

The early Vallesian vertebrates of Atzelsdorf (Late Miocene, Austria). 10. Carnivora

By Doris NAGEL¹

(With 1 figure and 4 tables)

Manuscript submitted on July 28th 2008,
the revised manuscript on January 23th 2009

This article is dedicated to my dear colleague Dr. Ortwin SCHULTZ.

Abstract

In Atzelsdorf (MN9, Upper Miocene) eleven fossil specimens of carnivores have been found. Although the sample is rather small, three different genera could be identified, among them the first record of *Sansanosmilus vallesiensis* in Austria. *Plesiogulo* and *Semigenetta* were only determined to the genus level because of the low number of specimens.

Keywords: *Sansanosmilus*, *Semigenetta*, *Plesiogulo*, Mustelidae, Hyaenidae, MN9, Vallesium, Upper Miocene, Lower Austria.

Zusammenfassung

In Atzelsdorf (MN9, Obermiozän) wurden insgesamt elf Carnivorenreste gefunden. Obwohl diese ein recht geringe Fundmenge darstellt, konnten insgesamt drei Gattungen identifiziert werden, darunter zum ersten Mal in Österreich *Sansanosmilus vallesiensis*. *Plesiogulo* und *Semigenetta* konnten auf Grund der wenigen fragmentierten Funde nur auf Gattungsniveau bestimmt werden.

Schlüsselwörter: *Sansanosmilus*, *Semigenetta*, *Plesiogulo*, Mustelidae, Hyaenidae, Vallesium, MN9, Obermiozän, Niederösterreich.

Introduction

Atzelsdorf (Lower Austria) is about 35 km NW of Vienna (Lower Austria). Geologically, it is situated at the north-western margin of the Vienna Basin and belongs to the Hollabrunn-Mistelbach Formation. The sediments are interpreted as delta deposits of the palaeo-Danube, which filled material into the Pannonian lake during the Late Miocene. Based on biostratigraphical investigations (see HARZHAUSER 2009, this volume) the fauna from the gravel pit in Atzelsdorf belongs to the Vienna Basin Pannonian Zone C, basal MN9 (absolute age approximately 11.2–11.1 Ma) (see HARZHAUSER 2009, this volume).

¹ University of Vienna, Department of Palaeontology, Althanstrasse 14, 1090 Vienna, Austria; e-mail: doris.nagel@univie.ac.at

Most of the carnivores were found by the private collectors Gerald PENZ (Vienna) and Peter SCHEBECZEK (Pellendorf). Only recently Dr. Gudrun DAXNER-HÖCK, Natural History Museum of Vienna, Department of Palaeontology, undertook a scientific excavation to locate the exact layers bearing mammalian fossils. Casts of the material from the collectors are stored at the Natural History Museum Vienna, Geological-Palaeontological Department.

Methods

Lower teeth are referred to by small letters, as in “m1”, uppers by capitals, as in “P4”, lower canines as Cinf. and upper canines as Csup. Measurements were taken with a caliper to the closest 0.1 mm. Description of tooth morphology follows THENIUS (1989).

Abbreviations

NHMW – Natural History Museum Vienna

Systematic Part

Order Carnivora BOWDICH, 1821

Family Barbourfelidae SCHULTZ, SCHULTZ & MARTIN, 1970
(sensu MORLO, PEIGNÉ & NAGEL, 2004)

Genus *Sansanosmilus* KRETZOI, 1929

The genus *Sansanosmilus* is known in Europe from the Middle to the Upper Miocene (later MN5 to MN9) and consists of four species. *S. palmidens* (GINSBURG, 1961) is found from late MN5 to MN6, *S. jourdani* (FILHOL, 1883) is known in the Asteracian (from MN6 to MN7-8). BEAUMONT & CRUSAFONT-PAIRÓ (1982) regarded *S. vallesiensis* (MN9) as a species rather than a subspecies of *S. jourdani*. *Sansanosmilus piveteaui* (GERAADS & GÜLEÇ, 1997) is recorded from MN9 from Anatolia. The genus may be paraphyletic and *S. vallesiensis* as well as *S. piveteaui* are probably a European parallel evolution to the American *Barbourfelis* (FILHOL 1883; VILLALTA & CRUSAFONT 1943; GINSBURG 1961; HEIZMANN 1973; MORLO 2006).

The oldest Barbourfelids are currently found in Africa. Therefore it is assumed that *Sansanosmilus* migrated from Africa to Europe in MN4, where it co-existed with *Pro-sansanosmilus* in Europe (MORLO et al. 2004).

***Sansanosmilus vallesiensis* BEAUMONT & CRUSAFONT 1982**
(figs 1.1a-d)

H o l o t y p e : right mandible with m1 and alveoli of p4-p3 and of the incisors.

T y p e l o c a l i t y : Santiga, Spain.

M a t e r i a l: NHMW 2008z0059/0001: lower left mandibular fragment with flange, p4 (length x width: 17.9 x 7.6 mm) and m1 (length x width: ca 23.5 x 9.4 mm) distal part broken; NHMW 2008z0059/0002: fragment of lower right canine; NHMW 2008z0059/0003: atlas, NHMW 2008z0059/0004: fragment of caudal vertebra (length of the centrum = 38.9mm).

D e s c r i p t i o n: The mandible consists of two parts: the distal part of the flange and a mandible fragment with the alveolus of p3, p4 and m1. The latter is broken after the lower carnassial (figs 1.1a-c). The mandible has a strong inflexion only known in the most apomorphic species of the genus *Sansanosmilus*.

The lower jaw is robust. The foramina mandibulae are placed under the postcanine diastema. The teeth are very worn and no serration can be seen any more. The p3 is missing and only the broken alveolus is still present. One small opening in the alveolus seems to have been the former foramen for the blood vessel and nerve, suggesting a major root. The preservation of the alveolus is rather poor and therefore a small second root, very close to the main one cannot be excluded. The p4 and m1 are strongly rotated backwards. The p4 consists of four cuspids, the main cusp is about one third larger than the anterior one. It is worn, and the posterior cuspids form a small cutting blade at the end of the p4. The two accessory cuspids on p4 are still separated from the main cuspid. The paraconid blade of m1 is 10.6 mm in length but it is partly broken and it was approximately about 13.5 mm long. A notch separates the two cuspids. Since the protoconid is broken it is not possible to discern if a metaconid or talonid was present. The mandible below m1 measures 30.6 mm and the smallest flange depth is 31.2 mm.

The atlas is of similar size to a recent lion. The articulation facets for the axis are rounded but more closed than in the canids or hyaenids and shallower than in the recent large cats. The transverse processes are broken. The caudal vertebra consists of a compact centrum with no transverse processi (fig. 1.1d). Due to its size and the location of discovery, it is tentatively assigned to the *Sansanosmilus* from Atzelsdorf.

Sansanosmilus vallesiensis differs from *S. palmidens* and *S. jourdani* by a larger size, the larger protoconid of m1 in comparison to the paraconid and the larger p4. In *S. jourdani* the protoconid blade becomes longer. This trend continues in *S. vallesiensis* and *S. piveteaui*, the latter has almost no notch between the protoconid and paraconid, while the m1 from Atzelsdorf still carries a notch. The flange is not fully preserved, therefore its length is not measurable.

GERAADS & GÜLEÇ (1997) calculated the index p4/m1 for *Sansanosmilus*: the index is > 0.85 for *S. sansaniensis* and < 0.72 for *S. jourdani*. The p4/m1 index for the Atzelsdorf lower jaw is 0.75, between the values given above. The material from Atzelsdorf falls into the size variation of *S. vallesiensis*, and is approximately 10 % larger than *S. palmidens* and *S. jourdani* (tab. 1). The Atzelsdorf material is apomorphic compared to *S. jourdani* with a longer protoconid on m1 but not as evolved as *S. piveteaui* (OZAN-SOY, 1965). The latter has a reduced notch on m1 and higher cuspids on p4, which are closer together than in the specimen from Atzelsdorf. The size, the apomorphic m1 and the strongly backwards-rotated teeth are typical for *S. vallesiensis*. The larger p3, although only judged by the alveolus and the p4/m1 index, indicate a primitive form of *S. vallesiensis*, less evolved than that from Santiga.

Sansanosmilus vallesiensis is known from MN9 from Spain, Ukraine and now from Austria. This genus is the last member of the Barbourfelidae, which migrated from Africa to Europe in MN4 with *Prosansanosmilus* (MORLO et al. 2004).

Family Viverridae GRAY, 1821

Genus *Semigenetta* HELBING, 1927

The genus *Semigenetta* is very similar to the recent *Genetta* but it is characterized by apomorphic features such as the complete reduction of the M2 and the strong reduction of the m2. At least two different lineages can be distinguished through time (HEIZMANN 1973; GINSBURG 1999; NAGEL 2003).

***Semigenetta* sp.**

(figs 1.4a-b)

M a t e r i a l: NHMW 2008z0071/0001, left P4 (length x width: 10.1 x 4.9 mm).

D e s c r i p t i o n: The upper carnassial bears a cutting metacone blade approximately the same length as the paracone. A cingulum is well visible on the lingual side and also on the buccal side of the metacone, a tiny parastyle and a reduced paracone. A cingulum is well visible (figs 1.4a-b).

On P4 from Atzelsdorf, the paracone is higher than the metacone blade and the parastyl is quite small, as typical for *Semigenetta*. The P4 is larger than that of *Semigenetta laugnacensis* (BONIS, 1973) and *S. elegans* DEHM, 1950 but slightly smaller than the material from La Grive (MN 7/8). It is comparable to the average size of *S. sansanienis* (LARTET, 1851) from Steinheim (MN7/8, HEIZMANN 1973), the latest occurrence of this

Tab. 1. *Sansanosmilus vallesiensis* from Atzelsdorf compared. * from depiction. ° roots. All measurements in mm.

	p4		m1	
	length	width	length	width
<i>S. vallesiensis</i> , NHMW 2008z0059/0001, Atzelsdorf	17.9	7.6	(23.5)	9.4
<i>S. piveteaui</i> , 06-AKM-0276, Sinap, GERAADS & GÜLEÇ 1997	17.7	7.2	26.6	10.8
<i>S. palmidens</i> , 454, Sansan, GINSBURG 1961*	15.0	-	16.2	-
460, Sansan, GINSBURG 1961*	-	-	18.2	-
459, Sansan, GINSBURG 1961*	-	-	18.5	-
456, Sansan, GINSBURG 1961*	16.2	5.8	-	-
<i>S. vallesiensis</i> , Santiga, BEAUMONT & CRUSAFONT-PAIRÓ 1982	16.6	5.9	23.9	10.0
<i>S. jourdani</i> , La Grive-St. Alban, FILHOL 1883*	17.2	-	23.6	-
<i>S. jourdani</i> , BSP 1951 I 42, Massenhausen°, MORLO 2006	13.7	7.4	-	-

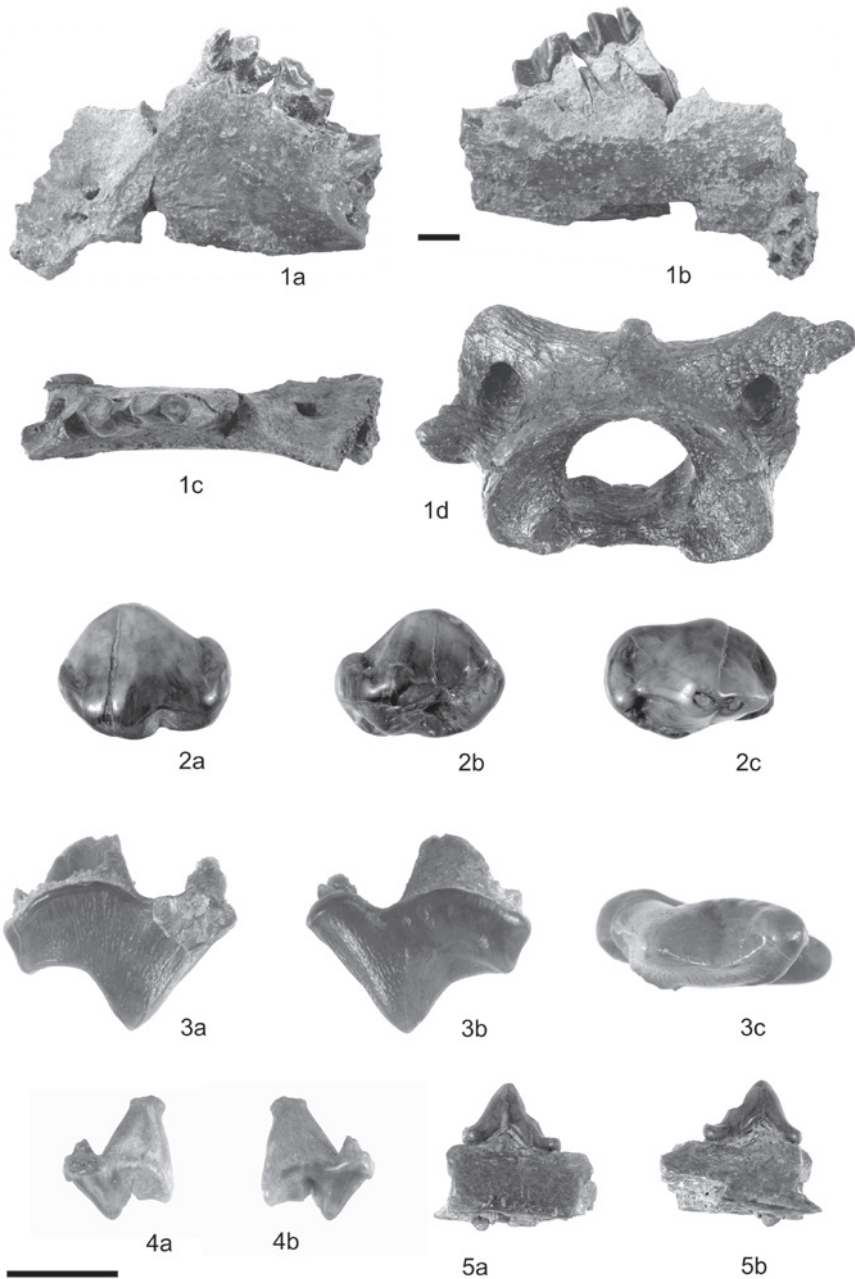


Fig. 1. Carnivora from the Late Miocene (Early Vallesian, MN9) of Atzelsdorf (Lower Austria). 1a-d: *Sansanosmilus vallesiensis* (NHMW 2008z0059/0001), a-c: left lower mandible with p4 and m1; d: atlas (NHMW 2008z0059/0004). 2a-c: Hyaenidae indet. (NHMW 2008z0073/0001), right P3. 3a-c: *Plesiogulo* sp. (NHMW 2008z0072/0001), upper right P4. 4a-b: *Semigenetta* sp. (NHMW 2008z0071/0001), left P4. 5a-b: Mustelidae indet. aff. *Martes* sp. (NHMW 2008z0072/0004: right mandible fragment with p4. a: buccal view, b: lingual view, c: occlusal view. Scale bars equals 5 mm.

species so far (tab. 2). The posterior buccal alveolus of M1 is placed strongly more lingually than the anterior one, indicating a slender tooth, more slender than e.g. known from *Plioverropros*.

Atzelsdorf is dated into the lower Vallesian (MN9). *Semigenetta* is known in MN9 by two taxa. One is from Can Llobateres (MN9, Spain), *S. ripolli* PETTER (1976), and the other one is *S. grandis* (CRUSAFONT & GOLPE 1981) from Castell de Barberà (MN9, Spain). *Semigenetta ripolli* is even smaller than *S. laugnacensis* and *S. grandis* is, as the name indicates, is the largest known *Semigenetta* so far. Both are only known by lower dentition but are far out of the size range of the Atzelsdorf specimen. Maybe *Semigenetta sansaniensis* persisted in Vallesian (MN9) or the size range of *S. grandis* is overlapping with *S. sansaniensis*.

Family Mustelidae FISCHER, 1817

Genus *Plesiogulo* ZDANSKY, 1924

The genus was erected by ZDANSKY (1924) on *Gulo*-like material from China. Differences mainly seen in M1 and m1 lead to the split from *Gulo* on the genus level. While ZDANSKY discussed these differences seen in *Plesiogulo* as apomorphic, DUBOIS & STEHLIN (1933) regarded them as plesiomorphic and considered *Plesiogulo* as ancestral to *Gulo*. A later work on *Plesiogulo crassa* by KROTKEVICH & SEMENOV (1975) ruled out this possibility again. They argued for a different chewing specialisation which makes an ancestry of *Gulo* impossible. *Plesiogulo* is known from MN9 of Hritsev/Gritsev, Ukraine (KOROTKEVICH & SEMENOV 1975) to MN13 in Las Casiones, Spain (ALCALÁ et al. 1994).

During the Upper Miocene, a second *Gulo*-like form was present: *Eomellivora* (MN9 to MN12). This musteline mustelid is characterized by a combination of features (see ZDANSKY 1924 and WOLSAN & SEMENOV 1996 for details), e.g. its very large size and the auditory bulla built relatively small. The upper teeth, premolars and molar, are sur-

Tab. 2. *Semigenetta* from Atzelsdorf compared to different *Semigenetta* species. *S. ripolli* and *S. grande* are only known from lower dentition. () = measured at the alveoli. * measurement from the depiction. All measurements in mm.

	P4 length x width	M1 length x width
<i>Semigenetta</i> spp. Atzelsdorf	10.1 x 4.9	(3.5 x 6.4)
<i>S. laugnacensis</i> Lg 285, Laugnac, BONIS de, 1994	8.0 x 4.4	3.2 x 6.2
<i>S. elegans</i> 13 37, Winterhof-West, DEHM 1950	8.7 x 4.8	3.7 x 7.3
<i>S. sansaniensis</i> Vieux-Collogne; VIRET 1958	9.7 x 6.0	3.8 x 7.4 to 5.0 x 9.6
<i>S. sansaniensis</i> GRU-B1-1, Grund, NAGEL 2003	10.3 x 5.5	-
<i>S. sansaniensis</i> 814, Sansan, GINSBURG 1961	10.6 x 5.6	5.2 x 7.4*
<i>S. sansaniensis</i> 1307, La Grive, VIRET 1951*	10.8 x 6.3	5.1 x 7.4
<i>S. steinheimensis</i> , Stuttgart, HEIZMANN 1973	10.1 x 5.5	4.7 x 8.6

rounded by a prominent cingulum and on P4 an bulging buccal base is visible. The protocone of P4 is well-separated from the main cusp. The m1 lacks the metacone or it has a vestigial one. *Plesiogulo* is smaller in size, the upper teeth, premolars and molar, are surrounded by prominent cingulum on the buccal side, rarely on the lingual one. The protocone on P4 is weakly separated from the paracone. The metacone is smaller than the paracone on M1 but still present. The teeth have rugose enamel (ZDANSKY 1924; KURTÉN 1970). Although the specimen from Atzelsdorf is partly broken, its size, the rugose enamel and the well-developed buccal cingulum allow its attribution to the genus *Plesiogulo*.

***Plesiogulo* sp.**

(figs 1.3a-c)

M a t e r i a l: NHMW 2008z0072/0001: upper right P4 (length x width of the paracone blade: 19.7 x 8.5 mm); NHMW 2008z0072/0003: left Cinf.; NHMW 2008z0072/0002: fragment of axis.

D e s c r i p t i o n: On the P4, the paracone is higher than the metacone. The protocone is missing. There is a small buccal cingulum. The enamel shows a slightly rugose structure on the buccal side and some small folds are visible on the lingual-posterior part. The roots are broken and were not fully developed. This and the fact that no wear facets can be seen lead to the assumption that the P4 was from a young and not fully grown individual (figs 1.3a-c).

Five species of *Plesiogulo* are accepted in the Eurasian record: *P. brachygnathus* ZDANSKY, 1924, *P. minor* TEILHARD & LEROY, 1945, *P. crassa* TEILHARD & LEROY, 1945, *P. praecocidens* KURTÉN, 1970 and *P. monspessulans* VIRET, 1939. *Plesiogulo major* was described by TEILHARD & LEROY, 1945. HENDEY (1978) first proposed the possibility that *P. major* is a synonym of *P. monspessulanus* and ALCALÁ et al. (1994) as well as HAILE-SELASSIE (2004) supported this. Furthermore, *Plesiogulo* is known from North America with *P. marshalli* and *P. lindsayi* (HARRISON 1981) as well as from Africa with *P. botori* (HAILE-SELASSIE et al., 2004) and maybe with *P. praecocidens* (MORALES et al. 2004).

Plesiogulo monspessulanus is a large form of *Plesiogulo*, the cusps on M1-trigon are smaller, although the tooth in general is larger than all other known ones and the metaconid on m1 is still present. *Plesiogulo crassa* has stocky premolars and a P4 with the same length/width ratio as *P. botori* and *P. marshalli*. *P. praecocidens* is smaller than *P. crassa*, the metaconid is absent on m1 and the M1 has completely different proportions (KURTÉN 1970). *Plesiogulo brachygnathus* is the smallest known form (KOUFOS 1982).

The P4 from Atzelsdorf fits in size (tab. 3) and morphology within the range of *P. crassa*, but since no M1 is known from Atzelsdorf to allow a more detailed investigation, the P4 is assigned to *Plesiogulo* sp. For further size comparison of the different *Plesiogulo* species see KOUFOS (2006).

Plesiogulo ist known from Europe (KOUFOS 1982; KOROTKEVICH & SEMENOV 1974), Asia (ZDANSKY 1924; VIRET 1939; TEILHARD & LEROY 1945; KURTÉN 1970), Afrika (HAILE-SELASSIE et al. 2004) from MN 9 to MN 13 and from North America where the

immigration of this animal is one criteria of determining the Late Hemiphillian (HARRISON 1981).

Mustelidae indet. aff. *Martes*

(figs 1.5a-b)

M a t e r i a l : Colln PENZ No. 53: left mandible fragment with distal root fragment of m1 and alveoli of m2. NHMW 2008z0072/0004: right mandibular fragment with p4 (length x width x height: 9.1 x 4.1 x 5.2 mm).

D e s c r i p t i o n : The p4 bears a tiny anterior accessory cuspid and a posterior cuspid closely attached to the main cusp. The tip of the latter is broken. A weak cingulum surrounds the tooth on the buccal side only rising a little bit at the posterior end, there forming a small cuspid (figs 1.5a-b). The tiny anterior cusp and the larger size of the tooth distinguish it from the Viverridae and Herpestidae, which are smaller and/or have a larger anterior cusp. The size and especially the height of the tooth, compared to its length exclude Melinae, Mephitinae, Gulolinae and Lutrinae. Within the Mustelinae, the specimen is closest to the *Martes*-group (KOUFOS 2006; PETTER 1976; GINSBURG 1961).

Mustelidae indet.

M a t e r i a l : NHMW 2008z0072/0005: left C inf.

D e s c r i p t i o n : canine of medium size, slender and slightly curved. The assignment to the mustelids was made due to size and form of the canine.

Tab. 3. *Plesiogulo* sp. from Atzelsdorf compared to different *Plesiogulo* species. All measurements in mm.

	P4	
	length	width
<i>Plesiogulo</i> sp. Atzelsdorf	19.7	8.5
<i>P. minor</i> K'ingyang, KURTÉN 1970	17.0	10.5
<i>P. praecocidens</i> , Loc.49, China, KURTÉN 1979	17.2	10.9
<i>P. brachygnathus</i> ZDANSKY 1924, Loc.49, Ex.5	17.1	11.1
<i>P. crassa</i> China Loc.49, KURTÉN 1970	20.5	14.0
<i>P. crassa</i> Yushe, KURTÉN 1970	18.5	13.8
<i>P. crassa</i> , Cherevichnoe, KOROTKEVICH & SEMENOV 1974	17.0 -18.0	-
<i>P. monspessulanus</i> , Teruel Basin, ALCALÁ 1994	23.2	15.6
<i>P. botori</i> , Narol, Africa, HAILE-SELASSIE et.al 2004	24.2	16.7
<i>P. marshalli</i> , North America, HARRISON 1981	18.5 - 21.7	12.1 - 15.0
<i>P. lindsayi</i> , North America, HARRISON 1981	23.5	17.3

Family Hyaenidae GRAY, 1821

Hyaenidae indet.

(figs 1.2a-c)

Material: NHMW 2008z0073/0001: right P3 (length x width: 15.8 x 11 mm).

Description: Only the crown of P3 is preserved, the roots are missing. A strong cingulum surrounds the tooth. On the anterior side, a small cuspid is visible sitting on the broad cingular projection of the tooth, together with several cingular folds. Posterior, a strong cusp is developed. The cingulum surrounds the whole tooth, which has a convex shape in the lingual posterior part (figs 1.2a-c).

The tooth is larger than known from *Plioviverrops* KRETZOI, 1938 or *Protictitherium* KRETZOI, 1938 but smaller than *Adcrocuta* (ROTH & WAGNER 1854). Despite recent works, there is still no consensus about the medium-sized hyaenids in the Upper Miocene. TURNER et al. (2008) accept *Ictitherium* WAGNER 1848, *Thalassictis* GERVAIS, 1850 ex NORDMANN, *Hyaenictitherium* KRETZOI, 1938, all with a canid-like dentition (Ecomorph Group 3), and *Lycaena* HENSEL, 1863, *Hyaenictis* GAUDRY, 1861 and *Chasmaporthetes* HAY, 1921. These three have a bone-cracking tendency (Ecomorph Group 4). SEMENOV (2008) additionally lists *Miohyaenotherium* SEMENOV, 1989 and *Hyaenotherium* SEMENOV, 1989 and together with *Hyaenictitherium* he attributes them to the subfamily Hyaenotheriini, while in his opinion the subfamily Ictitheriini consists of *Ictitherium* and *Thalassictis*. *Miohyaenotherium* is also mentioned in TSENG & WANG (2007) for Western Eurasia.

Other Upper Miocene hyaenas are: *Metahyaena* VIRANTA & WERDELIN, 2003, known from a single mandibular ramus found in the Sinap Formation (Locality 12, MN9), *Belbus* WERDELIN & SOLOUNIAS, 1991, the Asian *Palinhyana* QIU et al., 1979 and *Leecyaena* YOUNG & LIU, 1948 (= ?*Pliocrocuta* after TURNER et al. 2008) as well as the African *Ikelohyaena* WERDELIN & SOLOUNIAS, 1991. They are referred to as transitional bone-cracking hyaenas (TURNER et al. 2008).

The genera *Ictitherium*, *Hyaenictitherium* and *Thalassictis* all have slender P3 (see tab. 3), *Lycaena*, *Metahyaena*, *Belbus* and *Ikelohyaena* are only known from lower dentition. The latter is comparable in size to *Hyaenictitherium* (WERDELIN 2004). *Palinhyana* has not been reported in Europe and the ecological niche was probably taken by *Bel-*

Tab. 4. Hyaenidae indet. from Atzelsdorf compared to the common genera from Europe in the Upper Miocene. All measurements in mm.

	P3	
	length	width
Hyaenidae indet., Atzelsdorf	15.8	11
<i>Thalassictis robusta</i> , Dorn-Dürkheim 1, MORLO 1997	11.6	7.0
<i>Thalassictis robusta</i> , Kishinev, SEMENOV 1989	12.2	6.2
<i>Hyaenictitherium wongi</i> , Greece, KOUFOS 2000	15.5 - 17.7	8.4 - 10.0
<i>Ictitherium viverrinum</i> , Greece, WERDELIN, 1988; KOUFOS 2000	14.0 - 15.5	6.7 - 7.9

bus (WERDELIN & SOLOUNIAS 1991). *Lycaena* is a larger form, probably larger than the specimen from Atzelsdorf (BONIS et al. 2008).

As presented above, this single specimen from Atzelsdorf cannot be compared with all genera known so far from the Upper Miocene of Europe. Therefore the author refers it to Hyaenidae indet.

Carnivora indet.

Material: NHMW 2008z0074/0000: large third phalange; NHMW 2008z0074/0000: proximal fragment of axis, dent is broad and flat; ATZ S145: first phalange, about the size of a large mustelid; NHMW 2008z0074/0000: fragment of the distal metapodial joint; NHMW 2008z0074/0000: lumbal vertebra

Remarks: This postcranial material is placed into Carnivora indet. because of the general morphology of the specimens but no further determination is possible.

Conclusion

Although only few carnivore remains were discovered in Atzelsdorf, an interesting variety of different taxa was found. Unfortunately, the poor and fragmentary material does not allow a specific determination of several taxa, like *Semigenetta* and *Plesiogulo* which can only be identified to the genus level. However, *Sansanosmilus vallesiensis* is reported for the first time from Austria and *Plesiogulo* cf. *crassa* from MN9 has been known only from Eastern Europe and Asian localities and now for the first time from Central Europe.

Acknowledgements

I want to thank Gudrun HÖCK (Natural History Museum Vienna), Gerald PENZ (Vienna) and Peter SCHEBECZEK (Pellendorf) for entrusting me with the material and Ursula GÖHLICH for her help with the inventory numbers. Yuriy SEMENOV (Academy of Sciences, Kiev) was so kind to compare the *Plesiogulo* find from Atzelsdorf with his material from Hritsev. I am grateful for the constructive remarks of the reviewers George KOUFOS and Stéphane PEIGNÉ. Rudolf GOLD (Department of Palaeontology, Vienna) compiled the figure and arranged the plate. Christina RÖMER corrected the English.

References

- ALCALÁ, L. MONTROYA, P. & MORALES, J. (1994): New large mustelids from the Late Miocene of the Teruel Basin (Spain). – *Comptes Rendues de l'Académie des Sciences*, (II) **319**: 1093-1100.
- BEAUMONT, G. de (1986): Les Carnivore (Mammifères) du Néogène de Höwenegg/Hegau, Baden-Württemberg. – *Carolinea*, **44**: 35-45.
- & CRUSAFONT-PAIRÓ, M. (1982): Les félidés (Mammifères, Carnivores) du Vallésien du Vallès, Catalogne, Espagne. – *Archives des Sciences Genève* **35/1**: 41-64.

- BONIS, L. de, (1973): Contribution à l'étude des mammifères de l'Aquitainien de l'Agenais. Rongeurs-Carnivores-Périssoctyles. – Mémoires du Muséum national d'Histoire naturelle, Nouvelle series (C) **28**: 1-192.
- CRUSAFONT, M. & GOLPE, J. (1981): Hallazgo de una especie del genero *Semigenetta* del Vindoboniense terminal de Castell de Barberà (Depresion prelitoral catalana; Espana). – Boletin de la Real Sociedad Espanola de Historia Natural (Geologia), **79**: 67-76.
- DE BONIS, L., PEIGNÉ, St., MACKAYE, H.T., LIKIUS, A., VIGNAUD, P. & BRUNET, M. (2008): The fossil vertebrate locality Kossom Bougoudi, Djurab desert, Chad: A window in the distribution of the carnivoran faunas at the Mio-Pliocene boundary in Africa. – Comptes rendu Palevol **7**: 571-581.
- DEHM, R. (1950): Die Raubtiere aus dem Mittel-Miozän (Burdigalium) von Wintershof-West bei Eichstätt in Bayern. – Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, Neue Folge, **58**: 1-141.
- DUBOIS, A. & STEHLIN, H.G. (1933): La grotte de Cotencher, station moustérienne. – Mémoires du Société Paléontologie Suisse, **52-53**: 1-22.
- FILHOL, H. (1883): Notes sur quelques Mammifères fossiles de l'époque Miocène. III: Observations relatives à divers Carnassiers fossiles provenant de La Grive Saint-Alban. – Archives du Muséum d'Histoire Naturelle de Lyon, **3**: 56-69.
- GAUDRY, A. (1861): Note sur les carnassiers fossiles de Pikermi (Grèce). – Bulletin de la Société géologique de France, **18**: 527-538.
- GERAADS D. & GÜLEÇ E. (1997): Relationship of *Barbourofelis piveteaui* (Ozansoy, 1965), a late Miocene nimravid (Carnivora, Mammalia) from Central Turkey. – Journal of Vertebrate Paleontology **17/2**: 370-375.
- GERVAIS, P. (1850): Zoologie et Paléontologie Française. – 1^e Édition: 1-271.
- GINSBURG, L. (1961): La faune des carnivores miocènes de Sansan (Gers). – Mémoires du Muséum national d'Histoire naturelle, Nouvelle Serie (C) **9**: 1-190.
- (1999): Order Carnivora. – In: RÖSSNER, G. & HEISSIG, K. (eds): The Miocene. Land Mammals of Europe. – pp. 109-168, München (Dr. Friedrich Pfeil Verlag).
- HAILE-SELASSIE, Y., HLUSKO, L. & HOWELL, C. (2004): A new species of *Plesiogulo* (Mustelidae: Carnivora) from the Late Miocene of Africa. – Paleontologia Africana, **40**: 85-88.
- HARRISON, J.A. (1981): A review of the extinct wolverine, *Plesiogulo* (Carnivora: Mustelidae), from North America. – Smithsonian Contribution to Paleobiology, **46**: 1-27.
- HARZHAUSER, M. (2009). The Early Vallesian vertebrates from Atzelsdorf (Austria, Late Miocene). 2. Geology. – Annalen des Naturhistorischen Museum Wien, Serie A, **111**: 479-488.
- HAY, O.P. (1921): Description of species of Pleistocene Vertebrata, type or specimens most of which are preserved in the United States National Museum. – Proceedings of the United States National Museum, **59**: 599-642.
- HELBING, H. (1927): Une genette miocène trouvée dans les argiles de Captieux (Gironde). – Verhandlungen der Naturforschenden Gesellschaft in Basel, **38**: 305-315.
- HENDEY, Q.B. (1978): Late Tertiary Mustelidae (Mammalia, Carnivora) from Langebaanweg, South Africa. Annals of the South African Museum, **76**: 329-357.

- HENSEL, R. (1862): Über die Reste einiger Säugethierarten von Pikermi in der Münchener Sammlung. – Monatsberichte der königlich. preussischen Akademie der Wissenschaften Berlin, **14**: 560-569.
- HEIZMANN, E. (1973): Die Carnivoren des Steinheimer Beckens. – Palaeontographica, Supplement **8** (5, B): 1-95.
- KOUFOS, G. (1982): *Plesiogulo crassa* from the Upper Miocene (Lower Turolian) of Northern Greece. – Annales Zoologici Fennici, **19**: 193-197.
- (2006): The late Miocene vertebrate locality of Perivolaki, Thessaly, Greece. – Palaeontographica A **276**: 39-74.
- KRETZOI, M. (1929): Materialien zur phylogenetischen Klassifikation der Aeluroiiden. – 10. Congress internationale Zoologie Budapest, **1927**: 1293-1355.
- KROTOKEVICH, E.L. & SEMENOV, Y.A. (1975): First findings of Neogene *Plesiogulo crassa* in the Northern Black Sea area. – Vestnik Zoologii, **4**: 33-38. [in Russian]
- KURTÉN, B. (1970): The neogene wolverine *Plesiogulo* and the origin of *Gulo* (Carnivora, Mammalia). – Acta Zoologica Fennica, **131**: 1-22.
- LARTET, E. (1851): Notice sur la colline de Sansan. – pp. 1-45, Auch (J.A. Portes).
- MORALES, J. PICKFORD, M., SORIA, D. & SELESA, M.J. (2004): Carnivores from the Late Miocene and basal Pliocene of the Tugen Hills, Kenya. – 32nd International Geological Congress, Florence 2004 – Scientific Sessions, abstract (part1): 380.
- MORLO, M. (1997): Die Raubtiere (Mammalia, Carnivora) aus dem Turolium von Dorn-Dürkheim 1 (Rheinhessen). Teil 1: Mustelidae, Hyaenidae, Percrocutidae, Felidae). – Courier Forschungsinstitut Senckenberg, **197**: 11-47.
- (2006): New remains of Barbourfelidae (Mammalia, Carnivora) from the Miocene of Southern Germany: implication for the history of barbourfelid migration. – Beiträge zur Paläontologie **30**: 339-346.
- , PEIGNÉ, S. & NAGEL, D. (2004): A new species of *Prosansanosmilus*: implication for the systematic relationship of the family Barbourfelidae new rank (Carnivora, Mammalia). – Zoological Journal of the Linnean Society **140**: 43-61.
- NAGEL, D. (2003): Carnivores from the Middle Miocene deposits of Grund (Lower Austria). – Annalen des Naturhistorischen Museums Wien, Serie A, **104**: 297-305.
- OZANSOY, F. (1965): Etude des gisements continentaux et des Mammifères du Cénozoïque de Turquie. – Mémoires de la Société géologique de France, N.S., **44**: 1-92.
- PETTER, G. (1976): Étude d'un nouvel ensemble de petits carnivores du Miocène d'Espagne. – Géologie méditerranéenne, **3/2**: 135-154.
- QIU, Z., HUANG, W. & GUO, Z. (1979): Hyaenidae of Qingyang (K'ingyang) Hipparion fauna. – Vertebrata Palasiatica, **17**: 200-221. [in Chinese with English summary]
- SCHLOSSER, M. (1903): Die fossilen Säugetiere Chinas nebst einer Odontographie der recenten Antilopen. – Abhandlungen der mathematisch-physikalischen Klasse der königlich bayrischen Akademie der Wissenschaften, **22/1**: 1-221.
- SEMENOV, Y.A. (1989): Ictitheres and morphologically similar hyaenas from the Neogene of the USSR. – Naukova dumka: 1-180. [in Russian with English summary]
- (2008): Taxonomical reappraisal of "ictitheres" (Mammalia, Carnivora) from the Late Miocene of Kenya. – Comptes Rendus Palevol, **7** (8): 529-539.

- THENIUS, E. 1989. Zähne und Gebiß der Säugetiere. – In: NIETHAMMER, J., SCHLIEMANN, H. & STARCK, D. (eds): *Handbuch der Zoologie. VIII Mammalia.* – 513 pp., Berlin (Walter de Gruyter).
- TEILHARD DE CHARDIN, P. & LEROY, P. (1945): Les Mustélidés de Chine. – *Institut de Géobiologie*, **12/2**: 1-56.
- TSENG, Z.J. & WANG, X. (2007): The first record of the Late Miocene *Hyaenictitherium hyaenoides* ZDANSKY (Carnivora: Hyaenidae) in inner Mongolia and an evaluation of the genus. – *Journal of Vertebrate Paleontology*, **27/3**: 699-708.
- TURNER, A., ANTÓN, M. & WERDELIN, L. (2008): Taxonomy and evolutionary patterns in the Hyaenidae of Europe. – *Geobios*, **41**: 677-687.
- VILLALTA, J.F. DE & CRUSAFONT, M. (1943): Los Vertebratos del Mioceno continental de la Cuenca Vallés-Penedés (Provincia Barcelona). I: Insectivora. II: Carnívoros. – *Boletín del Instituto geológico y Minero de España* (3), **56**: 145-336.
- VIRANTA, S. & WERDELIN, L. (2003): Carnivora. – In: FORTELIUS, M., KAPPELMANN, J., SEN, S. & BERNOR, R.L. (eds): *Geology and Paleontology of the Miocene Sinap Formation, Turkey.* – pp. 178-193, New York (Columbia University Press).
- VIRET, J. (1939): Monographie paleontologique de la aune de Vertébrés des Sables de Montpellier. III: Carnivora, Fissipedia. – *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon*, **37/2**: 1-26.
- VON NORDMANN, A. (1850): see GERVAIS (1850).
- WERDELIN, L. (2004): Carnivora. – In: LEAKEY, M.G. & HARRIS, J.M. (eds): *Lothagam: The dawn of humanity in Eastern Africa.* – pp. 261-330, New York (Columbia University Press).
- & SOLOUNIAS, N. (1991): The Hyaenidae: taxonomy, systematics and evolution. – *Fossils and Strata*, **30**: 1-104.
- WOLSAN, M. & SEMENOV Y.A. (1996): A revision of the late Miocene mustelid carnivoran *Eomellivora*. – *Acta zoologica cracoviensia*, **30/1**: 593-604.
- YOUNG, C.C. & LIU, P.T. (1948): Notes on a mammalian collection probably from the Yushe series (Pliocene), Yushe, Shansi, China. – *Contributions of the Institute of Geology, Nanking*, **8**: 273-291.
- ZDANSKY, O. (1924): Jungtertiäre Carnivoren Chinas. – *Paleontologica Sinica* (C), **2/1**: 1-149.

