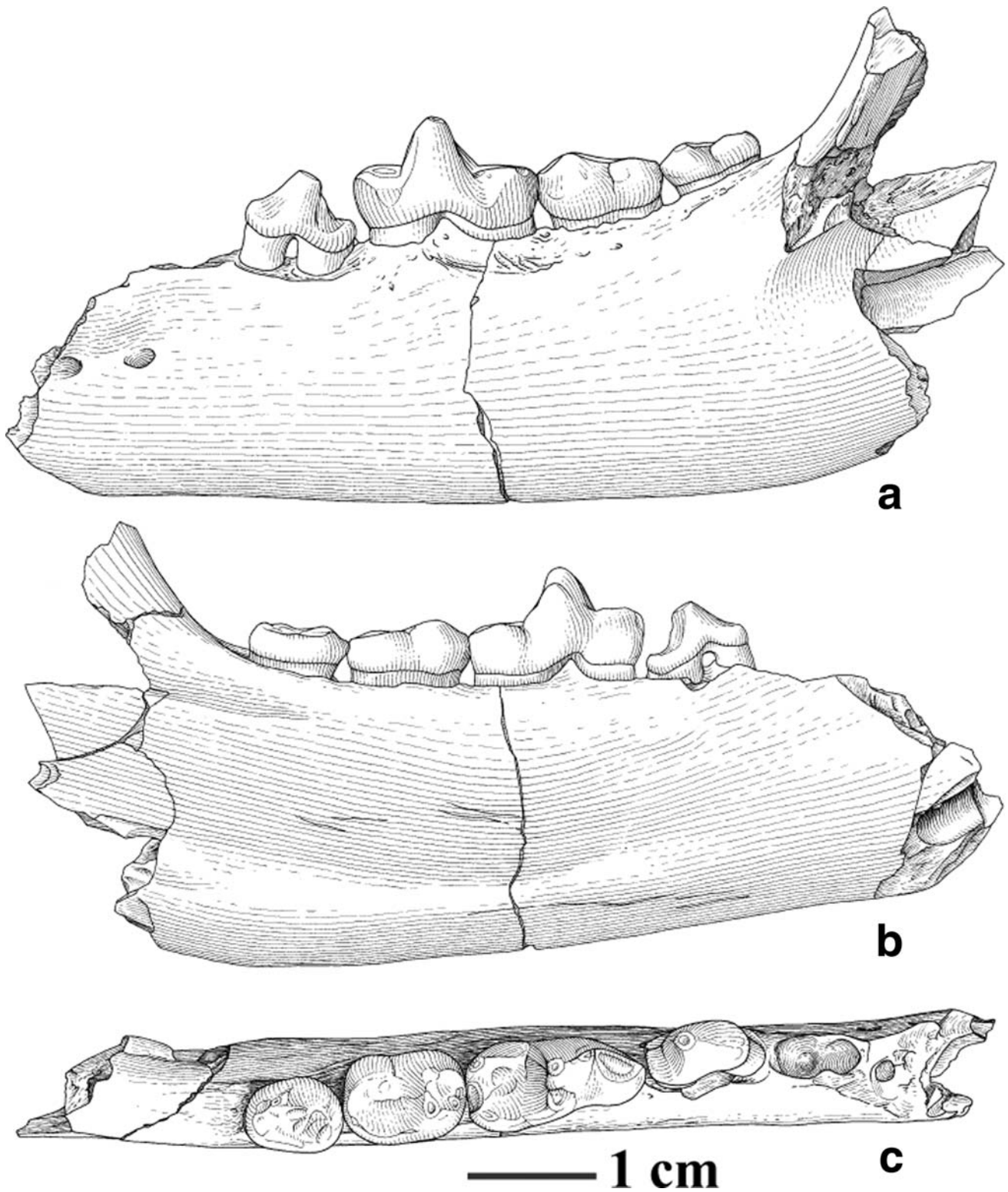


Fig. 4 *Pseudarctos bavaricus* (Schlosser, 1899) (8061: left mandible with alveoli of c inf., p3, p4-m3) from Sandelzhausen. a buccal view; b lingual view; c occlusal view

The genus *Pseudarctos* is thought to decrease in size from MN3 to MN9. Ginsburg (1992) split the genus into two species and lineages: the older and larger one,

Ictiocyon socialis (retaining four lower premolars) from MN3 to MN4 and the younger and smaller *P. bavaricus* (with three lower premolars only) from MN4b to MN9.

Table 1 Teeth measurements (mm) from *Amphicyon major* Blainville, 1841

Coll. no.	Element	Max. length	Max. width	Length metastyle blade	Width metastyle blade	Height
Upper dentition						
2198	Csup dext	22.6	16.7			(86.7)
2222	Csup dext	22.5	17.5			104
8100	Csup sin	27.4	19.7			90.5
8101	Csup sin	22.1	17.4			–
2202	P4 dext	26.6	16.8	25.0	13.5	
2224	P4 dext	29.1	17.7	26.2	13.4	
2225	P4 dext	24.5	14.4	23.2	11.0	
2213	M1 dext	24.9	30.8			
2226	M1 dext	22.8	30.4			
8099	M1 sin	–	21.8			
8097	M1 dext	22.0	25.7			
8102	M1 dext	20.2	–			
16202	M1 sin	–	(21.4)			
8098	M2 sin	17.4	26.6			
8220	M2 dext	18.6	29.7			
88	M2 dext	17.5	(25.8)			
8222	M3 dext	10.7	14.1			
Lower dentition						
	Element	Max. length	Max. width	Trigonid length	Trigonid width	
2199	Cinf dext	20.3	17.8			
8223	p4 sin	19.1	10.4			
8095 md dext	p4	20.5	(8.9)			
2200 md sin	p4	17.9	10.4			
2200 md sin	m1	30.7	16.5	21.2	14.5	
2236	m1 dext	–	17.2			
2227	m1 dext	–	16.2			
8095 md dext	m1	34.1	15.9	21.5	15.5	
8095 md dext	m2	23.5	17			
2214	m2 sin	20.4	15.5			
8082	m3 sin	19.0	14.1			
2229	m3 sin	16.6	12.8			
2235	m3 dext	19.0	15.0			
2244	m3 dext	16.1	11.7			

Specimens in brackets represent broken

Pseudarctos bavaricus Schlosser, 1899.

*1899 *Pseudarctos* sp. Schlosser: 117, pl. 13 figs. 17, 21, 22.

1961 *P. bavaricus* Schlosser—Ginsburg: 52–53, pl. 16, fig. 1.

1992 *P. bavaricus* Schlosser—Ginsburg: 305–310, figs. 1–15.

Material

8060: right mandible fragment with alveoli for p2-p3, p4-m1, posterior part of the talonid broken, and anterior alveole of m2 (Fig. 11t–v); 8061: left mandible fragment with alveoli of c inf., p3, p4-m3 (Fig. 4); 8081: right m1 (Fig. 11w–y); 5295: right m3 with missing roots; 16203:

left m3, damaged; 8238: left M1, buccal-posterior part broken (Fig. 11z).

Pseudarctos bavaricus is the only member of the genus *Pseudarctos* sensu stricto, but was divided by Ginsburg (1992) into three stratigraphically based, subsequent subspecies: *P. b. beaucensis* (MN4b), *P. b. pontignensis* (MN5), and *P. b. bavaricus* (MN6–MN8). The differences mainly concern size and variations of the talonid of m1 and the entoconid of m1. Material from, e.g., Häder (Germany, MN5) and Sansan (France, MN6) was assigned to the third subspecies. This subspecies division is followed here only for reasons of discussion.

Description: Only the alveoli of a single-rooted p2 (8060) and a double-rooted p3 (8060, 8061) are present among the material from Sandelzhausen. In 8060 and 8061,

Table 2 Postcranial measurements (mm) of the teeth from *Amphicyon major* Blainville, 1841

Coll. no.	Element	Total length	Length proximal ant/post	Width proximal lat/med	Length distal ant/post	Width distal lat/med	Diaphysis lateral	Diaphysis medial	Total width
3717	Femur dext	310.0	(91)		70.6		37.4	(24.4)	
2201	Femur sin	325.0	78.8		–		40.3	–	
8247	Radius dext	259.0	40.0	33.4	51.3	30.6	29.4	17.3	38.8
2204	Calcaneus dext	78.0							40.4
2222	Calcaneus sin	77.8							45.0
8249	Calcaneus	–							45.2
8107	Astragalus sin	50.0							43.9
2203	Astragalus sin	45.0					9.4		
8256	Mc1 dext	42.4	15.8	15.6	11.8	13.5	10.9		
2242	Mc2 sin	64.2	19.6	14.1	17.7	17.5	–		
8258	Mc4 dext	–	22.8	19.8	–	–	–		
2240	Mc5 sin	61.2	15.5	18.6	–	–	8.9		
2241	Mc5 dext	61.8	16.1	18.0	15.2	14.5	11.2	9.2	
8159	Mt1 dext	45.4	13.6	18.5	11.0	13.0	10.2		
8169	Mt2 dext	(63.5)	18.9	13	–	16.0	9.8		
2243	Mt3 dext	79.5	21.3	16.6	13.3	16.5	10.4		
8173	Mt4 dext	78.0	20.2	11.9	13.7	17.2	–		
8340	Mt4 dext	–	18.6	12.6	–	–	10.6		
2215	Mt5 dext	71.4	15.4	22.4	13.1	15.4			18.0
8257	Tarsale 3 sin	30.9							

Specimens in brackets represent broken

p4 have no anterior accessory cusps but 8061 carries the remnant of a posterior accessory cusp (Fig. 4). Both p4 have a strong posterior base. The trigonid of m1 (8060, 8061, and 8081) reveals a metaconid, which is higher than the paraconid and placed slightly posteriorly to the protoconid. The talonid of m1 is broader than the trigonid, with a hypoconid not larger than a swelling. The entoconid can be identified as a small enhancement of the lingual talonid border (8081). The lingual side of the talonid displays no rugose enamel or cuspid. As in m1, the m2 has a larger talonid with no distinct cusps. On the trigonid, protoconid and metaconid are of equal size and the paraconid is only a small cusplet on the anterior border of the tooth. In m3, the small protoconid forms a crest on the lingual as well as on the buccal side. The talonid of the m3 narrows into the posterior lingual part. The M1 is slightly asymmetrical with the anterior side being broader than the posterior one. The paracone is well developed, but the part carrying the metacone is broken and can therefore not be compared. No real protocone is developed in M1, only a crest starting on the anterior side of the paracone and extending to the posterior part of the tooth. M1 has a strong lingual cingulum.

Discussion: For the differences from *Amphicyon*, see discussion above. The material from Sandelzhausen differs from *Cynelos* and *Ysengrinia* (Kuss 1965) in having no

accessory cusps on the premolars, a shorter talonid in m1, and a noncutting hypoconid. Additionally, *Cynelos* carries cusplets on the lingual part of the m1 talonid, which is not present among the Sandelzhausen material.

No m1 from Sandelzhausen has a strong hypoconid and the entoconid is not elongated as in *P. bavaricus beaucensis*. The metaconid is placed slightly further back than the protoconid and no cusps are developed in the lingual part of the m1 talonid as is the case in *P. bavaricus bavaricus*. Metrically, the m1 from Sandelzhausen fits well within the size range given for *P. bavaricus*, in particular the subspecies *pontignensis* from the Faluns de l'Anjou, France (Ginsburg 1992) (Fig. 5). The lower m1 from Baigneaux (France) assigned to *P. b. beaucensis*, and from Flinz (Germany) assigned to *P. b. bavaricus* by Ginsburg (1992), are also comparable in size.

Pseudarctos bavaricus is known from only a few remains in Central Europe from MN5 to MN8 (Werdelin 1996) and has been recorded from, e.g., Göriach, Austria (Helbing 1936), Sansan (Ginsburg 1961), and Häder (Schlosser 1899). The material falls within *P. b. pontignensis*. However, based on the few known specimens, it remains unclear whether the subspecies represents a systematically separate taxon or just variability within *P. bavaricus* (Table 3).

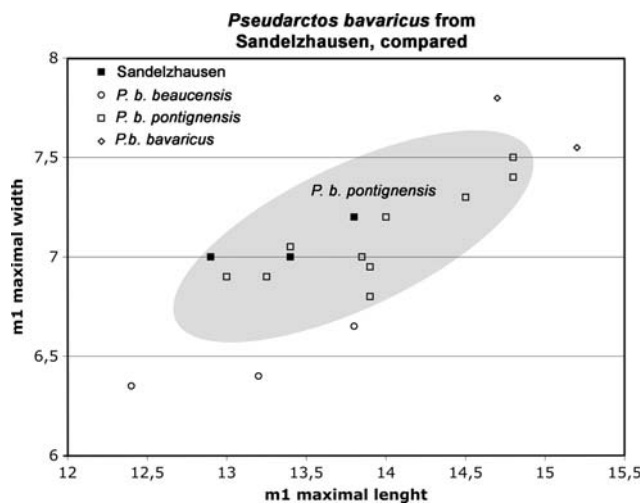


Fig. 5 Scatter diagram of m1 from *Pseudarctos bavaricus*, different subspecies compared [comparative measurements after Ginsburg (1992)]. Each point represents an individual specimen

Table 3 Teeth measurements (mm) from *Pseudarctos bavaricus* Schlosser, 1899

Coll. no.	Element	Max. length	Max. width	Trigonid length	Trigonid width
8238	M1 sin	7.8	12.4		
8060 md dext	p4	8.0	4.1		
8060 md dext	m1	13.4	(7)	8.7	7.0
8061 md sin	p4	8.4	4.5		
8061 md sin	m1	13.8	7.2	9.2	6.5
8061 md sin	m2	9.6	7.1		
8061 md sin	m3	7.5	5.8		
8081 sin	m1	12.9	7.0	8.5	6.4
5295	m3	8.7	6.8		
16203	m3 sin	(7.4)	(6.1)		

Specimens in brackets represent broken

Family Ursidae Gray, 1825.

Subfamily Hemicyoninae Frick, 1926.

Genus *Hemicyon* Lartet, 1851.

Type species: *Hemicyon sansaniensis* Lartet, 1851.

The Hemicyoninae were characterized by Frick (1926) as ursids lacking the M3. Several revisions of the subfamily were undertaken (Hürzeler 1944, Ginsburg 1955, and Ginsburg and Morales 1998). *Cephalogale* (Jourdan 1862) is considered the most plesiomorphic member of the Hemicyoninae (Ginsburg and Morales 1998a, b; Hunt 1998). According to Ginsburg and Morales (1998a, b), the Hemicyoninae consists of the genera *Zaragocyon* (Ginsburg and Morales 1995), *Hemicyon*, and *Dinocyon* (Jourdan 1861) only, while *Plithocyon* (Ginsburg 1955), *Phoberocyon* (Ginsburg 1955), and *Phoberogale* (Ginsburg

and Morales 1995) are placed in a separate subfamily, the Phoberocyoninae. *Phoberocyon* and probably *Phoberogale* show an increasing tendency toward carnivory and are therefore clearly distinct from *Hemicyon*. The separation at the genus level is justified but a differentiation as a subfamily would create unfounded taxonomic complexity. *Plithocyon* and *Hemicyon* are morphologically more similar, which sheds some doubt on the necessity to separate these genera into different subfamilies. We prefer to place all the cited genera into the subfamily Hemicyoninae, thereby omitting the subfamily Phoberocyoninae (Ginsburg and Morales 1998a, b; Nagel 2003).

Hemicyon was established by Lartet (1851) on the basis of material coming from the locality of Sansan. After some taxonomic problems it was re-established by Ginsburg (1955). It is characterized by a strong lingual cingulum on the square-shaped upper molars. The medial crest on the upper molars is derived, being elongated with a reduced protocone. The protocone of P4 is situated close to the paracone.

The other hemicyonine genera (except *Phoberocyon*, *Phoberogale* discussed above) differ as follows: *Dinocyon* is the largest hemicyonine known so far and differs in this respect clearly from the Sandelzhausen material. *Zaragocyon* is smaller in size and has a bigger and nondetached protocone in P4. *Plithocyon* has a small parastyle developed in P4, which is absent in the Sandelzhausen material. We therefore assign the material from Sandelzhausen to the genus *Hemicyon*.

Hemicyon stehlini.

Hürzeler, 1944.

*1944 *Hemicyon stehlini* Hürzeler: fig. 10–12.

“*Hemicyon*” *stehlini* Hürzeler, 1944 has always been referred to *Hemicyon*, but shows dental characters typical for *Plithocyon* (see above) and therefore was assigned to the latter genus by Heizmann (1973), and accepted by Werdelin (1996). Ginsburg and Morales (1998a, b) still used the genus *Hemicyon* in their summary of the European Hemicyoninae and also in Astibia et al. (2000); the authors address the material as *Hemicyon*.

Material: 8032: skull fragment with left alveoli of I2 and I3, C, P1, root fragments of P2-3, P4-M2 and right alveolus for I2, M1-M2 (Fig. 13a); 8084: right M2; 2234: left M2; 8033: right mandible with root fragments of c inf., alveolus of p2, p3-m3 (Fig. 13b–d); 8034: left mandible with p3-m2; 8045: isolated right m1; 8046: left m2; 8047: right m2; 8174: left astragalus; 8171: right astragalus; 8252: left calcaneus; 8180: juvenile right Mc2; 8172: right Mc3; 8192: juvenile right Mc5.

Description: The upper canine is slightly flattened and the P1 is a peg-like tooth. The P3 is small and reduced with a main cusp almost equal in size to the posterior part of the cingulum and no anterior cusp. A small cingulum is visible

at the posterior part. The protocone of P4 is placed as posterior as the paracone. It is small, almost elongated, and detached from the main cusp by a small notch. The metastyle blade is shorter than the paracone (blade 6.6 mm; paracone 11.3 mm); no parastyle is developed. The cingulum is not very strong on its buccal side and not very visible on the lingual side due to of the state of preservation. The P3 is about half the size of P4. M1 is trapezoid, with a paracone better developed than the metacone. The protocone and metastyle form a crest; the cingulum is strong on the buccal side and forms a cusp on its lingual part. M2 is square-shaped with the paracone being the main cusp. Protocone and metastyle form a sinus-shaped crest, but the protocone is not as well developed as in M1. The tooth is surrounded by a pronounced cingulum, which forms a cusp on the anterior side of the tooth.

The p3 is slender with no accessory cusps. The p4 carries a distinct crest at its anterior part and a small accessory cusp on the linguo-posterior side of the main cusp. A cingulid is present but weak on its lingual side. The m1 is elongated with a trigonid (19.4 mm length) more than double the size of the talonid (8.7 mm). The metaconid is posterior to the protoconid. The talonid is formed by a low hypoconid on the buccal side with a very small entoconid and entoconulid on the lingual side. The trigonid of m2 bears a protoconid and a slightly smaller metaconid. No trace of a paraconid is visible. The talonid is elongated and basined. A swelling on its lingual side might represent the remnant of a former hypoconid.

Comparison: Despite the well-preserved material, the question whether *stehlini* belongs to *Plithocyon* or *Hemicyon* is still open. The material from Sandelzhausen shows a mixture of characters. The P4 has an elongated protocone at about the same level as the paracone, the M1 is trapezoid and has no flat inner basin as described by Heizmann (1973) for the *stehlini* specimen from Engelswies (Germany, MN5), and the metaconid on m1 is more posterior than the protoconid. All these characteristics are typical for the genus *Hemicyon*. Additionally, the M1 has a larger paracone than metacone and the M2 is rectangular with a weak developed metacone and the protoconid and metaconid on m2 are of equal size. These characteristics are typical for the genus *Plithocyon* (Heizmann 1973, Ginsburg and Morales 1998a, b). Therefore a clean assignment to one of the two genera is still difficult and we prefer to keep the name given by Huerzeler (1944): *Hemicyon stehlini*. This species is known from France, Germany, and probably from Czech Republic (Huerzeler 1944, Ginsburg and Bulot 1982, Heizmann 1973, Roth 1989, Fejfar et al. 2003).

H. stehlini is intermediate in size between *H. gargan* (Ginsburg and Morales 1998), *H. sansaniensis* (Lartet 1851), and *H. goeriachensis* (Toula 1884), respectively.

The amount of variation of the m2 trigonid concerning development of protoconid and metaconid represents an ancestral feature, similar to the pattern in *H. sansaniensis* and *H. goeriachensis* (Ginsburg and Morales 1998a, b). *H. goeriachensis* is almost equal in size to *H. sansaniensis* and is more common in Central Europe from MN6 to MN9. *H. sansaniensis* is more abundant in Western Europe from MN5 to MN6 (Werdelin 1996, Ginsburg 1999, Nagel 2003).

H. sansaniensis from MN6 (Sansan) is larger and differs in several morphological details. In M2, the protocone is smaller than the metacone. The P4 has a smaller protocone, which is placed further back, while no cusps are developed on the anterior cingulum. In m2, the protoconid is larger than the metaconid while on the Sandelzhausen specimens the two cusps are of equal size. *H. goeriachensis* is interpreted as being more advanced (Heizmann 1973). Its teeth are more elongated due to the weaker cingulids. The protoconid of m2 is smaller than the metaconid. *H. gargan* is the smallest known species of *Hemicyon* to date. The protocone of P4 has a more labial insertion, is more pronounced, while a small crest connects the metacone with the metaconule of M1. *H. mayoralis* (Astibia et al. 2000) from MN4 (Tarazona de Aragón, Spain), the largest species of *Hemicyon* species known so far, differs from the Sandelzhausen specimen in size, in the lack of any antero-lingual crest in P4, and in having M2 oriented less obliquely in relation to the long axis of the tooth row. *Hemicyon teilhardi* (Huerzeler 1944) is larger than *Hemicyon* from Sandelzhausen. Furthermore, the protocone of *H. teilhardi* is situated very far back, a unique character among hemicyonines (Colbert 1939).

H. stehlini is known in Europe from France (Pontlevoy, Baigneaux, Bézian, Pellicahus, Montréal-du-Gers, Travers), Spain (Buñol), Portugal (Quinta da Barbacena, Quinta da Conceicao, Quinta do Pombeiro), and Germany (Engelswies, Stätzling, Georgensgmünd) (Heizmann 1973; Roth 1989). An overview can be found in Ginsburg and Morales (1998a, b). Stratigraphically, the material comes from the lower Middle Miocene (MN4–MN5) (Table 4).

Family Mustelidae (Fischer, 1817) Swainsson, 1835.

Subfamily Guloninae (Gray, 1825) Miller, 1912.

Genus *Ischyriactis* Helbing, 1930.

Type species: *Viverra zibethoides* Blainville, 1842.

Within the large Middle Miocene mustelids of Europe, Ginsburg (1999) distinguishes three basic lineages: *Trochictis*, *Iberictis*, and *Ischyriactis*. The latter is characterized by a round lingual side of M1. Qiu (2003) summarized the stratigraphic occurrence of *Ischyriactis* in Europe from MN3 to MN9. Within the genus *Ischyriactis* three subgenera are often separated: *Ischyriactis (Ischyriactis)*, *Ischyriactis (Laphictis)*, and *Ischyriactis (Hoplectis)* (Schmidt-Kittler 1976, Ginsburg 1999). *I. zibethoides* is referred to the

Table 4 Teeth measurements (mm) from *Hemicyon stehlini* Huerzeler, 1936

Coll. no.	Element	Max. length	Max. width	Trigonid length	Trigonid width
8032 max	M1	17.9	20.1		
8032 max	M2	14.3	18.0		
8032 max	C	12.7	8.5		
8032 max	P1 (?)	7.9	3.0		
8032 max	P4	20.0	10.4		
8032 max	P3				
8032 max	M1	–			
8032 max	M2	14.0	19.0		
8084	M2 dext	17.1	–		
8033 md sin	p3	9.6	4.4		
8033 md sin	p4	12.6	6.4		
8033 md sin	m1	28.2	11.5	19.5	9.9
8033 md sin	m2	17.3	10.6		
8033 md sin	m3	9.9	8.5		
8034 md dext	p3	9.5	4.1		
8034 md dext	p4	(13.1)	6.2		
8034 md dext	m1	27.5	11.4	19.0	9.3
8034 md dext	m2	18.0	11.4		
8045	m1 dext	27.9	11.5	29.6	10.5
8047	m2 dext	17.4	11.6		
8046	m2 sin	17.2	11.8		

Specimens in brackets represent broken

subgenus *Ischyriactis*, *I. mustelinus* to the subgenus *Laphictis* (Crusafont 1972, Heizmann 1973, Roth 1989), and *I. anatolicus* from Çandir (Turkey, MN5) to the subgenus *Hoplictis* (Schmidt-Kittler 1976; Nagel 2003). The latter assignment to the subgenera is followed herein.

Ischyriactis (Ischyriactis) zibethoides (Blainville, 1842).

*1842 *Viverra zibethoides* Blainville: pl. VI fig. 1–15.

1859 *Amphicyon zibethoide* (Blainville, 1842)—Gervais: pl. XXVIII fig. 13.

1891 *Mustela zibethoides* (Blainville, 1842)—Filhol: 98.

1930 *Ischyriactis zibethoides* (Blainville, 1842)—Helbing: 637.

Material: 8246: maxillar fragment with right P3; 8044: left P4 (Fig. 13p–r), right M1 (Fig. 13n), left M1 broken (Fig. 13o); 8080: right P4, protocone missing; 8059: right P4, protocone missing; 8085: left P4, protocone missing; 8072: right M1, layer C; 8073: left M1, layer C; 8083: right P4-fragment; 8037: left lower jaw, most complete specimen, with c-m1, alveolus of m2, layer C (Fig. 13h–j); 8038: left lower jaw, distal part of ramus well preserved, with p1-m1, alveolus of m2 layer B; height of coronoid process 58.3 mm; 8039: right lower jaw fragment with broken roots of p3-p4, m1, alveolus of m2, layer B; 40:

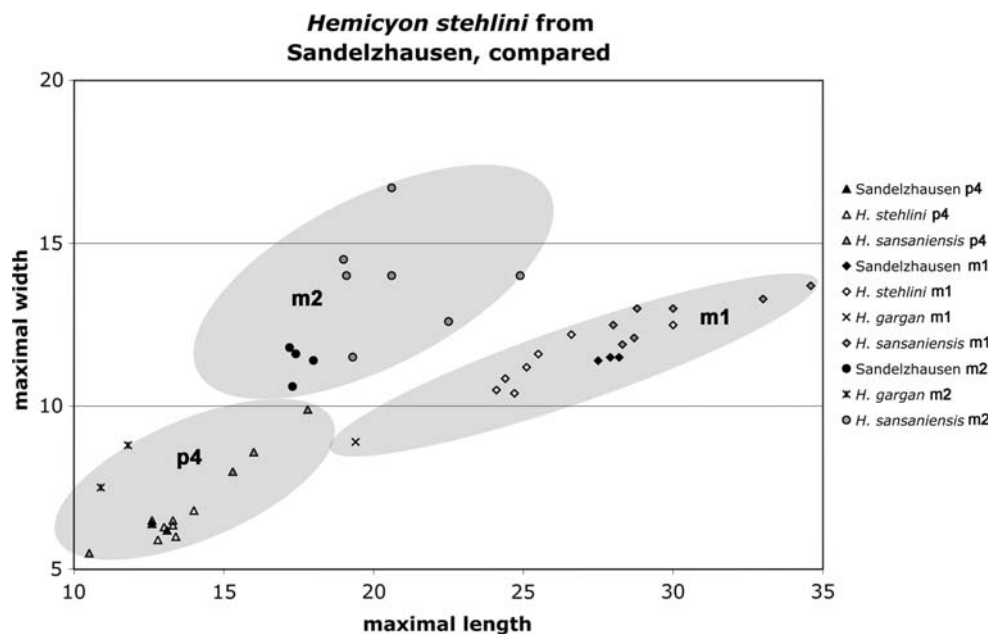
right lower jaw fragment with m1; 8040: left lower jaw fragment with alveolus of p1, p2-m1, layer B (Fig. 13e–g); 8041: right lower jaw fragment with alveoli of c inf. and p1, p2-m1, alveolus of m2; 8042: left lower jaw fragment with p4-m1, alveolus of m2, layer B; 8086: left lower jaw with alveolus of p1, p3-p4, m1 broken; 8043: right lower jaw fragment with broken p3, p4, proximal part of m1 and alveolus of m2; 8049: right lower jaw fragment with p2-p4, layer B/C; 8234: left p4; 8235: left p4; 8149: right astragalus; 8236: right p3. 8254: left astragalus; 8255: left astragalus fragment; 8168: left calcaneus; 8251: left calcaneus; 8353: left calcaneus; 8141: right metatarsal 3; 8343: left metatarsal 3 proximal part.

Description: One mandible is nearly complete (8037), with c-m1 in place and the condylus and most of the coronoid process preserved. The massetric fossa is a deep groove starting with a clear rim ventral to m2. Ventrally, the mandibular ramus is straight.

The premolars are spaced with the wider diastemes between p2 and p3 (1.5–4.2 mm) and the lesser between p3 and p4 (0.5–0.9 mm). As is typical for *Ischyriactis*, p1 is a very small, peg-like, slightly flattened tooth, which is much smaller than p2–4. These increase progressively in size and also progressively add an anterior and posterior cingulid. The first three premolars carry no anterior or posterior cusps. In p2, the main cusp is rotated anteriorly, in p3 it is placed more in the centre, and in p4 the protocone is slightly retrorse. The p4 bears a posterior accessory cusp and is surrounded by a cingulid at its anterior part. The tips of the main cusps in p2–p4 are all blunt and rounded, mostly with little wear; p4 usually shows more wear than the other premolars. All premolars except p1 display a small ridge in the midline.

The length of the m1 trigonid is about two-thirds of the overall tooth length with the protoconid being the highest cusp. The metaconid is distinctly lower than the protoconid. It is as high as the paraconid and placed close to the protoconid. The talonid is low and surrounded by a cingulid. Two different talonid morphologies can be observed among the material from Sandelzhausen. Three molars (8039, 8037, and 8042) have a relatively flat talonid, which is encircled by a well-developed cingulid, extending from the base of the protoconid to the base of the metaconid. Along the midline of the talonid is a noticeable though minor crest (most pronounced in 8037), but no additional cusp such as a hypoconid or entoconid can be observed (Fig. 13h–j). A similar morphology is present in *I. zibethoides* from Sansan [depicted by Filhol (1891): pl. VI], while the material described and depicted by Ginsburg (1961) mainly has a hypoconid. Four other lower molars from Sandelzhausen (8038, 8041, and 8040) show a well-developed cingulid around the talonid and a well-developed hypoconid (40: Fig. 13k–m). All m1 are of

Fig. 6 Scatter diagram of lower dentition of *Hemicyon stehlini* from Sandelzhausen, compared [comparative measurements from Ginsburg (1965) and Ginsburg and Morales (1998)]. Each point represents an individual specimen



similar size; only one lower molar is more massive and larger than the others (40: Figs. 4k–m, 7).

The upper carnassial has a slender, elongated cutting blade. The protocone is placed more lingually and connected to the protocone through a relatively narrow neck. This lingual projection of the protocone is the reason for the large breadth of the tooth, whereas the cutting blade itself is much more slender. The breadth of P4 posterior to the protocone is only about 6–7 mm, compared with 11–12 mm of maximum breadth. The parastyle is developed only as a low tip, formed by the cingulum. It is connected to the protocone by a slight rim.

All preserved M1 are transversely elongated, fairly flat, and display different amounts of wear. Paracone, metacone, the lingual protocone, and the elevated lingual cingulum are about equally pronounced. In the trigon the paracone is predominant. It takes up about three-quarters of the space and is more pronounced than the metacone. The metacone is connected to the paracone by a crest, which is cut by a deep narrow trough. The marked cingulum on the buccal outer rim of the M1 also shows a clear notch between paracone and metacone. Both paracone and metacone show a short and steep decline lingually toward the talon, but there is a narrow, crest-like line connecting paracone and protocone. No metaconule or paraconule is developed (Fig. 6).

Discussion and comparisons: Ginsburg (1999) described an evolutionary sequence from *I. bezianensis* Ginsburg and Bulot, 1982 from Bézian (France, MN4b), to *I. zibethoides* (Blainville 1842) from Sansan (France, MN6) to *I. mustelinus* (Viret 1933) from Steinheim (Germany, MN7) and La Grive-Saint-Alban (France; mostly MN7/8, but including faunal elements from MN5, see below).

The material of *I. (I.) zibethoides* from Sandelzhausen represents the most numerous material of this species from a single locality so far. From Sansan, a good set of mandibles from (*I.*) *zibethoides* were described (Ginsburg 1961; Roth 1989), but only a little is known about the upper dentition. Thus, the Sandelzhausen material allows a better understanding of the variability in size and form of the individual teeth. For the first time two morphological variations of the talonid are described for *Ischyriactis (I.) zibethoides*. The occurrence of this variation is not correlated with a specific stratigraphic layer in the section and thus does not represent an evolutionary difference. Instead, it is interpreted as intraspecific variation. This is corroborated by the otherwise morphological and metrical uniformity of the teeth.

In *Ischyriactis* three evolutionary lines have been recognized as subgenera so far: *Hopliactis*, *Laphiactis*, and *Ischyriactis*. *Hopliactis* was described with a felinoid tendency (Ginsburg 1961; Ginsburg and Morales 1992). *I. (H.) floriancei* (Mayet 1908) was described from Thenay (France, MN5), and *Ischyriactis (H.) anatolicus* (Schmidt-Kittler 1976) is endemic in Anatolia (Nagel 2003). The carnassials tend more toward hypercarnivory, with the protocone of P4 being smaller and not projecting lingually and anteriorly and the crest-like hypoconid of m1 being inserted more centrally on the talonid. Furthermore, the metaconid of the lower molars is higher and more detached from the protoconid. Diastemes between the lower premolars are not present, but these premolars carry posterior cusps. Metrically, m1 of *I. (H.) anatolicus* and *I. (I.) zibethoides* are very similar in length and width, with *I. anatolicus* being slightly smaller (Figs. 7, 8).

Fig. 7 Scatter diagram of lower dentition of *I. (I.) zibethoides* from Sandelzhausen, compared [comparative measurements from Helbing (1930), Ginsburg (1961), Heizmann (1973), and Roth (1989)]. Each point represents an individual specimen

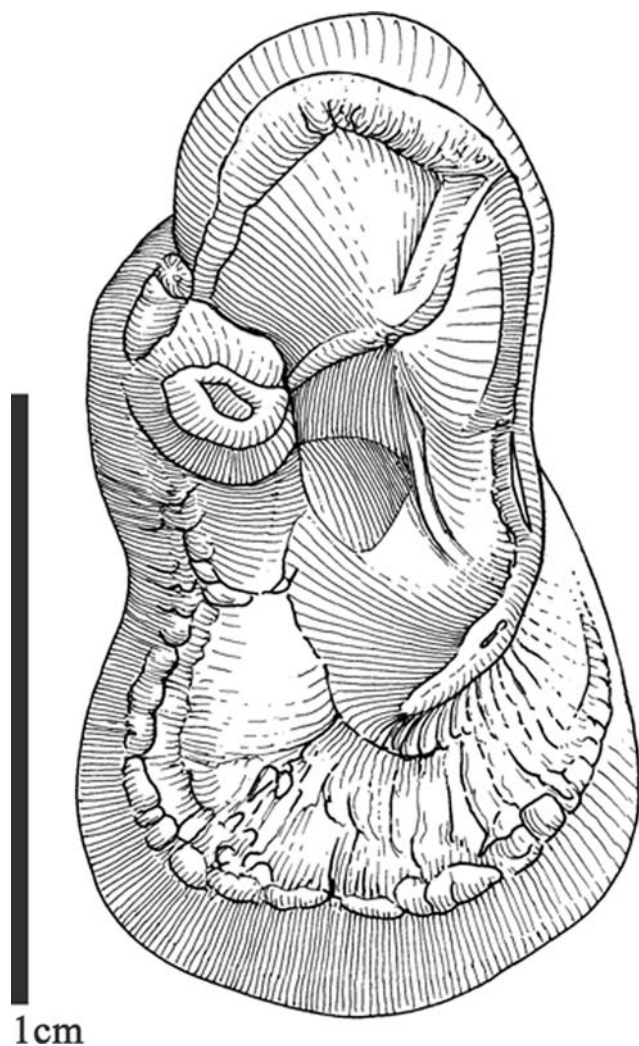
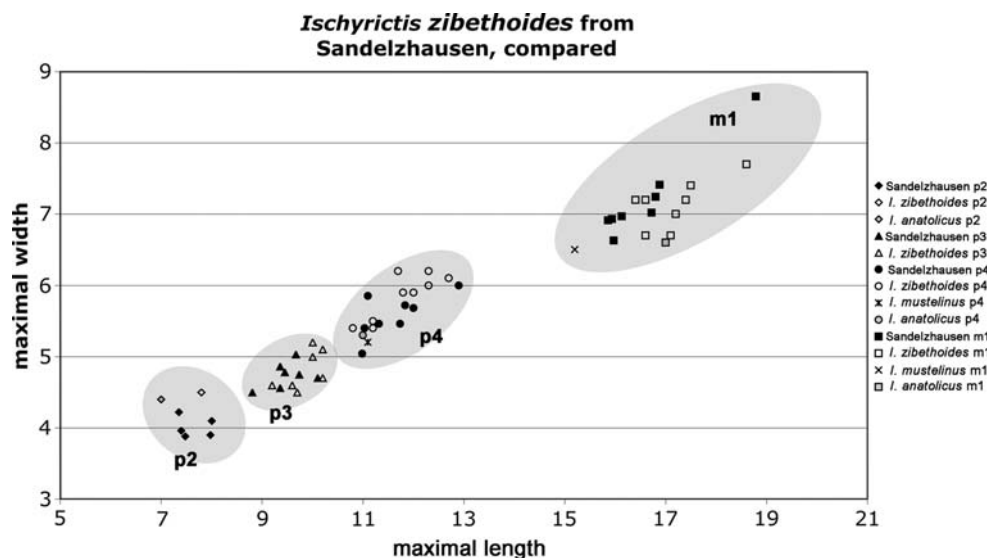


Fig. 8 *Ischyriactis zibethoides* (Blainville, 1842) from Sandelzhausen. 8072: right M1

The subgenus *Laphictis* was erected as a genus (type species *Laphictis mustelinus*) by Viret (1933) from La Grive-Saint Alban (France), but Helbing (1936) placed this genus in the *Ischyriactis* group. Dehm (1950) assigned the material from Winterhof-West to *I. (L.) mustelinus* and reported the missing p1 as an autapomorphy. Ginsburg and Morales (1992) assigned this species to a new genus, *Dehmictis*.

Helbing (1930) noted for *Ischyriactis (L.) mustelinus* from Steinheim a hypoconid, which is steeper lingually than buccally. This is different from *I. (I.) zibethoides* from Sandelzhausen where the hypoconid, if present, is symmetrically shaped. The m1 of *I. (L.) mustelinus* described by Viret (1951) from La Grive-Saint-Alban has a higher talonid than that from the Sandelzhausen material. In *I. (L.) mustelinus* the mandibular teeth are closer together, leaving only a narrow gap between p2 and p3. Also in p4 the second cusp attached to the protoconid seems to be more strongly developed (Helbing 1936, fig. 6). Roth (1989) mentioned three foramina mentalia in contrast to only two in *I. zibethoides*. In general, *I. (L.) mustelinus* is a bit smaller in size (Fig. 7).

I. bezianensis (Ginsburg and Bulot 1982) from Bezian is only known by one upper M1 which bears a metaconule. This is not the case in any Sandelzhausen M1. The specimen from Bezian was not assigned to any of the subgenera but was described as being more similar to the *Laphictis* group by the authors.

Ischyriactis is known from Europe from MN3 to MN9. It also occurs in North America (Qiu 2003). *Ischyriactis (I.) zibethoides* has been recorded from Western Europe (Spain, France, Germany) only, whereas *I. (H.) anatolicus* has been found only in Turkey (Pasalar, Çandır). This might indicate a different geographic distribution of the subgenera *Ischyriactis* and *Hoplictis* (Tables 5, 6).

Table 5 Postcranial measurements (mm) from *Hemicyon stehlini* Huerzeler, 1936

Coll. no.	Element	Total length	Total width	
8174	atragalus sin	42.0	30.0	
8171	atragalus dext	–	(24.5)	
8252	calcaneus sin	53.7	24.2	

Coll. no.	Element	Total length	Length proximal ant/post	Width proximal lat/med	Length distal ant/post	Width distal lat/med	Diaphysis lateral	Diaphysis medial
8180	Mc2 dext	–	15.2	10.1			8.1	6.2
8172	Mc3 dext	74.7	15.6	12.4	12.2	14.9	8.4	7.2
8192	Mc5 dext	–	16.8	13.6			8.8	7.2

Specimens in brackets represent broken

Genus *Martes* Pinel, 1982.

Type species: *Martes fiona* (Linneum, 1758).

Martes cf. munki Roger, 1900.

*1900 *Martes munki*—Roger: pl. 3 fig. 3.

1933 *Martes munki* Roger—Viret: 15, pl. 1 fig. 10–13.

1951 *Martes munki* Roger—Viret: 57, pl. 2 fig. 23.

Material (measurement in mm, length:width): 8087: left mandible with p2 (3.8:2.1), p3 (4.7:2.3), alveoli of p4, m1 (8.4:3.8) and m2 (3.3:3.2); 8074: fragment of right mandible with m1 (9.5:4.1) and alveolus of m2; 8108: isolated left m1 (9.5:4.1); 8088: right mandible with p3 (4.8 mm:2.3 mm), p4 (5.8 mm:2.7 mm), alveolus of anterior part of m1 and m1 talonid; 8133: fragment of left mandible with damaged p2, p3 (5.5:2.2); 8078: fragment of right maxilla with alveolus of P1, P2, fragment of P3, anterior alveolus of P4; 8112: isolated left P3 (5.0:2.1).

Description and comparisons: The specimens fit extremely well with the description of the species by, e.g., Stehlin and Helbing (1925), Viret (1951), and Ginsburg and Bulot (1982). It differs from the similar *M. sainjoni* (Mayet 1908) by a relatively long talonid. All Sandelzhausen specimens, however, are about 5–10% larger than previously described material of *M. munki*. We therefore refer the Sandelzhausen record only tentatively to *M. munki*.

Discussion: *Martes munki* is well known from MN4–5 in Europe (NOW) but also occurs in La Grive (France, traditionally placed in MN7/8, but see remarks below), Häder (Germany, MN5), and Pontlevoy (France, MN5) (Roger 1900; Stehlin and Helbing 1925; Viret 1951).

Family Mephitidae (Bonaparte, 1845).

Genus *Proputorius* Filhol, 1891.

Type species: *Proputorius sansaniensis* Filhol, 1891.

Proputorius pusillus (Viret, 1951).

*1951 *Martes pusilla* Viret: 58–60, fig. 11–13, pl. 2 fig. 24–25.

Material: 8136: fragment of right mandible with m1 (5.2 mm:2.2 mm) and alveolus of m2. A couple of very

small premolars also belong to the realm of Sandelzhausen carnivorans, but their unspecialized morphology does not allow an assignment, even if they may belong to *P. pusillus*, if only judging by size.

Description: In the very small m1, the trigonid consists of the dominant protoconid, the paraconid, which reaches about two-thirds of the height of the protoconid, and a small metaconid, which is placed slightly further back than the protoconid, from which it is separated by a little notch. The carnassial blade reaches the same height as the protoconid throughout its length. A short carnassial notch is developed. The talonid reaches a length of 2.0 mm. It is dominated by the hypoconid and has a little wall developed at its posterior and lingual margin which creates a very shallow basin. Cingulids are completely missing.

Discussion: This tiny *Martes*-like specimen differs from most other Middle Miocene musteloids (including *Martes munki*) by its small size. The only taxon of comparable size and morphology is *P. pusillus* (Viret 1951, figs. 11–13), even though the carnassial blade of the holotype does not extend to the same height as the protoconid but slopes down posteriorly. This difference, however, is caused by the high abrasion the holotype underwent, while the Sandelzhausen tooth is rather fresh. Besides size, the m1 differs from the slightly larger *Martes delphinensis* Depéret, 1892 in having the metaconid separated from the protoconid by a notch and having a relatively longer talonid. These characters also allow the separation of the taxon from Mustelidae and a placement into the Middle Miocene mephitid genus *Proputorius*. The holotype was described from La Grive-Saint-Alban (France), which generally is regarded to be MN7/8 in age (e.g., Ginsburg 1999). The presence of the gigantic hyaenodontid *Hyainailouros* and the gulonine *Martes munki* (see below), however, indicates that faunal elements of MN5 are present in the assemblage of La Grive as well. The occurrence of *P. pusillus* in MN5 of Sandelzhausen is therefore no surprise.

Suborder Feliformia Kretzoi, 1945.

Table 6 Teeth measurements (mm) from *Ischyriactis (I.) zibethoides* (Blainville, 1842)

Coll. no.	Element	Total length	Total width	Length metastyle blade	Width metastyle blade	
Upper dentition						
8236	P3 dext	11.5	6.5			
8044	P4 sin	6.5	11.0		6.6	
8044	M1 dext	9.0	15.5			
8059	P4 dext	14.0	7.9		4.6	
8080	P4 dext	14.9	–		6.5	
8083	P4 dext	(13.2)	–		6.4	
8085	P4 sin	16.0	–		6.3	
8073	M1 sin	7.6	14.4			
8072	M1 dext	9.1	16.3			
Lower dentition		Total length	Total width	Trigonid length	Trigonid width	Height
8037 md sin	p1	4.1	2,7			
8037 md sin	p2	7.4	4.0			5.6
8037 md sin	p3	9.4	4.9			5.1
8037 md sin	p4	11.3	5.5			6.9
8037 md sin	m1	15.9	6.9	10.3	6.2	8.9
8038 md sin	p1	3.2	3.0			3.3
8038 md sin	p2	7.5	3.9			4.7
8038 md sin	p3	9.4	4.6			5.0
8038 md sin	p4	12.0	5.7			4.7
8038 md sin	m1	16.8	7.2	11.3	6.2	8.2
8039 md dext	m1	16.7	7.0	12.0	5.9	7.4
8040 md sin	p2	7.4	4.2			4.3
8040 md sin	p3	9.7	5.0			5.3
8040 md sin	p4	11.1	5.9			6.5
8040 md sin	m1	16.1	7.0	10.9	6.3	9.0
8041 md dext	p2	7.9	3,9			4.3
8041 md dext	p3	9.5	4.8			5.0
8041 md dext	p4	11.8	5.7			6.6
8041 md dext	m1	16.9	7.4	12.1	5.9	8.2
8042 md sin	p4	11.0	5.0			5.4
8042 md sin	m1	15.9	6.6	10.9	6.0	6.7
8049 md dext	p2	8.0	4.1			
8049 md dext	p3	10.1	4.7			
8049 md dext	p4	12.9	6.0			
8086 md sin	p3	9.7	4.8			4.9
8086 md sin	p4	11.8	5.6			6.2
8086 md sin	m1	–				
8043 md dext	p3	–				
8043 md dext	p4	11.7	5.5			6.3
8043 md dext	m1	–				
40 md	m1 dext	18.8	8.7	13.2	6.9	8.4
8048	p3 sin	8.8	4.5	–		
8048	p4 sin	11.0	5.4			
8048	m1 sin	15.9	6.9	8.2		

Family Viverridae (Gray, 1825).

Genus *Leptoplesictis* Major, 1903.

Type species: *Leptoplesictis aurelianensis* (Schlosser, 1888).

Not many differences can be found between the extant *Herpestes* and *Leptoplesictis* (Major 1903), therefore this genus was not used for quite some time. Schmidt-Kittler (1987) re-established *Leptoplesictis* to distinguish between the fossil and the recent forms in his work about African carnivores. He described differences in the morphology such as a lower trigonid on m2 and higher anterior accessory cusps on p3 and p4. The details of these differences in the three fossil species are listed in Roth (1988).

Leptoplesictis* cf. *aurelianensis (Schlosser, 1988).

*1988 *Stenogale aurelianensis*—Schlosser: 153.

1907 *Stenogale aurelianensis* Schlosser—Stehlin: 526.

1908 *Stenogale aurelianensis* Schlosser—Stehlin: 223, fig. 72.

1925 *Herpestes aurelianensis* Schlosser—Stehlin & Helbing: 59, fig. 14.

1987 *Leptoplesictis* Schlosser—Schmidt-Kittler: 105.

1987 *Leptoplesictis aurelianensis* (Schlosser)—Roth: 175, fig. 137–138.

1988 *Leptoplesictis aurelianensis* (Schlosser)—Roth: 335, fig. 1–2.

Material: 8125: left isolated fragment of P4; 8146: left isolated fragment of P4; 9031: left M1 (2.9 mm:5.5 mm); 8132: isolated crown of m1 (length:width = 5.6 mm:2.2 mm).

Description and comparison: The M1 has a triangular shape with a pointed protocone, a well-developed paracone and metacone. The parastyle is very distant from the paracone and therefore the tooth seems elongated and slender. On the P4, only the posterior half is preserved with the paracone and the metastyle. A strong cingulum is developed on the buccal side. The lower carnassial consists of a high trigonid, where the protoconid is distinctly higher than the paraconid and the metaconid is the smallest cusp leaning posteriad. The talonid is much lower and narrower. The worn hypoconid is at the posterior end and the entoconid is very low.

Size and development of the talonid of m1 are typical for *Leptoplesictis*. In other Viverridae such as *Viverrictis* or *Jourdanictis* the talonid is characterized by three cusps, the entoconid being much larger than the other two. The material from Sandelzhausen is rather small and slender. The morphology of the talonid of m1 is similar to *aurelianensis* from La Grive (France, MN7/8) and Petersbuch 2 (Germany, MN4).

Roth (1988) revised the *Leptoplesictis* material and recognized three species: *L. aurelianensis* (Schlosser), *L. filholi* (Gaillard), and *L. atavus* (de Beaumont). *Leptoplesictis filholi* is characterized by its greater tooth length

but in general is smaller in size (Roth 1988; Viret 1951). In contrast to *aurelianensis*, in *L. atavus* the trigonid of m1 is stouter, the metaconid placed more anteriorly, and the talonid cusps are higher.

Leptoplesictis aurelianensis is rather rare and was known only from Spain (Hostalets de Pierola, MN7/8), France (La Grive Saint-Alban, MN7/8; Sansan, MN6; Vieux-Collognes, MN5), and Germany (Petersbuch 2, MN4; Stein/Rhein, MN6).

Family Felidae Gray, 1821.

Subfamily Felinae Trouessart, 1885.

Genus *Pseudaelurus* Gervais, 1850.

Type species: *Pseudaelurus quadridentatus* (Blainville, 1842).

Gervais (1850) erected the new genus *Pseudaelurus* for the Sansan material, while Ginsburg (1961) created the generic name *Sansanosmilus* for the barbourfelid remains from this locality to clarify the systematics of the hypercarnivorous taxa from the French MN6 reference site. The history of the correct assignment of the type material from Sansan was first summarized by Heizmann (1973) and later extended by Rothwell (2003) in his revision of North American *Pseudaelurus*. *Pseudaelurus* is known in Europe from MN3a to MN10 (Ginsburg 1999; NOW), with *P. cf. lorteti* (Gaillard 1899) from the Middle Sinap formation representing the last occurrence. However, if the smallest species, *P. turnauensis* (Hoernes 1882), is assigned to the subgenus *Schizailurus* (Viret 1951) (see Morlo 1997 for the most recent discussion on this topic), *Pseudaelurus* was present in Europe from MN4 to MN10.

Pseudaelurus romieviensis Roman and Viret, 1930.

1908 *Pseudaelurus quadridentatus*, Blainville—Mayet: 24.

*1930 *P. quadridentatus*, Blainv. mutation *romieviensis* Roman and Viret: 19–23, pl. II fig. 4–7 (Fig. 9).

1973 *Pseudailurus romieviensis*, Roman & Viret—Heizmann: 1–95, fig. 15b.

Material: 8050: right mandible with c inf., alveoli for p3, p3 with broken main cusp, m1 (Fig. 11q–s); 8052: left mandible with c inf., p3, p4 lingual side damaged, m1 (Fig. 10); 8209: right mandible fragment with m1 (Fig. 11k–m); 16219: left maxillar fragment with Csup., P2–P4; 8129: left maxillar fragment with P4 and alveoli of P3 (Fig. 11n–p); 8062: right cinf.; 8140: left P3 anterior part missing; 8237: left P4, only anterior part with protocone preserved; 8056: right P4, protocone broken; 8233: left P3.

Description and comparisons: On both lower jaw fragments the foramina mentalia are under the diasteme and under the posterior root of the p3. 8052 has a very small gap between the lower canine and p3 (7 mm). No alveolus of a p2 can be verified due to the poor condition of the mandible, but 8050 presents a tiny trace of an alveolus.

Fig. 9 Scatter diagram of upper dentition of *Hemicyon stehlini* from Sandelzhausen, compared [comparative measurements from Ginsburg (1965) and Ginsburg and Morales (1998)]. Each point represents an individual specimen

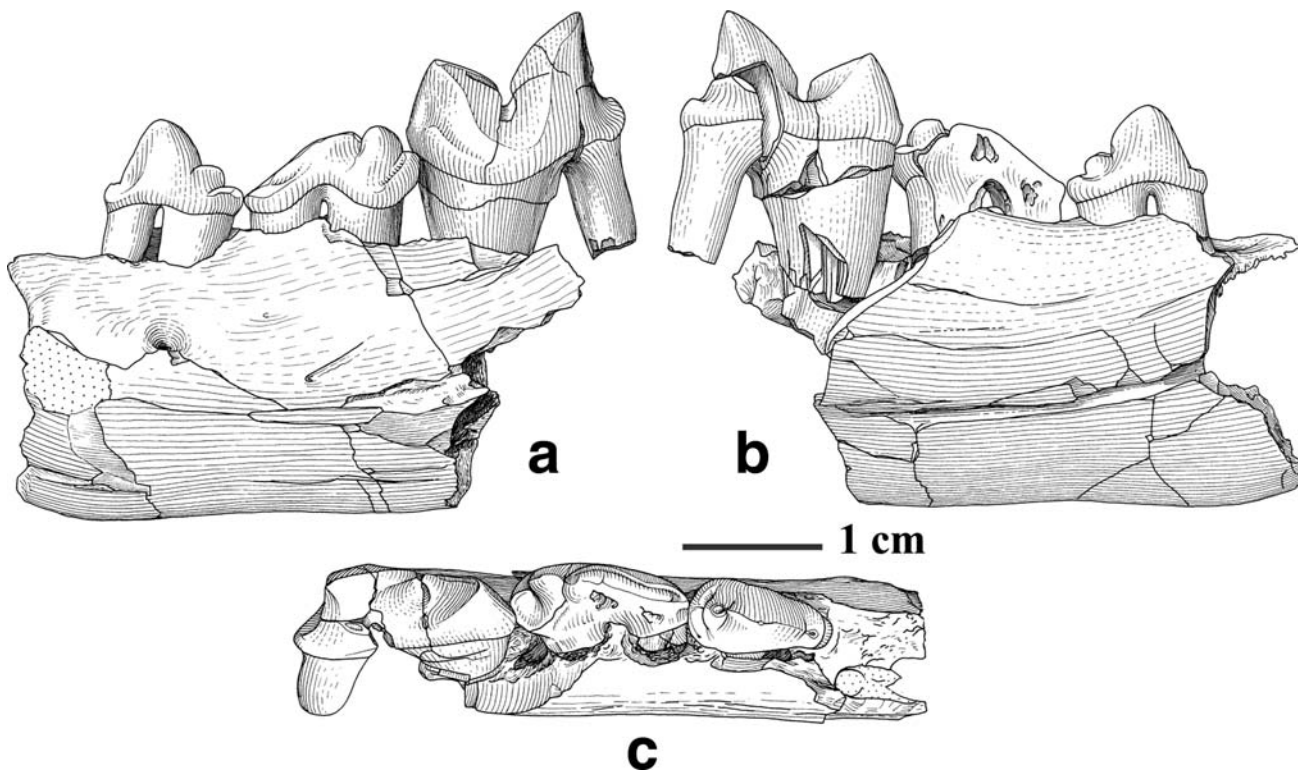
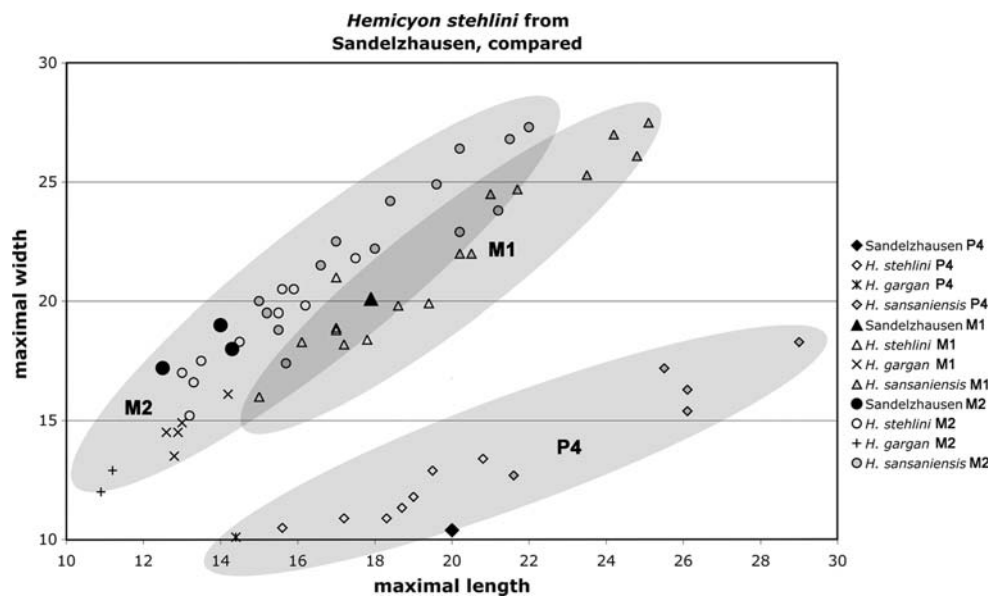
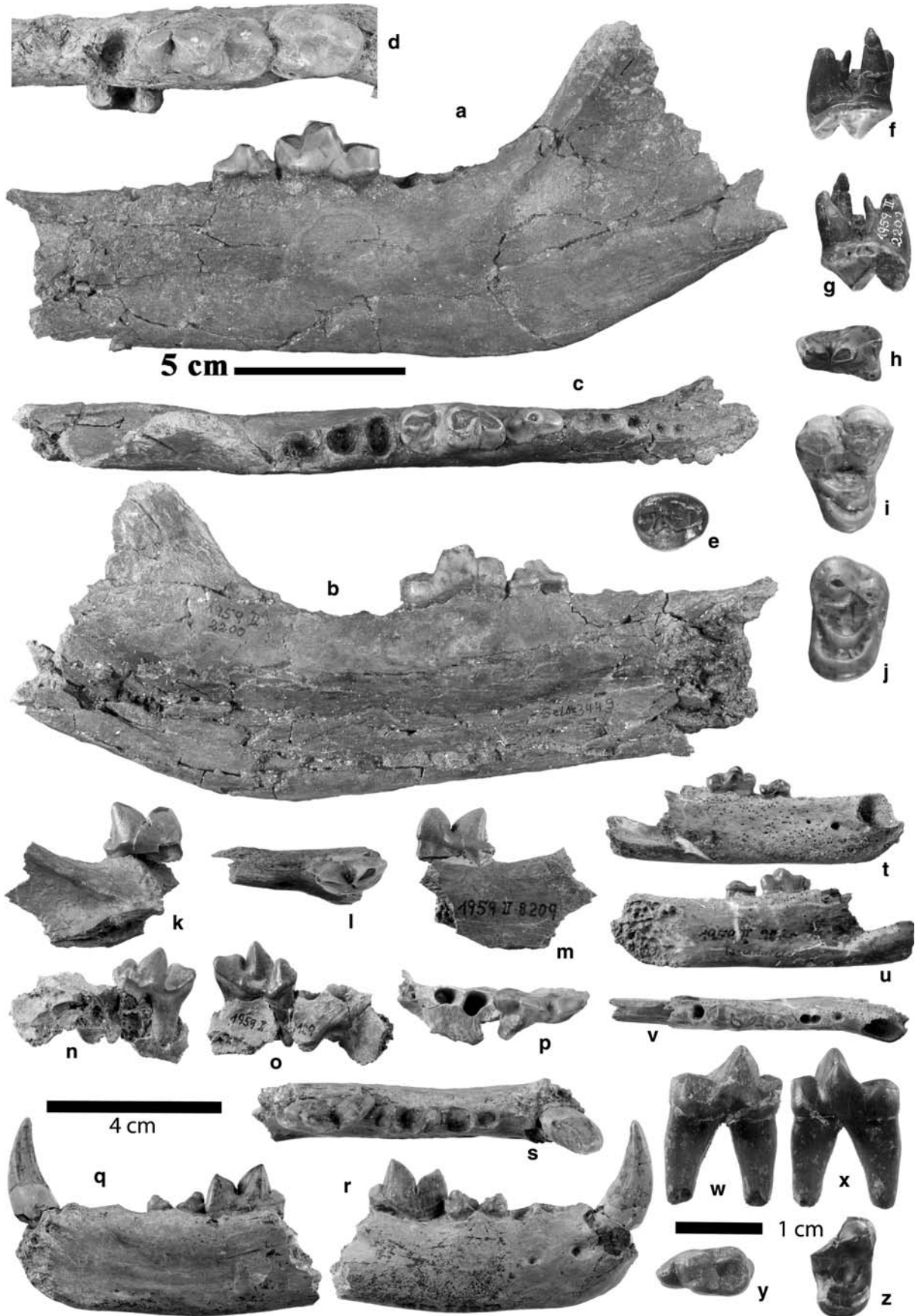


Fig. 10 *Pseudaelurus romieviensis* Roman and Viret, 1930: 8052. **a** Buccal view, **b** lingual view, **c** occlusal view

Therefore it is impossible to know whether a p2 was developed in 8052 or not.

The p3 is only preserved in 8052 and has a small anterior cusplet and posterior cusp as well as a cingulid specially developed at its posterior end. The main cusp of p4 is broken in 8050 but a small anterior cusp and a strong posterior cusp are still visible. The latter is also preserved

in 8052 where the lingual part is damaged. Posteriorly, the tooth displays a strong cingulid. The m1 is well preserved in 8050, 8052, and 8209. It overlaps the p4 slightly. The protoconid is taller than the paraconid; the metaconid is much reduced and blends into an abridged talonid. The talonid is very small in 8209 and 8052, but a bit larger in 8052. The P3 has no anterior cusp but a well-defined



◀ **Fig. 11** a–j *Amphicyon* cf. *major* (Blainville, 1841); a–c 2200, left mandible with p4–m1; a buccal view, b lingual view, c occlusal view, d 8095, right mandible with m1–m2, occlusal view, e 8082, left m3, occlusal view, f–h 2202, right P4, f buccal view, g lingual view, h occlusal view, i 2213, right M1, occlusal view; j 8098, right M2, occlusal view, k–s *Pseudaelurus romieviensis* Roman and Viret 1930, k–m 8209, right mandible fragment with m1, k buccal view, l occlusal view, m lingual view, n–p 8129, left maxillar fragment with P4, n buccal view, o lingual view, p occlusal view, q–s 8050, right mandible with p4–m1, q lingual view, r buccal view, s occlusal view, t–z *Pseudarctos b. bavaricus* (Schlosser 1899), t–v 8060, right mandible with p4–m1, t buccal view, u lingual view, v occlusal view, w–y 8081, right m1, w buccal view, x lingual view, y occlusal view, z 5295, right m3, occlusal view

posterior one and a strong posterior cingulum. The upper carnassial carries a strong slightly trenching protocone, which is implanted further forward than the parastyle. The parastyle is larger than the protocone but no preparastyle is developed. The paracone is high and of the same size as the metastyle blade.

The specimen differs from the similarly sized barbourfelid *Prosansanosmilus eggeri*, known from Sandelzhausen as well (see below), in lacking a preparastyle in P4, no metaconid present in m1, and lacking a flange.

Discussion: Heizmann (1973) revised the European *Pseudaelurus* and accepted four species based on an increase in size: *P. turnauensis*, *P. lorteti*, *P. romieviensis*, and *P. quadridentatus* and two different lineages. One is the *P. romieviensis*–*P. quadridentatus* lineage and the other leads from *P. turnauensis* to *P. lorteti*. However, Morlo (1997) argued for a close relationship of “*P.*” *turnauensis* to *Felis attica*, which would make *P. turnauensis* paraphyletic—the main argument to place it into *Schizailurus* (de Beaumont). While the African specimens all are summarized as *P. turnauensis* (Thomas et al. 1982), most of the Asian and North American forms are

described as different species (Cao et al. 1990; Wang et al. 1998; Rothwell 2003).

P. turnauensis is the smallest and earliest *Pseudaelurus* species. It may have p2 and the m1 metaconid completely reduced.

In *P. lorteti* the mental foramens are placed under the diasteme and under the anterior root of p3. The buccal part of the tooth is somewhat rugose and the p2 is either very reduced or lost. In p3 and p4 the main cusp is lower in comparison with *P. turnauensis* and *P. romieviensis*. Both premolars carry an anterior cusp as well as a posterior one. In m1, the paraconid is lower than the protoconid, the metaconid is small, and the talonid can be slightly or very reduced. In general it is intermediate in size between *P. turnauensis* and *P. romieviensis*.

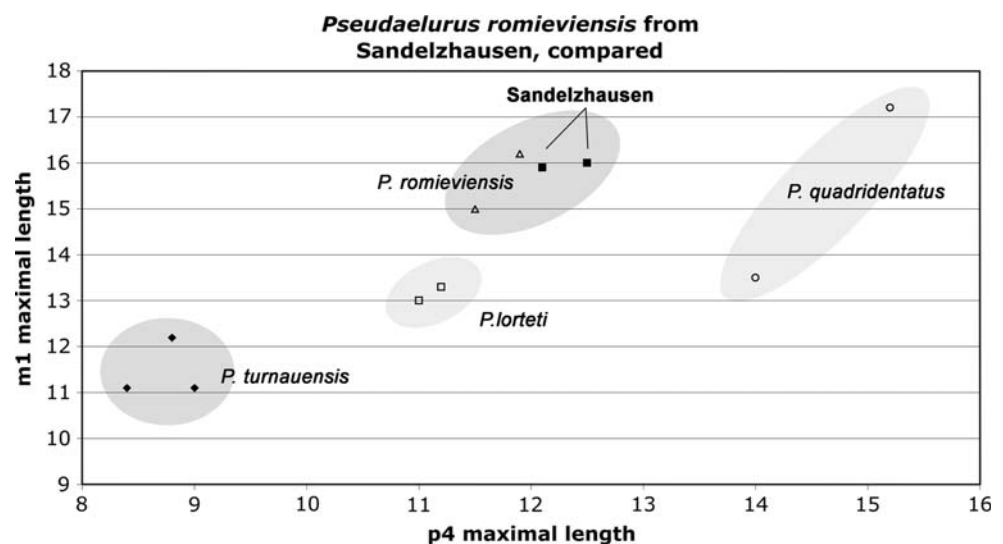
Pseudaelurus romieviensis has high premolars with an anterior cusp only in p3. In m1, the protoconid is higher than the paraconid, the metaconid already small and placed further back, with the talonid built as a cutting edge. In P4 of *P. romieviensis*, the protocone is the anteriormost part of the tooth and clearly detached. A cingulum can be found in the anterior buccal part, but no cusp is developed.

On *P. quadridentatus* the foramina mentalia are under the diastemes and under the posterior root of p3. The p4 is relatively longer than in all other species of *Pseudaelurus* (Fig. 12). The m1 has protoconid and paraconid of almost equal height and metaconid and talonid very reduced. In P4, the anterior cingulum is stronger while the preparastyle is smaller and the protocone is lower.

In *P. quadridentatus* the m1 overlaps the p4 slightly, the protoconid is a bit wider developed than the paraconid, and the metaconid is more reduced than in all the other *Pseudaelurus* species and almost a part of the talonid.

In *P. romieviensis*, the tooth dimensions are smaller than in *P. quadridentatus* and the mandible is less robust.

Fig. 12 Scatter diagram of the length of m1 versus length of p4 of different *Pseudaelurus* species. Comparative measurements were taken from Roman and Viret (1930), Heizmann (1973), and Ginsburg and Bulot (1982). Each point represents an individual specimen



No p2 (p1) is reported so far. The p3 bears a small and p4 a distinct posterior cusp. Additionally, both teeth have a cingulid, which is well developed posteriorly, and a main cusp higher than in *P. quadridentatus*. The protoconid on the m1 is higher than the paraconid and therefore the angle between the two cusps is narrower than in *P. quadridentatus*. The metaconid is strongly reduced and is part of the talonid, which is not yet as small as in *P. quadridentatus*.

The size of the mandible and teeth as well as the short diasteme put the material from Sandelzhausen into the *P. romieviensis* group (Fig. 12). The p3 has a high main cusp and the p4 has a distinct posterior cusp. Unfortunately, the main cusp of both preserved p4 is broken (8050, 8052), so nothing can be said about the height of this tooth. The *P. romieviensis*–*P. quadridentatus* line is characterized by an increase of the p4 in comparison with m1. The measurements of the length of p4 compared with the length of the m1 show strong similarities to *P. romieviensis* (Fig. 12). The protoconid on m1 is higher than the paraconid. The metaconid is very reduced and probably only visible as a part of the trenching talonid of 8050.

Distribution: *P. romieviensis* is known so far from France: Chevilly (MN4), La Romieu (MN4), Baigneaux-en-Beauce (MN5), Bézian (MN4), from Spain: Els Casots (MN4), and now from Sandelzhausen (MN5). Heizmann (1973) discussed also one specimen from Häder as a possible *P. romieviensis*, which was added by Ginsburg (1999) to his summary about the European *Pseudaelurus quadridentatus*. Based on the measurements and morphological details, though, it is reasonable to follow Heizmann in this matter. *P. romieviensis* is only known from Europe so far and only from MN4 to MN5, when it probably gave way to the next evolutionary step, *P. quadridentatus* (Table 7).

Family Barbourfelidae (Schultz et al. 1970) sensu Morlo et al. 2004.

Genus *Prosansanosmilus* Heizmann, Ginsburg, & Bulot, 1980.

Type species: *Prosansanosmilus peregrinus* Heizmann, Ginsburg, & Bulot, 1980.

Prosansanosmilus eggeri Morlo, Peigné, and Nagel, 2004.

1996 *Pseudailurus* sp.—Fahlbusch and Liebreich: 30, fig. 34b.

*2004 *P. eggeri* Morlo, Peigné, and Nagel: 45–50, fig. 1–3.

Material: 8051: right mandible with p3-m1 (holotyp); 11.553: left mandible fragment with p4-m1; 8058: right p3; 8053: fragment of right mandible with distal part of p3, p4-m1; 8054: fragment of left mandible with broken p4, m1; 8057: isolated fragment of left p4. 8058: isolated p4; 9041, fragment of left mandible; 8055: left maxillar fragment with P3-P4.

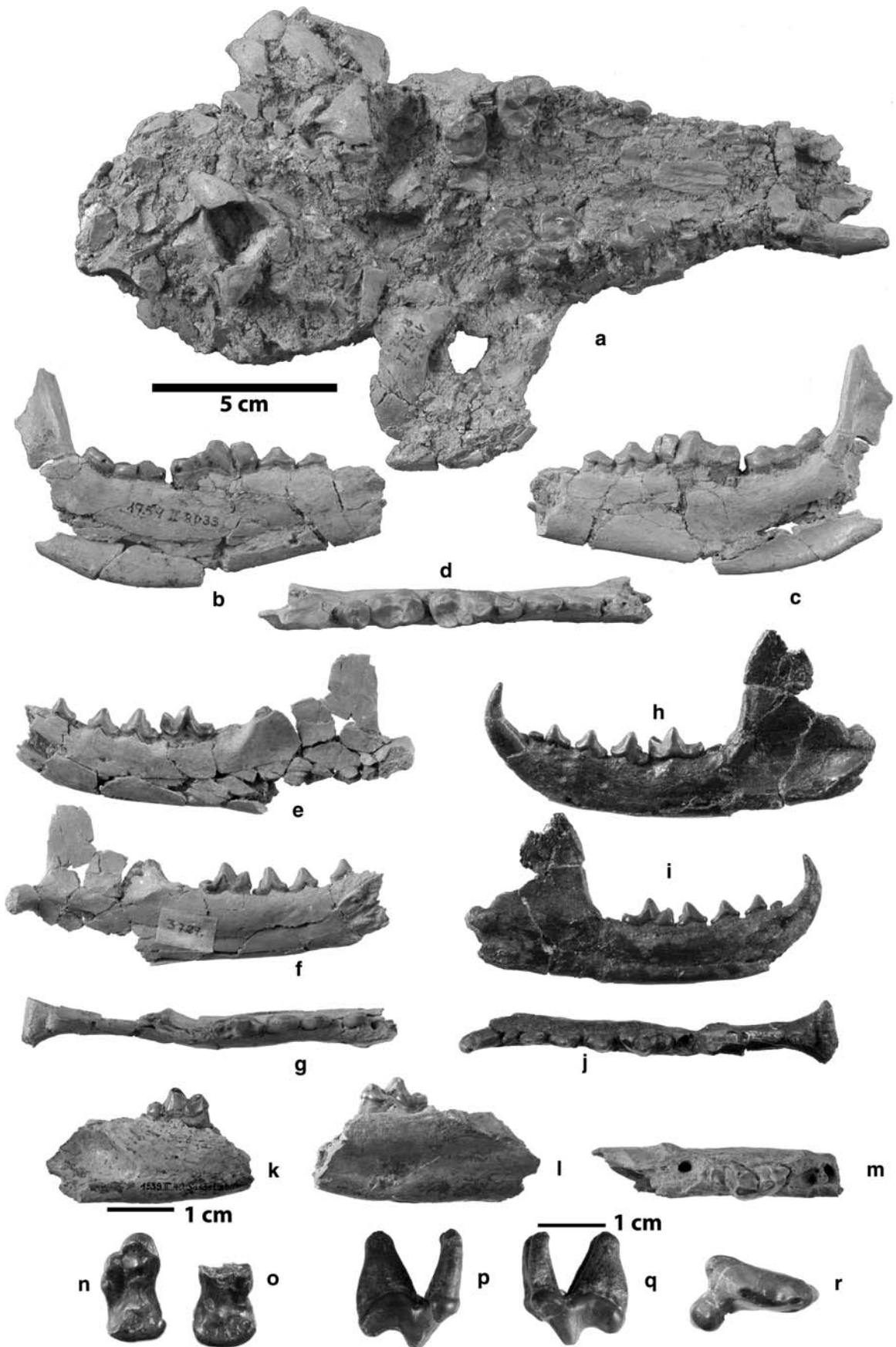
Table 7 Teeth measurements (mm) from *Pseudaelurus romieviensis* Roman and Viret, 1930

Coll. no.	Element	Total length	Total width	Trigonid length	Talonid width
8129 md sin	P3	11.3	4.7		
8129 md sin	P4	18.2	9.8		
8233 dext	P3	10.9	5.8		
8056 dext	P4	17.5	7.4		
8045 sin	Csup	12.0	8.2		
8045 sin	P2	3.2	2.4		
8045 sin	P3	11.1	6.8		
8045 sin	P4	16.2	–		
8052 md sin	cinf	10.8	8.1		
8052 md sin	p3	9.4	5.1		
8052 md sin	p4	12.1	–		
8052 md sin	m1	15.9	–	13.4	3.1
8209 dext	m1	15.3	–	13.7	2.9
8050 md dext	cinf	8.3	6.4		
8050 md dext	p3	9.8	5.1		
8050 md dext	p4	12.5	5.4		
8050 md dext	m1	16.0	–	13.4	3.7
8062 dext	cinf	8.0	6.4		

Description and comparisons: The holotype has been known since 1959 but because of its similarity to *Pseudaelurus*, it was not interpreted correctly. The complete material was described in detail by Morlo et al. (2004). The mandible is laterally compressed but nevertheless the flange is clearly visible. Minor differences such as a preparastyle in P4, the retrorse teeth, and the persistence of the metaconid enable the barbourfelid to be differentiated from its felid counterpart which is also present in Sandelzhausen.

The phylogenetic analysis places this species close to its larger relative, *Prosansanosmilus peregrinus*. *P. eggeri* probably came from Africa to Europe in MN5, after *P. peregrinus* which is known in Europe from MN4 to MN5 (Morlo 2006). Both may have originated from the African barbourfelid *Afrosmilus* (Kretzoi 1929), which itself migrated to Europe in MN4 by its species *A. hispanicus* (Morales et al. 2001), thereby representing the third

Fig. 13 a–d *Hemicyon stehlini* Huerzeler, 1944. **a** 8032, skull badly deformed, occlusal view, **b–d** 8033, left mandible with p3-m3, **b** lingual view, **c** buccal view, **d** occlusal view, **e–r** *Ischyriactis zibethoides* (Blainville, 1842), **e–g** 8040, left mandible with p2-m1, **e** buccal view, **f** lingual view, **g** occlusal view, **h–j** 8037, left mandible with p1-m1, **h** buccal view, **i** lingual view, **j** occlusal view, **k–m** 40, right lower jaw fragment with m1, **k** buccal view, **l** lingual view, **m** occlusal view, **n** 8044, right M1, occlusal view, **o** 8044, left M1; occlusal view, **p–r** 8044, left P4, **p** lingual view, **q** buccal view, **r** occlusal view



barbourofelid immigration into the early Middle Miocene of Europe (Morlo 2006). The question of whether *Sansanosmilus* descended from *P. eggeri* or represents another immigration of Barbourofelidae in MN6 cannot be answered yet.

Conclusion

The carnivoran species represented in the Sandelzhausen community range in the biochronology of Europe from MN4 to MN9. *P. eggeri* is only known from MN5 from Sandelzhausen so far. The similarly sized *P. romieviensis* was known only from MN4; therefore the Sandelzhausen specimen is the first reported occurrence from MN5. *Hemicyon stehlini* also is a species with a restricted stratigraphic range, being known from MN4 to MN5 only. The Sandelzhausen specimens of *P. bavaricus* are morphologically similar to the basal form of this species, known from MN5 to MN8. *Amphicyon major*, *Ischyriactis zibethoides*, *P. pusillus*, and *Martes munki* have a wider stratigraphic range and therefore do not help to pinpoint the stratigraphic age of the Sandelzhausen locality. Some faunal elements are only known from Europe, such as *Ischyriactis zibethoides*, *P. romieviensis*, and *Prosansanosmilus eggeri*, but the latter also marks an immigration event from Africa in MN5 (Morlo et al. 2004). In general, with the exception of *A. cf. major*, all other carnivorans from Sandelzhausen are quite small. Hyenids such as *Plioviverrops* or *Protictitherium* are missing, as is the large creodont *Hyainailouros*. These elements are usually known from more open landscapes. The composition of the Sandelzhausen carnivoran fauna indicates a more humid climate and a dense forest (Moser et al. 2009). Noticeable is the low diversity of musteloids, which is probably a result of the taphonomical processes that took place in Sandelzhausen. The material was usually very badly crushed during transportation in water and small specimens were likely to have been destroyed. Only by excellent preparation was it possible to retrieve the available information (see Fig. 13a). Nevertheless, the material was probably not transported very far, since elements from single individuals were found in close proximity. Skeletal remains from *Amphicyon*, *Hemicyon*, and *Pseudaelurus* seem to come from very few individuals rather than single elements from many different ones.

Acknowledgments We would like to thank Volker Fahlbusch for entrusting us with the material as well as Gertrud Rössner and Ursula Göhlich (all from Munich) for their patience with the ms and for their help with inventory numbers. Norbert Frotzler made the detailed black and white drawing and Rudolf Gold took the photos (both Vienna). We are grateful for the constructive remarks of our reviewers Elmar Heizmann (Stuttgart) and Lars Werdelin

(Stockholm), which helped to improve this paper. David Ferguson (Vienna) was kind enough to correct the English. The Deutsche Forschungsgemeinschaft is acknowledged for providing funds for C.S. to attend the Sandelzhausen Symposium 2005 in Mainburg (DFG GZ-4850/88/05).

References

- Astibia, H., J. Morales, and L. Ginsburg. 2000. *Hemicyon mayoralii* nov. sp., Ursidae du Miocène moyen de Tarazona de Aragon (basin de l'Ebre, Aragon, Espagne). *Annales de Paléontologie* 86(1):69–79.
- Blainville, H. 1842. Ostéographie ou description iconographique comparée du squelette et du système dentaire des cinq classes d'animaux vertébrés récents et fossils pour servir de base à la zoologie et à la géologie. *Mammifères Carnassiers: Des Mustelas (Genre Mustela L.)* 10:1–83.
- Cao, Z., H. Du, Q. Zhao, and J. Cheeng. 1990. Discovery of the Middle Miocene fossil mammals in Guanghe District, Gansu and their stratigraphic significance. *Geoscience* 4:16–32.
- Colbert, E.H. 1939. Carnivora of the Tung Gur Formation of Mongolia. *Bulletin of the American Museum of Natural History* 76:47–81.
- Crusafont, M. 1972. Les *Ischyriactis* de la transition Vindobonien-Vallésien. *Palaeovertebrata* 5:253–260.
- Daxner-Höck, G. 2003. Mammals from the Karpatian of the Central Paratethys. In *The Karpathian—a Lower Miocene Stage of the Central Paratethys*, ed. R. Brozobohaty, I. Cicha, M. Kovac, and F. Rögl. Brno: Masaryk University.
- Dehm, R. 1950. Die Raubtiere aus dem Mittel-Miocän (Burdigalium) von Wintershof-West bei Eichstätt in Bayern. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, Neue Folge* 58:1–141.
- Fahlbusch, V. 1974a. Aus Bayerns Tierwelt vor 15 Millionen Jahren. Ausgrabungen fossiler Säugetiere im Alpenvorland. *Aufschluss* 25:458–465.
- Fahlbusch, V. 1974b. Aus Bayerns Tierwelt vor 15 Millionen Jahren. Ausgrabungen fossiler Säugetiere im Alpenvorland. *Der Aufschluss* 25:458–464.
- Fahlbusch, V. 2003. Die miozäne Fossil-Lagerstätte Sandelzhausen. Die Ausgrabungen 1994–2001. *Zitteliana A* 43:109–121.
- Fahlbusch, V., and H. Gall. 1970. Die obermiozäne Fossil-Lagerstätte Sandelzhausen. 1. Entdeckung, Geologie, Faunenübersicht und Grabungsbericht für 1976. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* 10:365–396.
- Fahlbusch, V., and R. Liebreich. 1996. *Hasenhirsch und Hundebär*, 40. München: Pfeil.
- Fahlbusch, V., and R. Liebreich. 1999. Die Fossilfundstelle Sandelzhausen. Grabung 1998. Jahresbericht 1998 und Mitteilungen. *Freunde der Bayerischen Staatssammlung für Paläontologie und historische Geologie München e. V* 27:43–51.
- Fahlbusch, V., H. Gall, and N. Schmidt-Kittler. 1972. Die obermiozäne Fossil-Lagerstätte Sandelzhausen. 2. Sedimente und Fossilinhalt, Probleme der Genese und Ökologie. *Neues Jahrbuch für Geologie und Paläontologie. Monatshefte* 1972:331–343.
- Fahlbusch, V., H. Gall, and N. Schmidt-Kittler. 1974. Die obermiozäne Fossil-Lagerstätte Sandelzhausen. 10. Die Grabungen 1970–73, Beiträge zur Sedimentologie und Fauna. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* 14:103–128.
- Fejfar, O. Z. Dvorak, and E. Kadlecova. 2003. New record of Early Miocene (MN3a) mammals in open brown coal pit Merkur,

- North Bohemia, Czech Republic. In *Distribution and Migration of Tertiary Mammals in Eurasia, papers in honour of H.*, eds. Reumer, J., and W. Wessels, 10, 163–182. de Bruijn: Deinsea.
- Filhol, H.M. 1891. Études sur les mammifères fossils de Sansan. *Annales des Science Géologiques* XXI:319.
- Fraas, O. 1885. Beiträge zur Fauna von Steinheim. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* 41:313–326.
- Frick, C. 1926. The Hemicyoninae and an American Tertiary Bear. *Bulletin of the American Museum of Natural History* 56:1–120.
- Gervais, P. 1848–1852. Zoologie et Paléontologie françaises (animaux vertébrés) ou nouvelles recherches sur les animaux vivants et fossiles de la France. 1 réédition, 271. Paris.
- Ginsburg, L. 1955. De la subdivision du genre *Hemicyon* Lartet (Carnassier) du Miocène. *Bulletin de la Société Géologique de France* 6(5):85–99.
- Ginsburg, L. 1961. La faune des carnivores miocènes de Sansan (Gers). *Mémoires du Muséum National d'Histoire Naturelle, Séries C IX*:1–190.
- Ginsburg, L. 1992. Les genres *Pseudarctos* et *Ictiocyon*, Amphicyonidae (Carnivora, Mammalia) du Miocène européen. *Bulletin du Muséum National d'Histoire Naturelle (4C)* 14(3–4):301–317.
- Ginsburg, L. 1999. Order Carnivora. In *Land Mammals of Europe*, eds. Rössner, G.E., and K. Heissig., 109–148. München: Pfeil.
- Ginsburg, L., and C. Bulot. 1982. Les carnivores du miocène de Béziau près de la Romieu (Gers, France). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. B* 85(1):53–76.
- Ginsburg, L., and J. Morales. 1992. Contribution à la connaissance des Mustélinés (Carnivora, Mammalia) du Miocène d'Europe Trochictis et Ischyriactis, genres affines et genres nouveaux. *Comptes Rendus de l'Académie des Sciences Paris* 315(II):111–116.
- Ginsburg, L., and J. Morales. 1998a. *Zaragocyon daamsi* n. gen. sp. nov., Ursidae primitif du Miocène inférieur d'Espagne. *Comptes Rendus de l'Académie des Sciences Paris* 321(IIIa):811–815.
- Ginsburg, L., and J. Morales. 1998b. Les Hemicyoninae (Ursidae, Carnivora, Mammalia) et les formes apparentées de Miocene inférieur et moyen d'Europe occidentale. *Annales de Paléontologie* 84(1):71–123.
- Heizmann, E.P.J. 1973. Die tertiären Wirbeltiere des Steinheimer Beckens. *Palaeontographica Supplement* 8(5B):1–95.
- Heizmann, E.P.J., L. Ginsburg, and C. Bulot. 1980. *Prosansanosmilus peregrinus*, ein neuer machairodontider Felidae aus dem Miozän Deutschlands und Frankreichs. *Stuttgarter Beiträge zur Naturkunde B* 58:1–27.
- Helbing, H. 1930. Zur Kenntnis der miocänen „*Mustela*“ *zibethoides* Blainville. *Eclogae geologicae Helvetiae* 23(2):637–644.
- Helbing, H. 1936. Die Carnivoren des Steinheimer Beckens. A: Mustelidae. *Palaeontographica. Supplement* 8(VA):1–95.
- Huerzeler, J. 1944. Zur Revision der europäischen Hemicyoniden. *Verhandlung der Naturforschenden Gesellschaft in Basel* 55: 131–157.
- Hunt, R.M. 1998. *Ursidae. Evolution of tertiary mammals of North America. Volume 1: terrestrial carnivores, ungulates and unguateline mammals*, 174–195. London: Cambridge University Press.
- Jourdan, C. 1861. Description de restes fossiles de deux grands Mammifères constituant deux genres, l'un le genre *Rhizopron*, de l'ordre des Cétacés et du groupe des Delphinoïdes, l'autre le genre *Dinocyon*, de l'ordre des Carnassiers et de la famille des Canidés. *Comptes Rendus à l'Académie des Sciences* 53:959–963.
- Kuss, S.E. 1965. Revision der europäischen Amphicyoninae (Canidae, Carnivora, Mammalia) ausschließlich der voroberstampischen Formen. *Sitzungsberichte der Heidelberger Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse* 1:168.
- Lartet, E. 1851. Notice sur la colline des Sansan. Suivie d'une récapitulation de diverses espèces d'animaux vertébrés fossiles trouvés soit à Sansan, soit dans d'autres gisements du terrain tertiaire miocène dans le bassin sous-pyrénéen, 45. Auches: J.-A. Portes.
- Mayet, L. 1908. Études de Mammifères miocènes des sables de l'Orléanais et des faluns de la Touraine. *Annales de l'Université de Lyon, Nouvelle Série* 24:336.
- Morales, J., M. Pickford, D. Soria, and S. Fraile. 1998. New carnivores from the basal Middle Miocene of Arrisdrift, Namibia. *Eclogae Geologicae Helvetiae* 91:27–40.
- Morlo, M. 1997. Die Raubtiere (Mammalia, Carnivora) von Dorn-Dürkheim. 1. (Rheinessen) 1 Mustelida, Hyaenidae, Percrocutidae, Felidae. *Courier Forschungsinstitut Senckenberg* 197:11–47.
- Morlo, M. 2006. New remains of Barboourofelidae (Mammalia, Carnivora) from the Miocene of Southern Germany: implications for the history of barboourofelid migrations. *Berträge zur Paläontologie* 30:339–346.
- Morlo, M., St. Peigné, and D. Nagel. 2004. A new species of *Prosansanosmilus*: implication for the systematic relationship of the family Barboourofelidae new rank (Carnivora, Mammalia). *Zoological Journal of the Linnean Society* 140:43–61.
- Moser, M., G.E. Rössner, U.B. Göhlich, M. Böhme, and V. Fahlbusch. 2009 this volume. The fossil lagerstätte Sandelzhausen (Miocene; southern Germany): history of investigation, geology, fauna and age. In *Fossil lagerstätte Sandelzhausen (Miocene, southern Germany): Contributions to the fauna. Paläontologische Zeitschrift*, eds. Rössner, G.E., and U.B., Göhlich, 83 (1). 000–000.
- Nagel, D. 2003. Carnivora from the middle Miocene Hominoid locality of Çandir (Turkey). *Courier Forschungsinstitut Senckenberg* 240:113–131.
- Peigné, S., and E.P.J. Heizmann. 2003. The Amphicyonidae (Mammalia: Carnivora) from Ulm-Westtangente (MN2, Early Miocene), Baden-Württemberg, Germany, Systematics and ecomorphology. *Stuttgarter Beiträge zur Naturkunde B* 343:133.
- Qiu, Z. 2003. Dispersal of Neogene Carnivorans between Asia and North America. Chapter 2. *Bulletin American Museum of Natural History* 279:18–31.
- Roger, O. 1900. Wirbeltierreste aus dem Dinotheriensande der schwäbisch-bayerischen Hochebene. 3. Teil. *Berichte des naturwissenschaftlichen Vereins für Schwaben und Neuburg in Augsburg* 34:54–70.
- Roman, F., and J. Viret. 1930. Le Miocène continental de l'Armagnac et le gisement burdigalien de La Romieu (Gers). *Livre Jubilaire (Société Géologique de France)*: 577–604.
- Roth, C.H. 1988. *Leptoplesictis* Major 1903 (Mammalia, Carnivora, Viverridae) aus dem Orleanium und Asteracium/Miozän von Frankreich und Deutschland. *Paläontologische Zeitschrift* 62(3/4):333–343.
- Roth, C.H. 1989. Die Raubtierfauna (Carnivora, Mammalia) der untermiozänen Spaltenfüllung von Erkertshofen 2 bei Eichstätt/Bayern. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* 29:163–205.
- Rothwell, T. 2003. Phylogenetic Systematics of Northern American *Pseudailurus* (Carnivora: Felidae). *American Museum Novitates* 3403:64.
- Schlosser, M. 1899. Über die Bären und bärenähnlichen Formen des europäischen Tertiärs. *Palaeontographica* 45:95–147.
- Schmidt-Kittler, N. 1976. Raubtiere aus dem Jungtertiär Kleinasiens. *Palaeontographica Abt. A* 155(1–4):1–131.
- Schmidt-Kittler, N. 1987. The Carnivora (Fissipedia) from the Lower Miocene of East Africa. *Palaeontographica, A* 197:85–126.
- Stehlin, H.G., and H. Helbing. 1925. Catalogue des ossements de mammifères Tertiaires de la Collection Bourgeois à l'École de

- Pont-Levoy (Loir-et-Cher). *Bulletin de la Société naturelles et Anthropologie de Loir-et-Cher* 18:77–277.
- Thenius, E. 1989. Zähne und Gebiß der Säugetiere. In *Handbuch der Zoologie*, ed. J. Niethammer, H. Schliemann, and D. Starck, 513. VIII Mammalia: Walter de Gruyter.
- Thomas, H., S. Sen, M. Khan, B. Battail, and G. Ligabue. 1982. The lower Miocene fauna of Al-Sarrar (Eastern province, Saudi Arabia). *The Journal of Saudi Arabian Archaeology* 5:109–135.
- Toula, F. 1884. Über *Amphicyon*, *Hyaemoschus* und *Rhinoceros* (*Aceratherium*) von Göriach bei Turnau in der Steiermark. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Klasse* 90(5):405–428.
- Viranta, S. 1996. European Miocene Amphicyonidae—taxonomy, systematics and ecology. *Acta Zoologica Fennica* 204:1–61.
- Viret, J. 1933. Contribution à l'Étude des Carnassiers Miocènes de la Grive-Saint-Alban (Isère). *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon* 21(18):1–31.
- Viret, M.J. 1951. Catalogue critique de la faune des Mammifères Miocènes de la grive Saint-Alban (Isère). *Nouvelles archives du muséum d'histoire naturelle de Lyon* 3:1–104.
- Wang, X., J. Ye, J. Meng, W. Wu, L. Liu, and S. Bi. 1998. Carnivora from middle Miocene of northern Junggar Basin, Xinjiang Autonomous Region, China. *Vertebrata Palasiatica* 36:218–243.
- Werdelin, L. 1996. Carnivores, exclusive of Hyaenidae, from the Later Miocene of Europe and Western Asia. In *The Evolution of Western Eurasian Neogene Mammal Faunas*, ed. R. Bernor, V. Fahlbusch, and H.-W. Mittmann, 271–289. New York: Columbia University.