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The early Vallesian vertebrates of Atzelsdorf (Late Miocene, Austria) 8. *Anchitherium*, Suidae and Castoridae (Mammalia)

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(With 10 figures and 6 tables)

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Abstract

The early Late Miocene (Early Vallesian, MN9) locality Atzelsdorf in Lower Austria yielded a diverse collection of land mammals and lower vertebrates. Herein, we describe six mammalian species: two castorids *Trogontherium* (*Euroxenomys*) *minutum* and *Steneofiber* sp., three suids *Albanohyus* cf. *pygmaeus*, *Parachleuastochoerus kretzoii* and Suidae incertae sedis, and the equid *Anchitherium aurelianense*. The cooccurrence of the primitive brachydont equid *Anchitherium* and the newly immigrant hypsodont *Hippotherium* is an association of basal Vallesian (MN9) assemblages in Central Europe. Atzelsdorf provides a new evidence of this event from the early Late Miocene Palaeo-Danube delta in Lower Austria. In this area the cooccurrence of these two horses is limited to zone C of the Early Pannonian (indicated by the bivalve *Mytilopsis hoernesi* and the first occurrence of *Hippotherium*) with a maximum time range of 11.2 to 10.6 Ma.

Keywords: Taxonomy, biostratigraphy, Pannonian C, palaeoecology, Palaeo-Danube delta.

Zusammenfassung

Die Lokalität Atzelsdorf in Niederösterreich aus dem frühen Spät-Miozän (frühes Vallesium, MN9) erbrachte eine vielfältige Sammlung von Landsäugetieren und Niederen Wirbeltieren. Davon werden hier sechs Säugetierarten beschrieben: die Castoridae *Trogontherium* (*Euroxenomys*) *minutum* und *Steneofiber* sp., die Suidae *Albanohyus* cf. *pygmaeus*, *Parachleuastochoerus kretzoii* und Suidae incertae sedis, und als Vertreter der Equidae das *Anchitherium aurelianense*. Das gemeinsame Vorkommen des primitiven brachyodonten *Anchitherium* und des neu eingewanderten hypsodonten *Hippotherium* ist in Mitteleuropa auf Faunen des basalen Vallesium (MN9) beschränkt. Atzelsdorf liefert dafür einen neuen Beleg aus dem frühen Spät-Miozän im Delta der "Ur-Donau" in Niederösterreich. Hier ist das gemeinsame Vorkommen auf die Zone C des Frühen Pannonium beschränkt (die Zone C ist durch das Vorkommen der Muschel *Mytilopsis hoernesi* und durch das Erstauftreten von *Hippotherium* belegt). Der entsprechende Zeitabschnitt reicht von 11.2 bis höchstens 10.6 Millionen Jahre vor heute.

Schlüsselworte: Taxonomie, Biostratigraphie, Pannonium C, Paläoökologie, Delta der „Ur-Donau".

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Introduction

The fossil site Atzelsdorf in the Northern Vienna Basin includes vertebrate fossils of extraordinary importance. The majority of the assemblage was collected by two private collectors, P. Schebeczek and G. Penz, who consequently visited the abandoned sand- and gravel pit in Atzelsdorf over many years. Finally, in 2003 integrated geological and palaeontological field activities were carried out by the Museum of Natural History Vienna in the Late Miocene Palaeo-Danube delta in the Northern Vienna Basin. Within the framework of these investigations the Atzelsdorf section was studied (Harzhauser 2009), and systematic excavations were undertaken of the Atzelsdorf local fauna. Currently, the total Atzelsdorf collection includes a diverse assemblage of large mammals, only a few small mammals all with remarkably low individual numbers. Except for turtles, the record of lower vertebrates is poor. However, this unusual vertebrate-composition was obviously affected by taphonomical processes.

The locality Atzelsdorf is an old gravel pit NW of the village of Atzelsdorf near Mistelbach in Lower Austria (N 48°30'37", E 16° 32'39"). The site is situated in the marginal part of the late Miocene Palaeo-Danube delta and displays sand and gravels of the Hollabrunn-Mistelbach Formation (Nehyba & Roetzel 2004). For details on the locality's stratigraphy see Harzhauser (2009: fig. 1). From this region several time correlative fossil localities including Gaiselberg, Obersulz, Mistelbach, Mariathal, Magersdorf, and Pellendorf, have yielded diverse plant and vertebrate assemblages and provide a rich fossil record of warm-temparate mesophytic forests (Bernor et al., 1988; Daxner-Höck 1975, 2004a; Harzhauser et al. 2003; Zapfe 1948).The biostratigraphic correlation of Atzelsdorf is with the Early Pannonian (letter Zone C; Papp 1951) and the lowermost Vallesian (MN9) (fig. 1).

Material and methods

The investigated material includes six premolars, four molars and three incisor-fragments of two different beavers. There are two cheek teeth (one of them is badly damaged) and two incisors of the primitive equid *Anchitherium*. A mandible, four partly fragmentary incisors, two canines and two molars support the presence of at least two different suids *Albanohyus* sp. and *Parachleuastochoerus kretzoii*. The digital photos were taken by A. Schumacher and G. Daxner-Höck. The most interesting Atzelsdorf fossils from the private collections Schebeczek and Penz were molded, and the casts are integrated in the collections of the NHMW.

To facilitate easier comparisons all right side teeth of Castoridae are figured as mirror images, and their figure numbers are underlined, e.g fig. 10/1a-c (= right m1/2).

For classification and terminology of dental structures we follow: Hugueney (1999) for Castoridae, Abusch-Siewert (1983) for *Anchitherium*, and Bernor & Fessaha (2000), Bernor et al. (2004) and Fortelius et al. (2005). Additionally the following terminology is used for Suidae:

Innenhügel – the lingual cusp of the twinned main cusp found on p4;

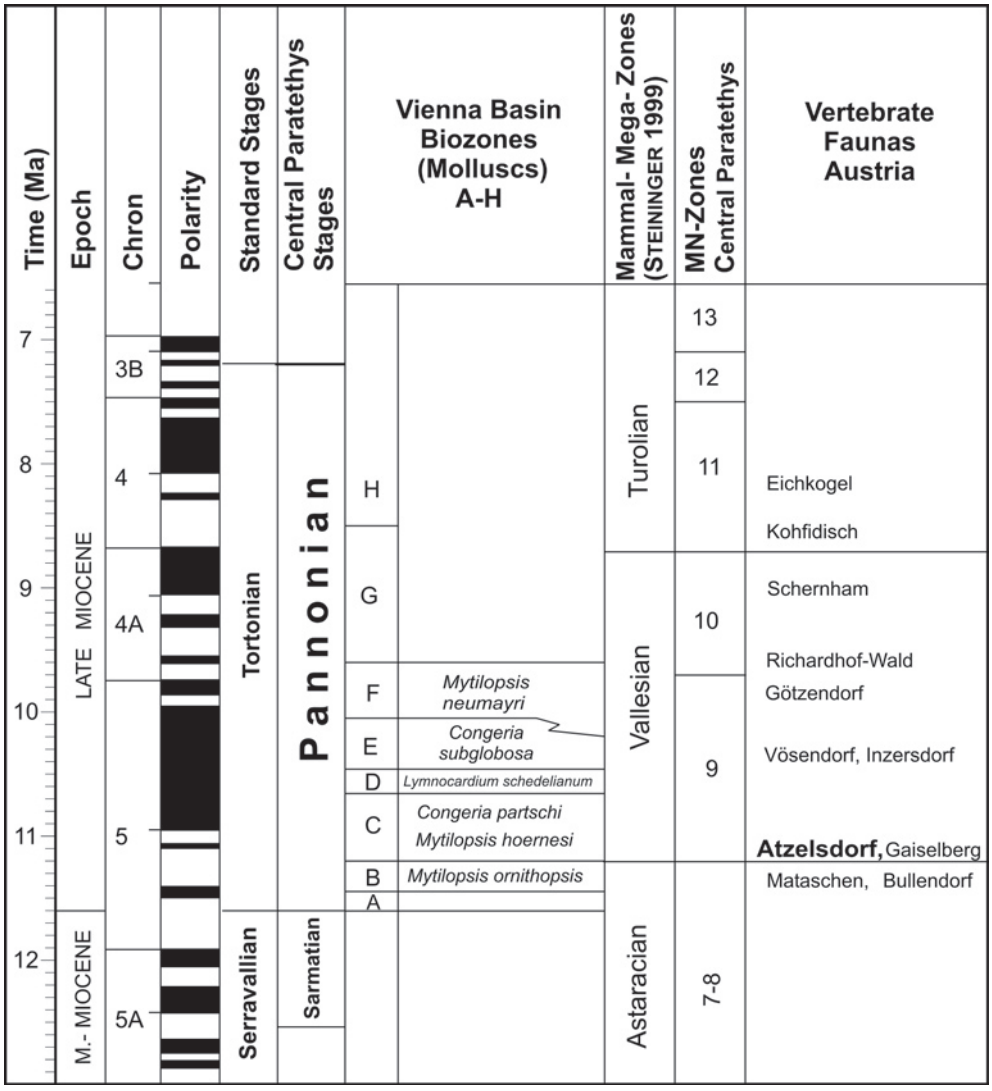

Fig. 1. Chronostratigraphy and biostratigraphy of the Pannonian; modified after MAGYAR et al. (1999) and DAXNER-HÖCK (2004a).

mesial ridge – the ridge descending on the mesial (anterior) surface of the mandibular premolar principal cusp to the base of the crown;

distal ridge – the ridge descending on the distal (posterior) surface of the mandibular premolar cusp to the base of the crown;

Furche – any one of the deep enamel folds or grooves that partition molar cusps in a regular pattern (Furchenmuster) as recognized by HÜNERMANN (1968), see also PICKFORD (1986, 1988). These are not to be confused with the shallow enamel wrinkles that are also commonly found on the surface of suid teeth.

Abbreviations

c	lower canine
C	upper canine
FOD	first occurrence datum
inc	lower incisor
Inc	upper incisor
l	left (from the left side)
LOD	last occurrence datum
m1-3	mandibular (lower) molars
M1-3	maxillary (upper) molars
NHMW	coll. Naturhistorisches Museum Wien
P.	coll. PENZ
p4	mandibular (lower) 4th premolar
P4	maxillary (upper) 4th premolar
r	right (from the right side)
S.	coll. SCHEBECZEK

Measurements of *Anchitherium* teeth:

BL	basal length of cheek teeth
Ht	height of the crown
MHt	mesostyle height
OL	occlusal length of incisors in mesial-distal direction
OW	occlusal width of incisors in labial-lingual direction
W	maximum width of cheek teeth

Measurements on Suidae teeth:

BERNOR & FESSAHA (2000) developed measurement methods for suids that were subsequently followed by BERNOR et al. (2004) and FORTELIUS et al. (2005). We use these same methods here for measuring the *Parachleuastochoerus* teeth and comparing them to the relevant Rudabánya sample.

M1 = basal length
M2 = occlusal length
M3 = mesial width (Wm)
M4 = mesial height
M5 = distal width (Wd)
M6 = distal height
M7 = on m3 talonid width
M8 = height

Measurements of Castoridae teeth:

L (m-d)	incisors length of the transversal section in mesial-distal direction
L	occlusal length of cheek teeth
W (la-li)	incisors width of the transversal section in labial-lingual direction
Wd	distal occlusal width of cheek teeth
Wm	mesial occlusal width of cheek teeth

Systematic part

Order Perissodactyla OWEN, 1848

Family Equidae Gray, 1821

Genus *Anchitherium* VON MEYER, 1844

Anchitherium aurelianense (CUVIER, 1812)

(fig. 2, tab. 1)

T y p e l o c a l i t y : Montabuzard (France), Early Miocene (MN4).

L o c a l i t y : Atzelsdorf in Lower Austria, Hollabrunn-Mistelbach Formation; Late Miocene (Early Pannonian, letter zone C; Early Vallesian, MN9).

M a t e r i a l (tab. 1): One right upper molar (M3), a fragmentary left upper cheek tooth (P/M), and two incisors from the collections SCHEBECZEK (S.1), PENZ (P. 20, 22) and from the NHMW (Inv.No. 2008z0063/0004).

D e s c r i p t i o n : The M3r (fig. 2/1-3) is trapezoidal in occlusal outline with a strongly reduced disto-labial corner. Thus, the mesial width extends almost one third beyond the distal width. The lophodont paracone and metacone are integrated in the ectoloph. The bunodont lingual cones protocone and hypocone are continuous with the S-shaped protoloph and metaloph, respectively. Protoloph and metaloph contact the ectoloph. Protoconule and crochet are present. Parastyle and mesostyle are prominent. The tooth is supplied with a semi-continuous cingulum. The labial cingulum is weak, it extends from parastyle towards mesostyle. The pronounced distal and lingual cingula are continuous. The mesial cingulum extends in lingual direction towards the base of protocone. Two pronounced conules are situated on the mesial and lingual cingulum, respectively. The prominent hypostyle consists of two arms contacting mesially at a right angle. Distally. The two arms are fused with the distal cingulum. No roots are preserved.

The fragment of a left premolar or molar (fig. 2/4) displays part of the labial cusps and the metaloph. There is a weak crochet and small metaconule on the metaloph.

The upper incisor (fig. 2/5-8) has a slightly asymmetrical crown-shape, and an almost straight root, indicating a 2nd incisor. The crown is almost as high as wide (in labial-lingual direction). The maximal length was measured close to the cutting edge of the

Tab. 1. *Anchitherium aurelianense* (CUVIER, 1812), measurements (in mm).

object	coll.	NHMW Inv.No. of (casts) and original	fig.	measurements (mm) BL	W	MHt
M3r	S. 1	(2008z0063/0001)	2/1-3	17.8	24.6	7.5
P/Ml	P. 22	(2008z0063/0002)	2/4	--	--	--
				OL	OW	Ht
Inc2r	P. 20	(2008z0063/0003)	2/5-6	8.6	7.9	7.5
inc2/3l	NHMW	2008z0063/0004	2/7-8	7.6	5.6	7.5

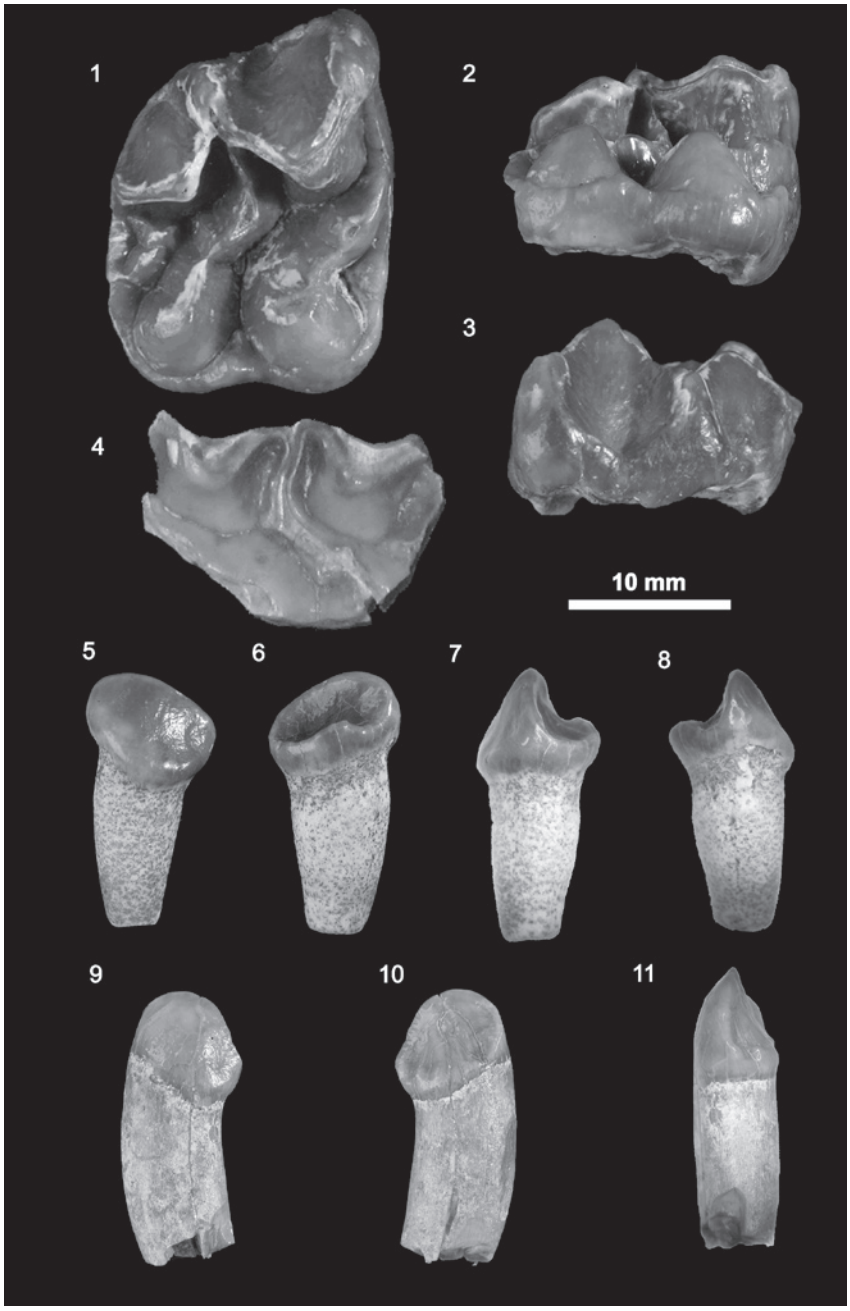

Fig. 2. *Anchitherium aurelianense* (Cuvier, 1812) from Atzelsdorf, Late Miocene (MN9). Scale bar equals 10 mm.
1-3 right M3; coll. Schebeczek (S. 1); 1: occlusal, 2: lingual, 3: labial.
4 left fragmentary P or M; coll. Penz (P. 22); occlusal.
5-6 right I2 sup.; coll. Penz (P. 20); 5: labial, 6: lingual, 7: distal, 8: mesial
7-8 left i2/3 inf.; coll. NHMW (2008z0063/0004); 9: labial, 10: lingual, 11: distal.

tooth. On the lingual side a prominent central basin is visible. It is surrounded by a strong lingual cingulum, which continues on both sides towards the cutting edge (fig. 2/6-7). The cutting edge is asymmetrical with its highest portion placed mesially. The deep central basin is indicative of upper incisors, and the slightly asymmetrical shape and straight root suggest that it is a 2nd upper incisor. The 1st would be more symmetrical, and the 3rd would be more asymmetrical (ABUSCH-SIEWERT 1983: Abb. 20-23).

The lower incisor (fig. 2/9-11) has no lingual basin but a pronounced cutting edge, indicating a lower incisor. The more asymmetrical shape of crown and root hints to a 2nd or 3rd lower incisor.

D i s c u s s i o n : Anchitheriine equids first extended their range into Eurasia in the early Miocene. The most diverse and broadly distributed genus *Anchitherium* is first recorded in Europe in the mammal-Zone MN3, including the localities Chitenay, Neuville and Chitelleurs (France) and Wintershof-West (Germany) and Merkur (Czech Republic; FEJFAR et al. 2003). Likewise, *Anchitherium* frequently occurs in Early- to Middle Miocene faunas and abruptly goes extinct shortly after basal Late Miocene (BERNOR & ARMOUR-CHELU 1999).

ABUSCH-SIEWERT (1983) recognized three clades of *Anchitherium*, including *A. aurelianensis* with three subspecies-lineages: *A. aurelianensis aurelianensis* (CUVIER, 1812) (ranging from Wintershof-West / MN3 to Sandelzhausen and Georgensgmünd / MN5), *A. aurelianensis steinheimensis* ABUSCH-SIEWERT, 1983 (recorded from Steinheim / MN7) and *A. aurelianensis hippoides* (LARTET, 1851) (recorded from Sansan / MN6 and La Grive / MN7). A second clade would be the large *A. ezquerrae* VON MEYER, 1844 with two subspecies known from the Miocene of Spain: *A. ezquerrae ezquerrae* VON MEYER, 1844 (Middle Miocene) and *A. ezquerrae sampelayoi* VILLALTA & CRUSAFONT, 1945 (Late Miocene). A third clade would be represented by the large *A. zitteli* SCHLOSSER, 1903 known from the Miocene of China.

Before, ZHAI (1962, 1963) recognized significant differences between the European *Anchitherium*-species and the Asian *A. zitteli*, and had established the genus *Sinohippus* for this species. *Sinohippus* differs by larger size and by some morphological features in the cheek teeth, such as the absence of lingual cingula in upper and lower cheek teeth and relatively high crowns (SALESA, SANCHÉZ & MORALES 2004: 193). Moreover, the width of the premolars of *Sinohippus* decreases from posterior towards anterior, and that of the molars towards posterior (YE et al. 2005). Recently the large sized species *A. ezquerrae sampelayoi* (sensu ABUSCH-SIEWERT 1983) from Nombrevilla I (Spain; MN9) with marked tendency towards hypsodonty and the absence of cingula on cheek teeth was determined as *Sinohippus sampelayoi*, whereas the conservative dental pattern of horses from Nombrevilla II (Spain; MN7/8) are characteristic of *Anchitherium* sensu stricto (SALESA, SANCHÉZ & MORALES 2004: 192). In their opinion also some large sized specimens from Vallesian sites in Turkey and from Soblay (France/MN10) would represent *Sinohippus*, indicating the dispersal of the Asian genus *Sinohippus* simultaneously with the North American *Hippotherium* towards the West, and immigrating in Asia Minor, France and Spain at the beginning of the Vallesian (SALESA, SANCHÉZ & MORALES 2004: 194).

The monospecific genus *Paranchitherium* BORISSIAK, 1938 from the Miocene of Georgia (Caucasus) is much closer to the New World *Parahippus* LEIDY, 1858 in having a

connected crochet, thin cement, and rather well-developed metaconid and metastylid (Forsten 1982).

All Central European occurrences belong to the evolutionary line of *Anchitherium aurelianensis*, showing a general trend towards size-increase and simplification of dental pattern. But only rich materials allow identification on the subspecies level, as they have a wide variability and overlap in morphology and measurements (Abusch-Siewert 1983). Some isolated teeth from Anwil (Switzerland) and from Wißberg, Esselborn, Salmendingen, Melchingen, Massenhausen, Wartenberg, Friedberg (Germany) (ranging from MN7/8 to MN9) with substantial differences in dental-morphology and dimensions were comprised as *A. aurelianensis* subspec. indet. by Abusch-Siewert (1983).

The Atzelsdorf fauna includes the primitive equid *Anchitherium*, characterized by its very low crowned cheek teeth, pronounced cingula, the presence of a distinct crochet and prominent hypostyle. The specimens described here are referred to *A. aurelianense* without subspecies-attribution. *Sinohippus* is certainly excluded on the basis of both morphology and size dimensions. In Austria, *Anchitherium* is one of the rare elements of Early- and Middle Miocene faunas, and discoveries in earliest Late Miocene deposits, are extraordinary. The specimens from Atzelsdorf, and also a left mandible with p3-m3 from Straß south of Lohnsburg in Upper Austria (Thenius 1952: fig.1) are referable to *A. aurelianense* based on dental characters. Moreover, some postcranial bones were described from four localities of the Palaeo-Danube delta in the vicinity of Atzelsdorf, including Mariathal, Gaiselberg, Magersdorf and Radlbrunn (Thenius 1950; Steininger 1963), and yet other postcranials of *Anchitherium* were recognized from three places in the Styrian Basin, Holzmannsdorfberg, Laßnitzhöhe, and Brunn b. Nestelbach (Mottl 1955, 1970). In almost all of these Austrian localities *Anchitherium* is associated with the second equid *Hippotherium*. The occurrences from Atzelsdorf, Gaiselberg, Mariathal, Magersdorf and Radlbrunn can be correlated with the earliest Vallesian (MN9, Pannonian C stage). There, *Anchitherium* (LOD) and *Hippotherium* (FOD) cooccur within the 11.2 to 10.6 Ma interval.

Order Artiodactyla Owen, 1848

Superfamily Suoidea Gray, 1821

Family Suidae Gray, 1821

Genus *Albanohyus* Ginsburg, 1974

Albanohyus cf. *pygmaeus* (Depéret, 1892)

(fig. 3, tab. 2)

T y p e l o c a l i t y : La Grive (France); Middle Miocene (MN7/8).

L o c a l i t y : Atzelsdorf in Lower Austria, Hollabrunn-Mistelbach Formation; Late Miocene (Early Pannonian, letter zone C; Early Vallesian, MN9).

M a t e r i a l (tab. 2): Two isolated maxillary molars from the collections Schebeczek (S.38) and the NHMW (Inv.No. 2008z0064/0001).

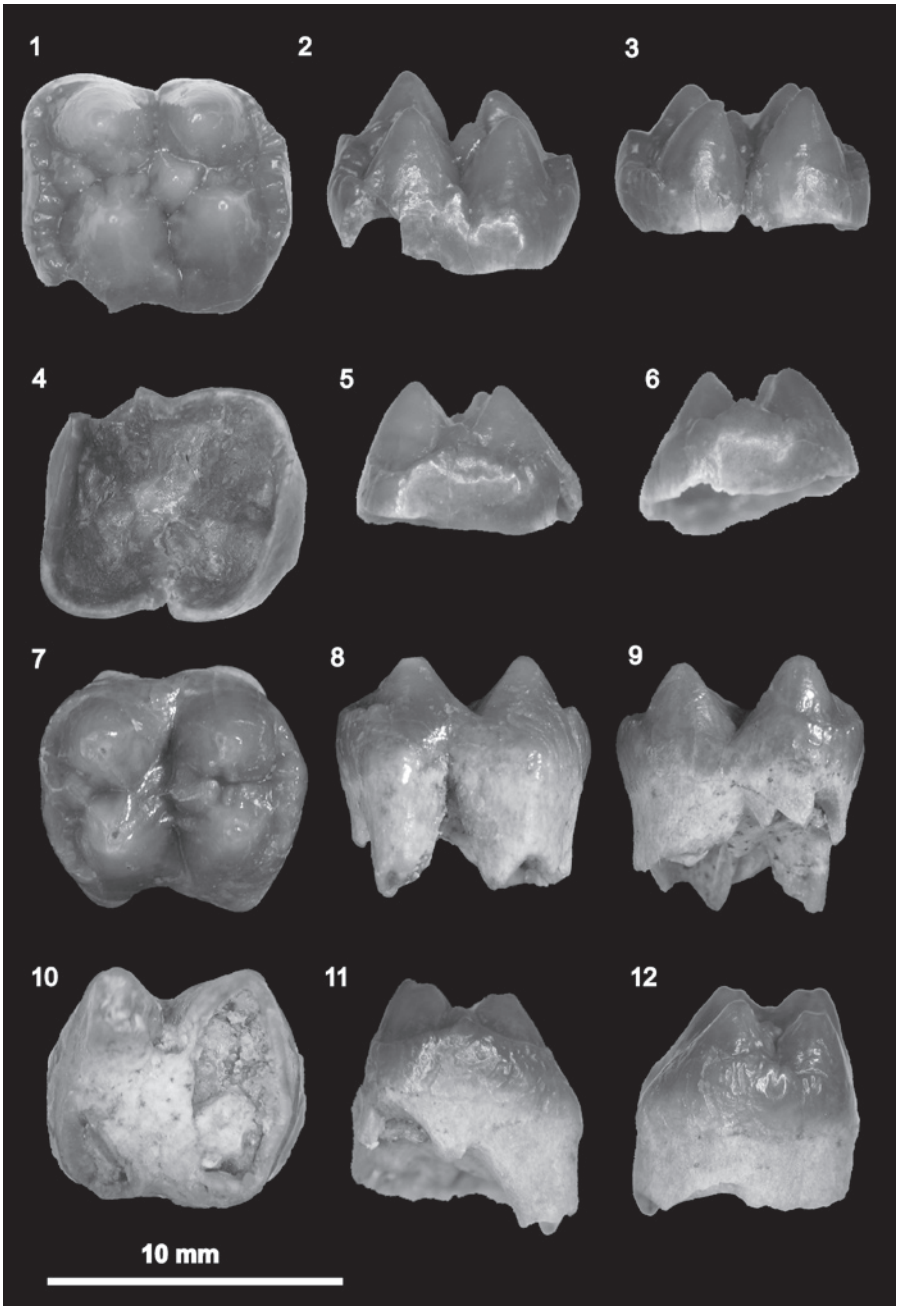

Fig. 3. *Albanohyus* cf. *pygmaeus* (DEPÉRET, 1892) from Atzelsdorf, Late Miocene (MN9). Scale bar equals 10 mm.

1-6 left M1/2; coll. NHMW (2008z0064/0001); 1: occlusal, 2: lingual, 3: labial, 4: basal, 5: mesial, 6: distal.

7-12 left M2; coll. SCHEBECZEK (S. 38); 7: occlusal, 8: lingual, 9: labial, 10: basal, 11: mesial, 12: distal.

D e s c r i p t i o n : M1/2 (fig. 3/1-6) is an unerupted first or second left molar lacking roots. It has four high cusps with sharp to subrounded apices, forming nearly symmetrical labio-lingual pairs. The lingual cusps are slightly more distally positioned than the labial ones. There is a strongly developed rounded central pillar positioned between the main cusps, and contacting the mesial surfaces of metacone and hypocone. It is accompanied by three small conules, two of them positioned mesial and one distal of it. A well developed crest descending from the mid-labial aspect of the protocone meets a similar crest descending from the paracone. The tooth has a strong, almost continuous cingulum, most heavily developed mesially and distally where it is presented as a beaded shelf. The mesial cingular shelf has a prominent conule lodged between paracone and protocone. There is also a swollen conule on the distal cingular shelf. Labially and lingually the cingulum is partly interrupted. The lingual, labial, mesial and distal views (fig. 3/2-3, 5-6) reveal that the main cusps are almost equal in elevation.

M2 (fig. 3/7-12) has high cusps that are slightly worn at their apices and a semi-continuous cingulum. The cingulum is very well developed mesially and distally; the distal shelf is beaded. The lingual and labial cingulum is semi-continuous, as in the previously described specimen, except for the lingual base of the hypocone where there is an accentuated bulge. The distal beaded cingulum is extended continuously mesialward between metacone and hypocone closely approaching the central pillar. The central pillar itself is not rounded as in M1/2 (fig. 3/1), but angular and trenchant mesialward (fig. 3/7). The paracone-protocone and metacone-hypocone are almost symmetrically aligned. The placement and development of the various conules and crests is also similar to M1/2 (fig. 3/7). The lingual roots are clearly separated.

D i s c u s s i o n : The left M1/2 and M2 from Atzelsdorf compare well with *Albanohyus pygmaeus* from La Grive (France; MN7/8) figured by VAN DER MADE (1996: fig. 2 Aa, Ab, Ac; right M1-3 specimen numbers LGr1559, LGr1560 and fig. 2 Ba, Bb, Bc, Bd; right M2 specimen number LGr 1563, also provided to us as digital photographs by ORLIAC). The teeth from Atzelsdorf and La Grive share the details of cusp and cingulum morphology and the placement of the accessory mesial conule, central pillar, distal conule, and the root numbers. The dimensions of M1/2 and M2 from Atzelsdorf are within the size range of M2 from La Grive, whereas M1 from La Grive is smaller (VAN DER MADE 1996: fig. 5).

VAN DER MADE (1996) has provided a useful review of the genus *Albanohyus* and its distinction from *Taucanamo*. GINSBURG (1974) was the first to recognize, and name *Albanohyus* from Artenay and La Grive. He gave a number of arguments for distinguishing *Taucanamo* and *Albanohyus*. GOLPE POSSE (1977) recognized a peccary at Castell de Barbera, which she referred to *Barberahyus castellensis*. CHEN (1984) tentatively

Tab. 2. *Albanohyus* cf. *pygmaeus* (DEPÉRET, 1892), measurements (in mm).

object	coll.	NHMW Inv.No. of original and (cast)	fig.	measurements (mm) L	Wm	Wd
M1/2l	NHMW	2008z0064/0001	3/1-6	8.55	7.80	7.80
M2l	S. 38	(2008z0064/0002)	3/7-12	8.70	7.50	8.10

recognized *Barberahyus castellensis* from Przeworno 2 which had previously been referred to *Taucanamo sansaniense* by KUBIAK (1981). VAN DER MADE (1996) referred these collections of "*Barberahyus*" to *Albanohyus. Albanohyus* is very easily mistaken as being *Taucanamo.*

Taucanamo species differ from *Albanohyus* in their tendency for molars to become quasi lophodont and elongate, whereas *Albanohyus* M1 and M2 are more quadrate. Also, the Atzelsdorf M1/2 and M2 compare closely with *Albanohyus* in their well individualized mesial conule (= paraconule of ORLIAC, pers. Commun.) being clearly distinct from the mesial cingulum. Also, *Albanohyus* has, as a rule, a more continuous cingulum around the base of the molar teeth than *Taucanamo.* Finally, as in *Albanohyus* but not *Taucanamo*, the Atzelsdorf M2 has roots that are not fused below the base of the crown. Clearly, *Albanohyus* and *Taucanamo* are distinct taxa, apparently belonging to separate families of Suoidea. According to ORLIAC et al. (2006: figure 12) *Albanohyus* belongs to a subfamily incertae sedis.

FORTELIUS et al. (1996) have calculated the body mass of *Taucanamo grandaevum* as being 9 kg, which would be the approximate (or slightly less) the size of the Atzelsdorf *Albanohyus* cf. *pygmaeum*.

The NOW database lists two species: the larger *Albanohyus castellensis* (GOLPE POSSE, 1977) from Castell de Barbera (Spain; MN 7-8), Nombrevilla I (Spain; MN 9) and Doué-la-Fontaine (France; MN 9) and the smaller *Albanohyus pygmaeus* is listed as occurring at La Grive St. Alban (France; MN7-8), Przeworno 2 (Poland; MN7-8) and Four (France; MN 6). If most closely related to the *Albanohyus pygmaeus* lineage as appears here, the Atzelsdorf *Albanohyus* cf. *pygmaeus* would represent the latest stratigraphic occurrence of the taxon. The association of *Anchitherium* + *Hippotherium* + *Albanohyus* is therefore characteristic of the Central European basal MN 9 – Pannonian C biozone.

Subfamily Tetraconodontinae SIMPSON, 1945

Genus *Parachleuastochoerus* GOLPE-POSSE, 1972

Parachleuastochoerus kretzoii FORTELIUS et al., 2005

(fig. 4-6, tab. 3)

T y p e l o c a l i t y : Rudabánya, locality II (Hungary), Late Miocene (MN9).

L o c a l i t y : Atzelsdorf in Lower Austria, Hollabrunn-Mistelbach Formation; Late Miocene (Early Pannonian, letter zone C; Early Vallesian, MN9).

M a t e r i a l (tab. 3): A left mandible with p4-m3 from the collection SCHEBECZEK (S. 96) (the cast: NHMW 2008z0065/0001).

Generic characters modified after PICKFORD (1981): Primitive tetraconondont suids in which the canines are sexually dimorphic; heteromorphism between the P1/p1-P2/p2 not as strong as in *Conohyus*; P2 much lower crowned than P3; P3 inflated with wrinkled enamel and complete lingual cingulum; P4 with two labial cusps closely applied to each other, but not completely fused and with wrinkled labial enamel and slight

labial cingulum; p3-4 not as inflated as those of other tetraconodonts; p4 lacking sagittal cusplets and with reduced Innenhügel, placed distal to the main cusp or conjoined with the principal cusp; labial cingula present on upper and lower molars; enamel thin compared to species of *Conohyus* (contrary to PICKFORD 1981); molar furchen shallow; postcranial skeleton generally gracile.

D e s c r i p t i o n (fig. 4): The p4 is likely 3-rooted, supporting an expanded distal heel, inflated labiolingually, with the widest part being immediately distal to the principal cuspid. Innenhügel is clearly fused with the principal cuspid, while the principal cuspid is high and separated from the distal heel by a deep labial and a shallow lingual invagination. The heel is raised more than half the height of the principal cusp and has two small, obliquely disposed facets oriented lingually and labially.

The m1 is a rectangular-shaped likely 4-rooted tooth. The dentine pools are well exposed for the protoconid, metaconid, hypoconid and entoconid which are themselves transversely aligned. The mesial cuspid pair has a narrower width dimension than the distal cuspid pair. The heel is composed of a tiny distal cuspid (= hypoconulid) also worn with extensively exposed dentine. There is a large, distinct cingular shelf present on the labial side developed labial to the valley between the two labial cusps.

The m2 is a larger, rectangular shaped and likely 4-rooted tooth. The mesial fovea is a restricted, V-shaped (oriented distalward) structure. The dentine pools are only beginning to show on the mesial pair of cuspids; the protoconid-metaconid and hypoconid-entoconid apices again rise high above the floor of the central portion of the tooth, and the lingual cuspids are substantially higher than their labial counterparts. The heel is marginally larger with a better developed hypoconulid than in m1, and there is again a well developed cingular shelf on the medio-labial aspect of the tooth.

The m3 is likely a 5-rooted, relatively broad tooth. The mesial fovea is very restricted. The metaconid cuspid is much higher than the protoconid while the hypoconid-entoconid are subequal in height. The elevation of cuspids above the floor of the crown are as in m1-2. The cingulum is more developed on the mesial and labial surfaces than found in m1 and m2, forming a beaded ledge between the protoconid and hypoconid cuspids. The heel is broad, short and cuspidate.

D i s c u s s i o n : *P. kretzoii* (from Rudabánya, Hungary; MN9) is larger than the type species *P. crusafonti* PICKFORD, 1981 (from Can Llobateres, Spain; MN9). The propor-

Tab. 3. *Parachleuastochoerus kretzoii* FORTELIUS et al., 2005, measurements (in mm).

	p4	m1	m2	m3
M1 = basal length	11.9	12.0	13.7	20.8
M2 = occlusal length	12.2	12.2	15.9	18.4
M3 = anterior width	9.7	10.9	12.2	12.8
M4 = anterior height	10.6	7.7	9.8	11.1
M5 = posterior width	9.2	10.2	12.2	11.9
M6 = posterior height	8.8	7.6	9.0	10.0
M7 = on m3 talonid width				8.8
M8 = height				5.5

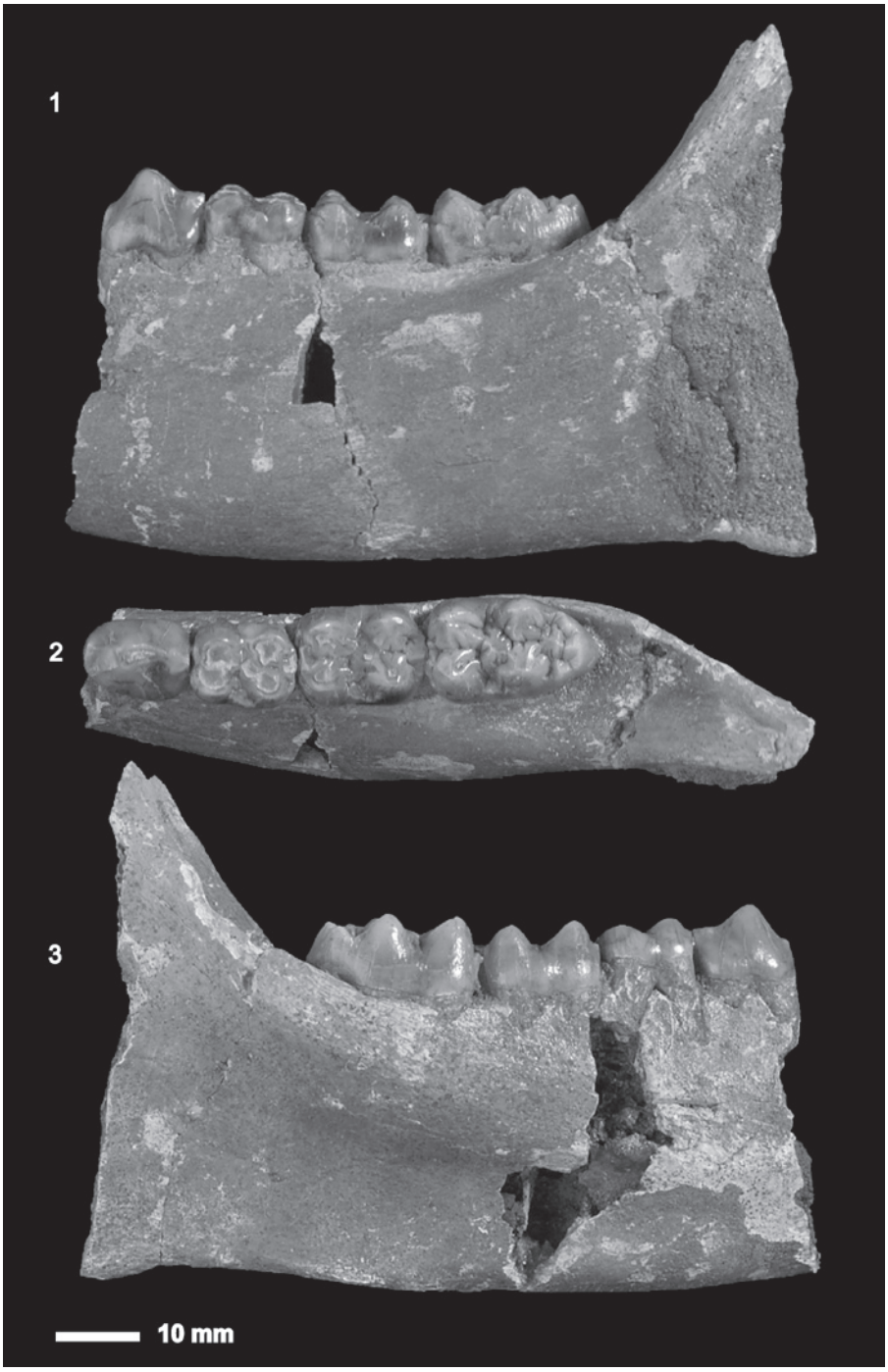

Fig. 4. *Parachleuastochoerus kretzoi* FORTELIUS et al., 2005 from Atzelsdorf, Late Miocene (MN9). Left mandible with p4-m3; coll. SCHEBECZEK (S. 96). 1: labial, 2: occlusal, 3: lingual. Scale bar equals 10 mm.

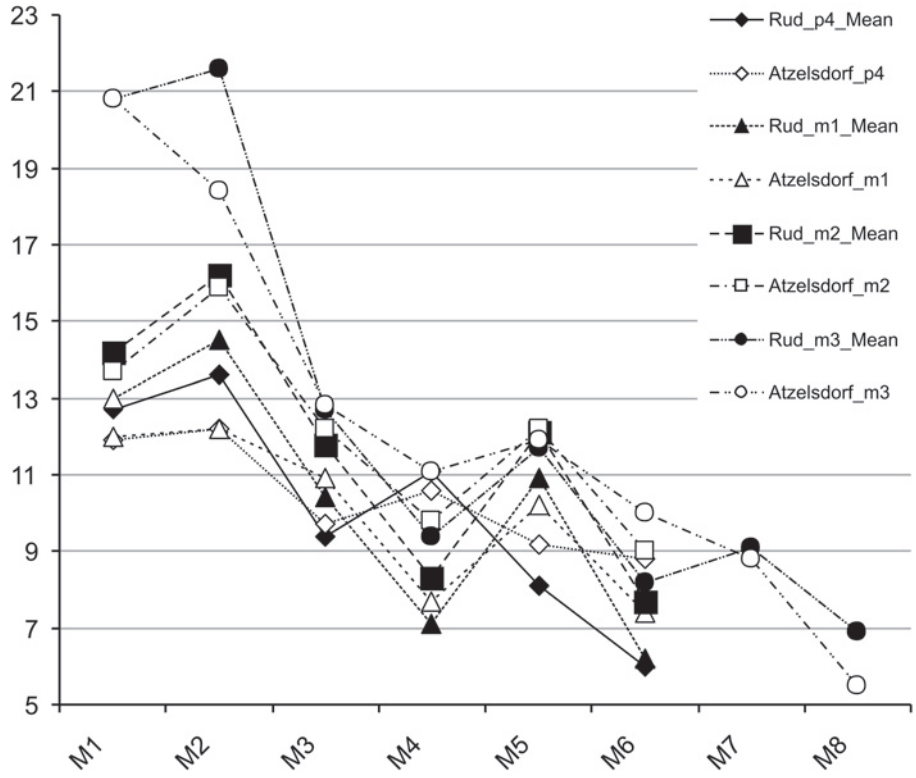

Fig. 5. *Parachleuastochoerus kretzoii* FORTELIUS et al., 2005. Comparison of mandibular cheek tooth measurements from Rudabánya and Atzelsdorf.

tions of p4-m3 are wider, p4 has a tall principal cuspid, with variably fused Innenhügel and tall distal heel, with greater labial and lingual swelling of the base. All these characters of the Atzelsdorf specimen resemble *P. kretzoii* rather than *P. crusafonti*.

Table 3 provides measurements of the Atzelsdorf cheek teeth. The paired measurements of the Atzeldorf p4-m1 measurements, as defined in the legend of tab. 3 (M1-M8) are plotted against the mean measurement for the Rudabánya sample (fig. 5). Fig. 6 graphs the variability seen in the range of the Rudabánya sample's measurements. The vast majority of measurements compare closely between the Atzelsdorf and Rudabánya samples. Substantial separation of measurement points between the two samples is largely confined to measurement of the occlusal length for m3 (M2): Rudabánya mean equals 21.6 mm; Rudabánya's range equals 20.3-22.8; Atzelsdorf's measurement equals 18.4 mm. Also, Atzeldorf's m3 height measurements (M4 and M6) are likewise outside the range of the Rudabánya sample. As FORTELIUS et al. (2005) remarked, *P. kretzoii* is a highly variable taxon, particularly in m3 size and shape. Therefore, the short length of the Atzeldorf specimen's m3 is best considered due to normal variability within *P. kretzoii*, and the greater heights of the lingual cusps due to wear stage.

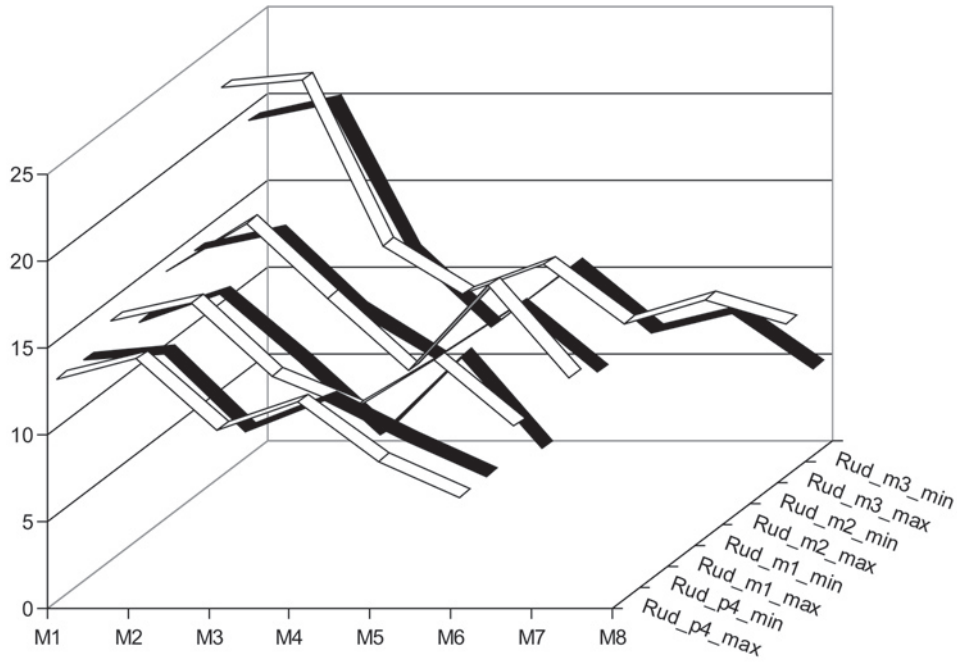

Fig. 6. Maximum and minimum cheek tooth measurements of *Parachleuastochoerus kretzoii* FORTELIUS et al., 2005 from the type locality Rudabánya (Hungary, MN9).

The Atzelsdorf tetraconodont is best referred to *Parachleuastochoerus* based on its close morphologic and size comparison to the type assemblage from Rudabánya. The Atzelsdorf sample is correlated to lowermost MN9 (ca. 11.2 Ma), while Rudabánya is correlated to upper MN 9 (ca. 10 Ma). This supports the earlier view by FORTELIUS et al. (2005) that *P. crusafonti* and *P. kretzoii* must have diverged from one another sometime during MN 7/8.

BERNOR et al. (2004) undertook extensive statistical analyses of a suite of Early to Late Miocene Eurasian hyotheriine and tetraconodont suids. They furthermore provided a cladistic analysis of selected hyotheriine, *Parachleuastochoerus* and *Conohyus* species. These analyses suggested that contrary to FORTELIUS et al.(1996), the genus *Parachleuastochoerus* could only be justified being applied to *P. crusafonti* and *P. kretzoii*. BERNOR et al. (2004) and FORTELIUS et al. (2005) further detailed the very close morphological similarities shared between *Hyotherium* and *Parachleuastochoerus* and observed that *Parachleuastochoerus* may occur in other, much older Eurasian assemblages but is misidentified as "*Hyotherium*". BERNOR et al.'s (2004) cladistic analyses, and resulting phylogenetic interpretations would predict that the divergence of the *Parachleuastochoerus* and *Conohyus* clades would have occurred in the late Early Miocene, perhaps as early as MN4/MN5. As such, these two species of *Parachleuastochoerus* represent a "ghost lineage" of considerable duration: MN4/5 to early MN9.

P. crusafonti is smaller than *P. kretzoii*, and in turn, *P. kretzoii* is about the same size or slightly smaller than *Conohyus huenermanni* HEISSIG, 1989. FORTELIUS et al. (1996) calculated the body mass of *C. huenermanni* as being 39 kilograms. We would estimate *P. kretzoii* to have been around 35 kg and belong to Class 2 body mass size (21-80 kg) of FORTELIUS et al. (1996). The Atzelsdorf specimen represents the best preserved mandible of this species. Its great depth compared to hyotherine suids suggests an adaptation to strong vertical forces. While *Parachleuastochoerus* did not have as thick enamel and as expanded cheek teeth as any species of *Conohyus*, it was more adapted to crushing food items than any species of hyotherine or schizotherine suoid (BERNOR et al. 2004). At Rudabánya, *P. kretzoii* is found in a swamp environment, and the Atzelsdorf locality also represents a wetland area within the delta of Palaeo-Danube.

Suidae incertae sedis
(fig. 7, tab. 4)

L o c a l i t y : Atzelsdorf in Lower Austria, Hollabrunn-Mistelbach Formation; Late Miocene (Early Pannonian, letter zone C; Early Vallesian, MN9).

M a t e r i a l : Four teeth (two of them are fragments) from the collections SCHEBECZEK (S. 65, 109, 112) PENZ (P. 32).

D e s c r i p t i o n : Two fragments of mandibular canines have well preserved smooth lingual surfaces (fig. 7/1, 4). The labial side is badly weathered in one specimen (fig. 7/2). The second specimen (fig. 7/3) is damaged on the labial side, but it displays a vertical ridge. These tooth fragments would appear to be the correct size and shape for attribution to *P. kretzoii*. Unfortunately, we have no knowledge of *Parachleuastochoerus* mandibular canines. However, the canine is very much like the slightly larger tetraconodont *Conohyus olujici* BERNOR et al., 2004 from Lucane (in Croatia; MN4/5). As with *C. olujici*, the canine (fig. 7/1-2) is strongly flattened labio-lingually and broad mesio-distally. In *C. olujici* the mandibular canine is obliquely set in the jaw with the mesial blade rotated laterally; the lingual side is very smooth while the labial side has two distinct surfaces separated by a strong vertical ridge.

There is a canine (fig. 7/5-6) in the Atzelsdorf assemblage, that would appear to be a left maxillary canine of a larger suid, perhaps the size of *Conohyus* or *Parachleuasto-*

Tab. 4. Suidae incertae sedis, measurements (in mm).

object	coll.	NHMW Inv.No. of (casts)	fig.	measurements (mm) L	W	H
c	S. 109	(2008z0066/0001)	7/1-2	----	----	----
c left	P. 32	(2008z0066/0002)	7/3-4	----	----	----
C left	S. 85	(2008z0067/0001)	7/5-6	11.0	>17.6	37.1
C sup.	P.112	(2008z0067/0002)	7/7-8	> 20	6.6	12.8

L = basal length, W = anterior width, H = anterior hight

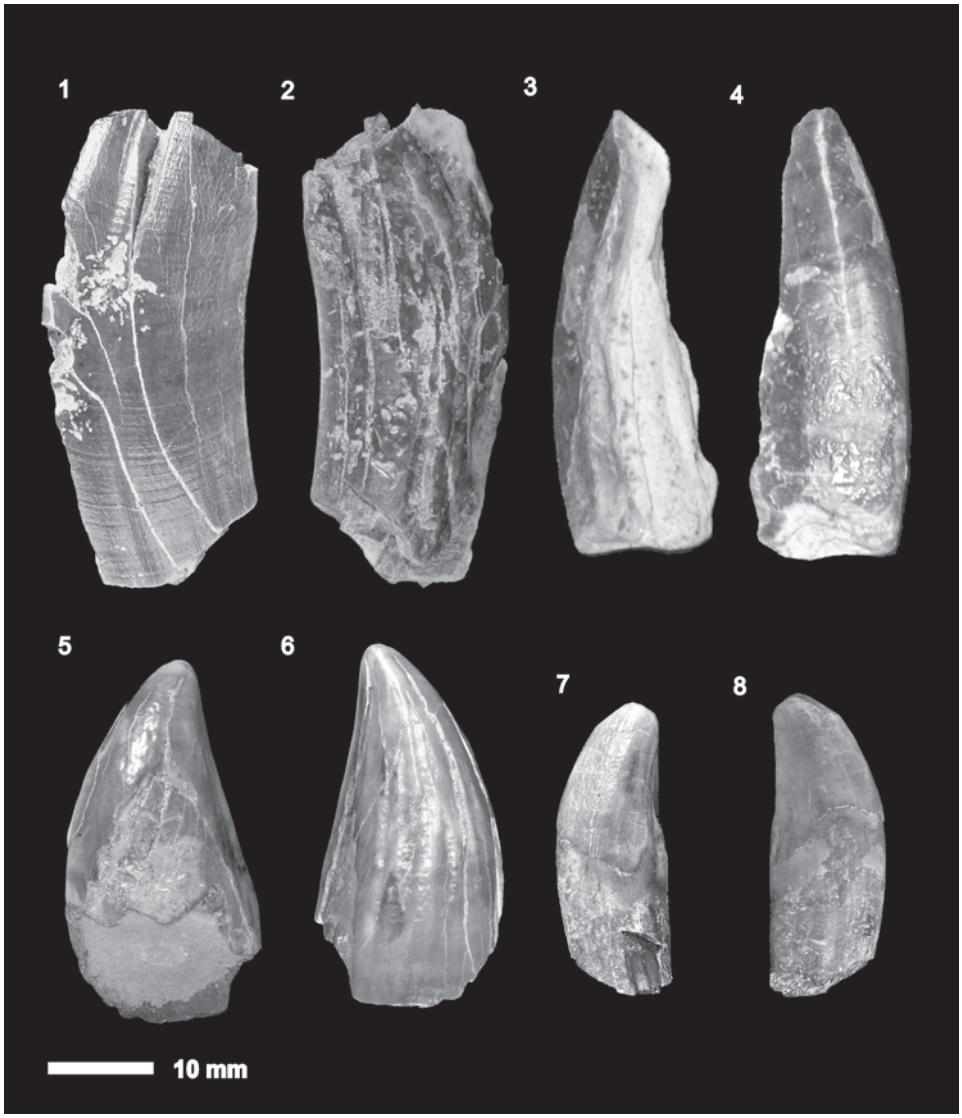

Fig. 7. Suidae incertae sedis from Atzelsdorf, Late Miocene (NM9). Fragments of lower canini. Scale bar equals 10 mm.
1-2 c inf. / distal fragment; coll. SCHEBECZEK (S. 109).
3-4 c inf. / proximal fragment; coll. PENZ (P. 32).
5-6 left C sup.; coll. SCHEBECZEK (S. 85).
7-8 C sup.; coll. SCHEBECZEK (S. 112).

choerus. The tooth has three enamel bands with strongly developed vertical ridges. A second but smaller maxillary canine (fig. 7/7-8) has smooth enamel bands. We have seen no teeth to directly compare them to and are therefore uncertain of their attribution.

Order Rodentia Bowdich, 1821

Family Castoridae Hemprich, 1820

Genus *Trogontherium* Fischer, 1809

Subgenus *Euroxenomys* Samson & Radulesco, 1973

***Trogontherium* (*Euroxenomys*) *minutum* (von Meyer, 1838)**
(figs 8-9, tab. 5)

T y p e l o c a l i t y : Elgg (Switzerland), Early-Middle Miocene (MN5).

L o c a l i t y : Atzelsdorf in Lower Austria, Hollabrunn-Mistelbach Formation; Late Miocene (Early Pannonian, letter zone C; Early Vallesian, MN9).

M a t e r i a l (tab. 5): Nine isolated teeth from the collections Schebeczek (S. 45-48, 52), Penz (P. 23-24) and from the Natural History Museum Vienna (NHMW).

D e n t a l c h a r a c t e r s of *Trogontherium* (*E.*) *minutum*: Small sized Castoridae with tetra-lophodont, high crowned but rooted teeth. The synclinclines(ids) are parallel to each other. Hypostria(ids) do not reach the basis of the crown. The lingual stria(ids) are considerably shorter or absent. The P4/p4 are much larger than the molars. The enlargement of P4 and M3 increased during the time of evolution from the Early to the Late Miocene (MN4 to MN11). The mesial surface of incisors is slightly convex but smooth. The trans-section of incisors is triangular or rounded depending on the age of these permanently growing teeth.

D e s c r i p t i o n : The fragmentary incisor has a rounded transversal section and a slightly convex anterior surface (fig. 8/4a, 4b). The enamel is smooth and thin.

The P4 is strongly enlarged and curved. Labially it is wider than lingually. One of the two specimens (fig. 8/1b) has a wide root in mesio-lingual position and a small labial-posterior root, the second specimen (fig.8/2) has no roots preserved. P4 is tetralophodont with a deep hypoflexus separating protocone and hypocone. Hypoflexus and paraflexus

Tab. 5. *Trogontherium* (*Euroxenomys*) *minutum* (von Meyer, 1838), measurements (in mm).

object	coll.	NHMW Inv.No. of original and (casts)	fig.	measurements (mm) L	Wm	Wd
P4r	NHMW	2008z0047/0001	8/2	4.05	3.75	3.75
P4r	S. 47	(2008z0047/0004)	8/1a-c	3.90	3.15	3.30
M3l	S. 51	(2008z0047/0006)	8/3a-c	3.30	2.70	2.25
p4r	S. 45			4.95	3.15	3.90
p4l	S. 46	(2008z0047/0003)	9/2a-c	4.20	2.85	3.15
p4r	S. 48			3.90	2.55	3.15
p4r	P. 24	(2008z0047/0002)	9/1a-c	4.20	2.85	3.45
m1/2l	P. 23	(2008z0047/0007)	9/3a-c	3.00	2.85	2.85
				L (m-d)	W (la-li)	
Inc	S. 52	(2008z0047/0005)	8/4a-b	3.90	3.60	

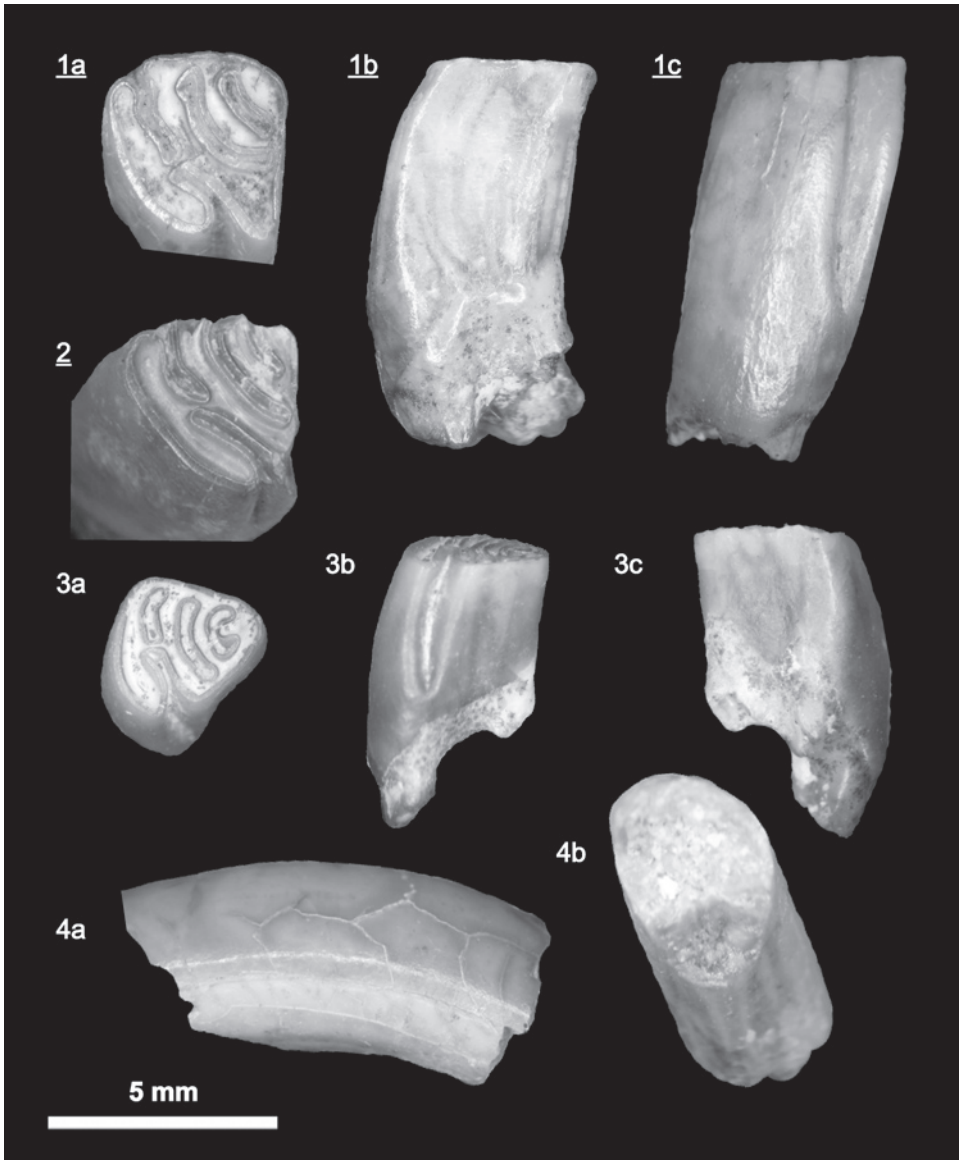

Fig. 8. *Trogontherium* (*Euroxenomys*) *minutum* (VON MEYER, 1883) from Atzelsdorf, Late Miocene (NM9). Scale bar equals 5mm (6x).
1a-c right P4; coll. SCHEBECZEK (S. 47); 1a: occlusal, 1b: labial, 1c: lingual.
2 right P4; coll. NHMW (2008z0047/0001); occlusal.
3a-c left M3; coll. SCHEBECZEK (S. 51); 3a: occlusal, 3b: lingual, 3c: labial.
4a-b fragmentary incisor; coll. SCHEBECZEK (S. 52); 4a: labial, 4b: transverse section.

are in opposite position and orientated obliquely. There is a curved mesofossette which extends from the labial to the distal margin of the tooth. The smaller metafossette separates metacone and posteroloph. Labial stria are absent. The lingual hypostria reaches

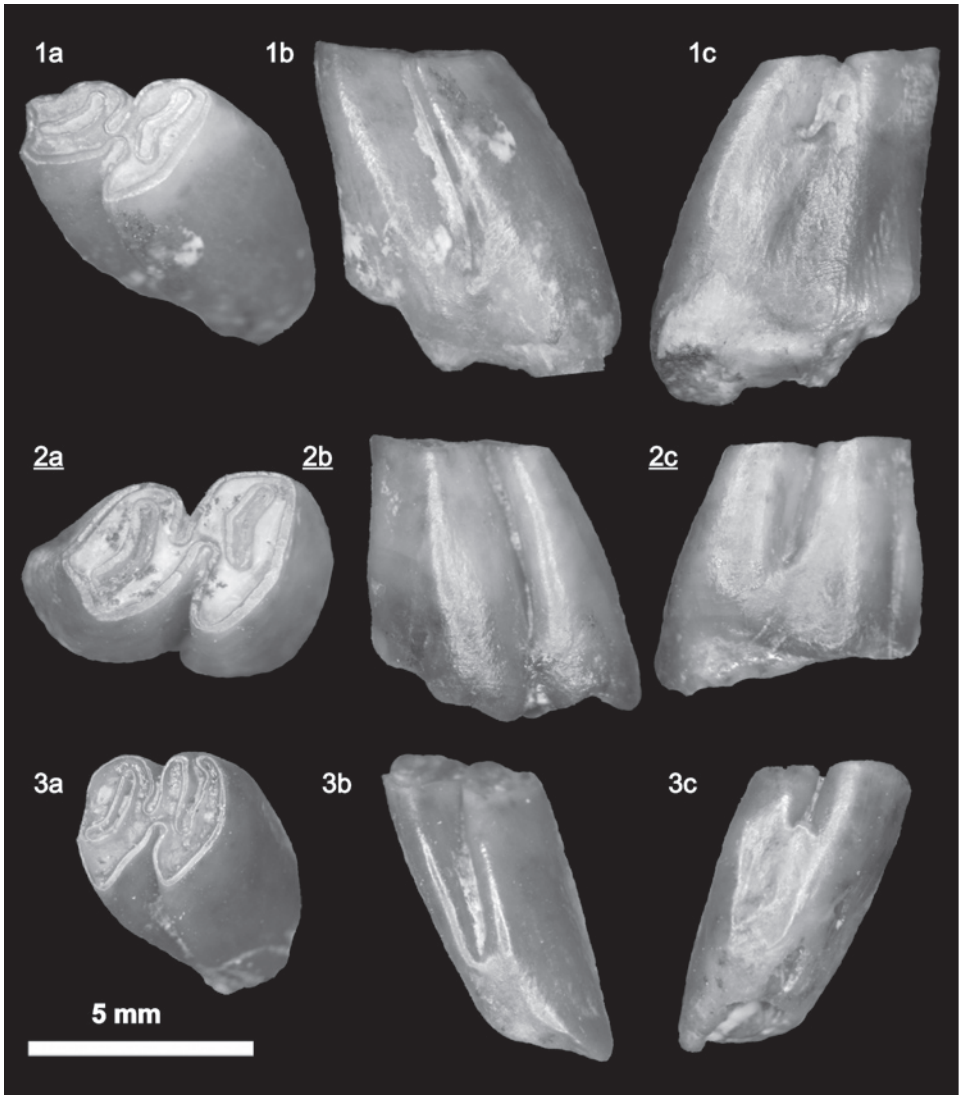

Fig. 9. *Trogontherium* (*Euroxenomys*) *minutum* (VON MEYER, 1883) from Atzelsdorf, Late Miocene (NM9). Scale bar equals 5 mm (6x).
1a-c left p4; coll. SCHEBECZEK (S. 46); 1a: occlusal, 1b: labial, 1c: lingual.
2a-c right p4; coll. PENZ (P. 24); 2a: occlusal, 2b: labial, 2c: lingual.
3a-c left m1/2; coll. PENZ (P. 23); 3a: occlusal, 3b: labial, 3c: lingual.

1/3rd of the crown-height in one specimen (2008z0047/0001), and almost 2/3rds in the second specimen (2008z0047/0002; fig. 8 /1c)

The M3 is triangular in outline (fig. 8/3a), with a wide mesial part and a narrow distal part. There is a strong mesio-lingual root, and two smaller labial ones. The occlusal pattern is similar to P4 having hypoflexus and parafossette in opposite positions. The

mesofossette and the smaller metafossette are obliquely orientated. The hypostria almost reaches the base of the crown (fig. 8/3b).

The four p4s differ in size but are uniform in dental pattern. If preserved there are two roots, one mesially, the other distally placed. The labial hypoflexid and the lingual mesoflexid are opposite one another, or slightly alternating (fig. 9/1a, 2a). There is a wide mesial parafossettid and a distal metafossettid. The labial hypostriid is long, it can almost reach the base of the crown (fig. 9/1b, 2b). The mesostriid is significantly shorter (fig. 9/1c, 2c).

The m1/2 is smaller than p4 and in its basal part strongly compressed in mesial-distal direction. No roots are preserved. The dental pattern resembles p4. However, there is no metafossettid but a lingually open metaflexid (fig. 9/3a). The hypostriid is long (fig. 9/3b), the mesostriid short (fig. 9/3c).

D i s c u s s i o n : Since its first description as *Chalicomys minutus* VON MEYER, 1838 the species was attributed to different genera, e.g. to *Monosaulax* STIRTON, 1935, to *Steneofiber* GEOFFROY-SAINT-HILAIRE, 1833, to *Trogontherium* FISCHER, 1809, and finally the new genus *Euroxenomys* SAMSON & RADULESCO, 1973 was erected for this species. HUGUENEY (1999: 290) emphasizes closest morphological affinities in dental pattern with *Trogontherium*, with the exception of smooth enamel surfaces on incisors, instead of the typical longitudinally-ribbed upper incisors of *Trogontherium* s. str. These differences point to an independent lineage justifying the nominal taxon *Euroxenomys* at least as a subgenus of *Trogontherium* (HUGUENEY 1999: 290). Other than HUGUENEY (1999), KORTH (2001) ranked *Euroxenomys* at the genus level. At the present time castorid phylogeny and taxonomy is still unclear. However, because of the scarcity of our material we cannot resolve this issue, but simply follow HUGUENEY (1999) and assign the teeth to *Trogontherium* (*Euroxenomys*) *minutum.* The species comprises two subspecies (HUGUENEY 1999: 291, fig. 28.7): i. e. *T.* (*E.*) *minutum rhenanum* described FRANZEN & STORCH (1975) from Dorn-Dürkheim, Germany (MN11), and *T.* (*E.*) *minutum minutum* identified by BAUDELOT (1972) from Sansan, France (MN6). The M3 from Atzelsdorf is relatively short and not significantly enlarged as it would be typical for *T.* (*E.*) *minutum rhenanum.* However, the material is too small to allow reliable subspecies identification.

In Europe *T.* (*E.*) *minutum* is found from a large number of localities, and ranges stratigraphically from the Early- to the Late Miocene (MN4 to MN11; for details see HUGUENEY 1999: fig. 28.9 and tab. 28.1). The Late Miocene occurrences in Austria are: Mataschen (uppermost part of MN7/8; DAXNER-HÖCK 2004b), Atzelsdorf, Vösendorf, Inzersdorf, Richardhof-Golfplatz and Götzendorf (all MN9), Schernham (MN10) (fig. 1). Sedimentological investigations from these Austrian localities suggest the presence of fluvial or lacustrine environments, which corresponds with the adaptation of *T.* (*E.*) *minutum* to semi-aquatic life.

Genus *Steneofiber* Geoffroy-Saint-Hilaire, 1833

***Steneofiber* sp.**
(fig. 10, tab. 6)

L o c a l i t y : Atzelsdorf in Lower Austria, Hollabrunn-Mistelbach Formation; Late Miocene (Early Pannonian, letter zone C; Early Vallesian, MN9).

M a t e r i a l (tab. 6): Two lower molars and two fragments of incisors from the collection Schebeczek (S. 42-43, 55, 57).

D e s c r i p t i o n : The trans-section of the incisor-fragment is sub-triangular with rounded corners and a flattened mesial side (fig.10/3a-c). The enamel is smooth and thin.

The m1/2 (fig.10/1a-c) is rectangular in outline and of tetralophodont pattern. The early wear stage is indicated by the presence of a proparafossettid, the extremely high crown and the absence of roots. Paraflexid reaches far towards mesio-labial (anterior to the protoconid). Mesoflexid and hypoflexid are opposite to each other. Metaflexid turns towards the hypoconid. An isolated mesostylid results from the constricted mesolophid. Hypostriid reaches almost as far as the basis of the crown, mesostriid is short, parastriid and metastriid are extremely short. The valleys are orientated obliquely and parallel to each other. The crown is twice as high as long. Cement is almost absent.

The m3 (fig. 10/2a-c) is similar with m1/2 but narrow in its posterior part. The lower crown-height and the absence of a proparafossettid indicate a later wear stage. Hypostriid is very long, para-, meso- and metastriids are very short. The valleys are orientated transversely and parallel to each other. There is a thin layer of cement in the hypoflexid. Roots are absent.

Discussion: The investigated specimens combine dental characters of the two genera *Steneofiber* Geoffroy-Saint-Hilaire, 1833 and *Chalicomys* Kaup, 1832. With *Steneofiber* they share the smaller size, the short lingual striids and the almost absent cement filling of the flexids. They resemble *Chalicomys* in hypsodonty and in the occlusal pattern but are distinctly smaller. For comparisons see Hugueney (1999), Steffen (1997) and Casanovas – Vilar (2007). In the Late Miocene of Austria *C. jaegeri* is evidenced from Mataschen (uppermost part of MN7/8; Daxner-Höck 2004b), Götzendorf (MN9), Schernham (MN10), Kohfidisch (MN11) and Eichkogel (MN11; Daxner-Höck 1980;

Tab. 6. *Steneofiber* sp., measurements (in mm).

object	coll.	NHMW Inv.No. of (casts)	fig.	measurements (mm) L	Wm	Wd
m1/2r	S. 42	(2008z0068/0001)	10/1a-c	5.70	4.20	4.35
m3r	S. 43	(2008z0068/0002)	10/2a-c	5.70	5.10	4.20
				L (m-d)	W (li-la)	
inc	S. 55	(2008z0068/0003)	10/3a-c	6.75	6.45	
inc	S. 57			7.50	7.35	

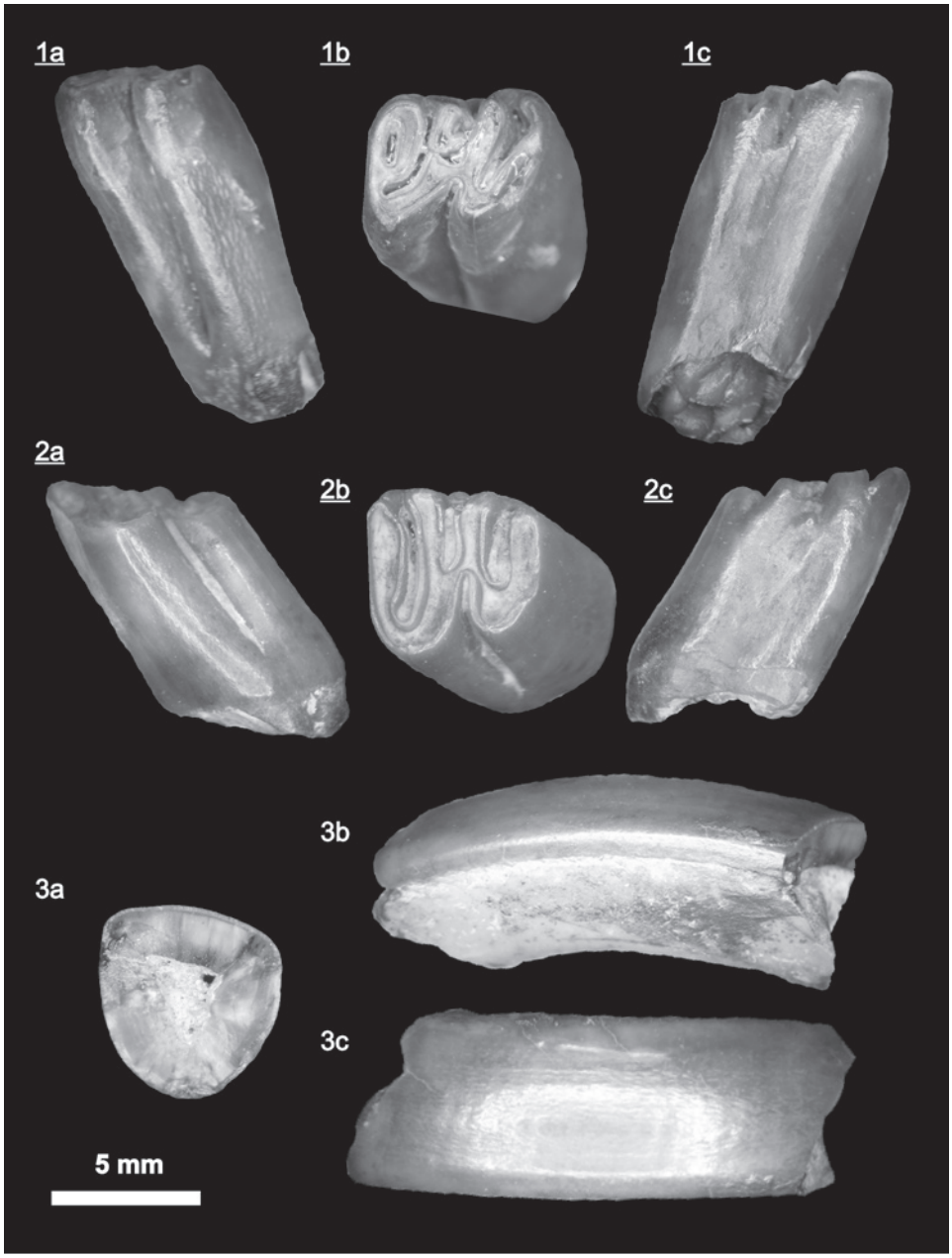

Fig. 10. *Steneofiber* sp. from Atzelsdorf, Late Miocene (NM9). Scale bar equals 5 mm (4x).
1a-c right m1/2; coll. SCHEBECZEK (S. 42); 1a: labial, 1b: occlusal, 1c: lingual.
2a-c right m3; coll. SCHEBECZEK (S. 43); 2a: labial, 2b: occlusal, 2c: lingual.
3a-c fragmentary incisor; coll. SCHEBECZEK (S. 55); 3a: transversal section, 3b: mesial, 3c: labial.

1996). All these specimens are considerably larger than the investigated material from Atzelsdorf, and differ also by abundant cement in the flexi(ds). The Atzelsdorf specimens resemble *Steneofiber* rather than *Chalicomys*, however, species identification remains open.

Conclusions

In recent years the gravel- and sandpits of the Hollabrunn-Mistelbach Formation have been recognized as an important area for investigating lowermost Vallesian vertebrate assemblages. Here the Palaeo-Danube terminated in a braided delta system in the Northern Vienna Basin. Freshwater ecosystems developed in the delta plain of the Mistelbach subbasin during the Early Pannonian lowstand of Lake Pannon in zone C (refined letter zones C1-C2) (Harzhauser et al. 2004: fig.3; Harzhauser et al. 2003). The delta displays vast forested and wetland environments indicated by characteristic azonal tree taxa and aquatic plants known from the locality Pellendorf (Harzhauser et al. 2003). However, within C3 (part of the *Mytilopsis hoernesi* zone C) the delta was flooded during a transgressive phase as evidenced in the Atzeldsorf and Pellendorf sections, and the riverine system retreated into the hinterland (Harzhauser et al. 2004: fig.3). As demonstrated by Harzhauser et al. (2004) and Harzhauser (2009) this latter event correlates with an absolute age of 11.0 to 11.1 Ma.

The biostratigraphic correlation of the Atzelsdorf assemblage with the Early Pannonian (letter Zone C; Papp 1951) and the lowermost Vallesian (MN9) is indicated by the occurrences of the bivalve *Mytilopsis hoernesi*, the equids *Anchitherium* (LOD) and *Hippotherium* (FOD) and the primitive suid *Albanohyus* (LOD).

The swampy, warm mesophytic forests of the Palaeo-Danube delta provided a broad spectrum of habitats for diverse vertebrate communities as elaborated in this volume. They served as a refugium for Middle Miocene survivors, here evidenced by the primitive browsing horse *Anchitherium*, the small pig *Albanohyus* and the beaver *Steneofiber*, and likewise provided favourable environments for newcomers, e.g. the second tridactyl horse *Hippotherium*.

Acknowledgements

We dedicate this paper to Ortwin Schultz for his extensive scientific contributions and for his invaluable support given to all his colleagues. We also wish to acknowledge the important efforts of the private collectors G. Penz and W. Schebeczek for providing us with several species that are key to this volume. We thank our colleagues G. Wessely, M. Harzhauser, J. Hir, the preparators F. Topka and A. Englert and many students for their contributions to the field-campaign, which was part of the FWF- Project P 15724-N06. R. Bernor thanks the National Science Foundation (grant number EAR-125009) and the Revealing Hominid Origins Initiative (NSF grant BCS-0321893) for supporting his research. This paper substantially improved by discussions with M. Fortelius, M. Orliac and J. Van der Made and by final critical remarks of the reviewer M. Fortelius.

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