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The early Vallesian vertebrates of Atzelsdorf (Late Miocene, Austria) 7. Ruminantia

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(With 5 plates and 8 tables)

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Abstract

The Ruminantia (Mammalia, Artiodactyla) is the quantitatively best represented mammal order in the Pannonian MN9 locality of Atzelsdorf. The fossil specimens can be referred to seven taxa, namely *Dorcatherium naui* KAUP & SCHOLL, 1834 (Tragulidae), *Micromeryx flourensianus* LARTET, 1851 (Moschidae), *Palaeomeryx* cf. *eminens* VON MEYER, 1847 (Palaeomerycidae), *Miotragocerus* sp. vel *Tethytragus* sp. (Bovidae), *Euprox* sp. (Cervidae), Pecora indet, and Ruminantia indet. The material comprises predominantly isolated teeth, postcranial bones and portions of two cranial appendages. In the present paper, we provide a detailed description of the fossils and their taxonomic classification. The collection of *D. naui* fossils from Atzelsdorf is the most extensive record of this species. The taxonomic faunal composition suggests a humid habitat with abundant cover.

Keywords: *Dorcatherium*, *Micromeryx*, *Miotragocerus*, *Tethytragus*, *Euprox*, *Palaeomeryx*, Lake Pannon, Hollabrunn-Mistelbach Formation

Zusammenfassung

Die Ruminantia (Mammalia, Artiodactyla) sind quantitativ die am besten belegte Säugetierordnung in der Pannon-Fundstelle Atzelsdorf (MN9). Die Fossilien können sieben Taxa zugeordnet werden, nämlich *Dorcatherium naui* KAUP & SCHOLL, 1834 (Tragulidae), *Micromeryx flourensianus* LARTET, 1851 (Moschidae), *Palaeomeryx* cf. *eminens* VON MEYER, 1847, *Miotragocerus* sp. vel *Tethytragus* sp. (Bovidae), *Euprox* sp. (Cervidae), Pecora indet und Ruminantia indet. Das Material besteht überwiegend aus isolierten Zähnen, postcranialen Knochen und zwei Schädelfortsätzen. Die vorliegende Arbeit beinhaltet eine detaillierte Beschreibung der Fossilien sowie ihre taxonomische Bestimmung. Das Fossilmaterial von *D. naui* aus Atzelsdorf ist, soweit bekannt, das Umfangreichste dieser Art. Die taxonomische Zusammensetzung zeigt einen feuchten bewaldeten Lebensraum an.

Schlüsselwörter: *Dorcatherium*, *Micromeryx*, *Miotragocerus*, *Tethytragus*, *Euprox*, *Palaeomeryx*, Pannon See, Hollabrunn-Mistelbach-Formation

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Introduction

The preceding systematic differentiation of extant ruminant families during the Miocene of the Old World is well recorded. Miocene ruminant communities differ considerably due to regio-temporal environment diversification caused by successive climatic cooling and geomorphologic events and due to the ecophysiological/ecomorphological habitat adaptation. In Europe, Late Miocene Austrian ruminant communities taxonomically hold a transitional position between central Europe and eastern and southeastern Europe, whereby central Europe was probably a forested province and eastern and southestern Europe a woodland province (e.g. FORTELIUS et al. 1996).

Miocene deposits in Austria are largely of marine origin, and ruminant faunas are therefore comparably uncommon. This makes the discovery of new material especially valuable. The here-described ruminant community from the fossil site of Atzelsdorf is even of particular importance among these rare fossils because it represents the very beginning of the Late Miocene (earliest European Land Mammal Unit MN9, earliest European Land Mammal Mega Zone Vallesian). This is known as a time of Eurasian mammal turnover.

This paper records the comparably small sample of isolated bones and teeth and attempts to verify or falsify the transitional position of Austrian faunas for the beginning of the Late Miocene.

The Atzelsdorf locality is an abandoned gravel pit located about 35 km NE of Vienna in Lower Austria. It is situated at the western margin of the Vienna Basin. Geologically, the deposits of the Atzelsdorf site belong to the Hollabrunn-Mistelbach Formation, which comprises deltaic deposits that were discharged by the palaeo-Danube River into Lake Pannon during the Late Miocene.

Biostratigraphic investigations and well-log correlations point to a correlation of the Aztelsdorf fauna with the Vienna Basin Pannonian Zone C, basal MN9, and an absolute age of about 11.2-11.1 Ma (for more details, see DAXNER-HÖCK & GÖHLICH 2009, this volume and HARZHAUSER 2009, this volume).

Material and methods

The present material largely belongs to the private collectors G. PENZ (Vienna) and P. SCHEBECZEK (Pellendorf). Some material was collected by the Natural History Museum of Vienna (NHMW) during an excavation in 2003. Most of the specimens from the private collections, including all figured specimens, are available as casts at the Naturhistorisches Museum Wien under the inventory numbers 2008z0049/0001 to 2008z0054/0015. Certain specimens from the private collections, often fragmentary ones, that were not molded, are indicated by S for collection SCHEBECZEK or P for collection PENZ, followed by an identification number.

The terminology and measurement of the ruminant teeth follow RÖSSNER 1995. The terminology for postcranials is after NICKEL et al. (1992), their measurements after JOUSSE (2004). All measurements are given in millimetres.

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Osteological comparisons of postcranials with extant ruminants were undertaken at the Zoological Department (NMW) of the Natural History Museum of Vienna. The specimens studied were: *Tragulus napu* (NMW 1923), *Hyemoschus aquaticus* (NMW 5407), *Antilope cervicapra* (NMW 2), *Giraffa camelopardalis* (NMW 28565), and *Cervus elaphus* (NMW 61335).

Abbreviations

Teeth:

D/d: upper/lower deciduous premolar

I/i: upper/lower incisive

M/m: upper/lower molar

P/p: upper/lower premolar

Collections:

BSPG: Bayerische Staatssammlung für Paläontologie und Geologie, München

HLMD: Hessisches Landesmuseum Darmstadt

MNHN: Muséum National d'Histoire Naturelle Paris

NHM: The Natural History Museum, London

NHMW: Naturhistorisches Museum Wien

P: colln PENZ

S: colln SCHEBECZEK

Other abbreviations:

ant.: anterior
aw: anterior width
cran.: cranial
dex: right
dist: distal
dors.: dorsal
l: length
lat.: lateral
max.: maximum
med.: medial
mid.: middle
min.: minimum
n: number
post.: posterior
proc.: processus
prox: proximal
sin: left
ventr.: ventral
w: width
w/l: width/length index.

Systematic Palaeontology

Suborder Ruminantia SCOPOLI, 1777

Infraorder Tragulina FLOWER, 1883

Family Tragulidae MILNE-EDWARDS, 1864

Genus *Dorcatherium* KAUP & SCHOLL, 1834

Type species: *Dorcatherium naui* KAUP & SCHOLL, 1834.

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Dorcatherium naui Kaup & Scholl, 1834
(pl. 1, figs 1-13; pl. 2, fig. 9)

H o l o t y p e : Right half of a mandible with p3–m3 from Eppelsheim (Germany), MN9, figured in Kaup (1839, pl. 23 fig. 1). The mandible is lost, but a cast is available at the NHM under the number M3714.

M a t e r i a l : Dentition: dex half of mandible with p1–m3 (NHMW 2008z0049/0031, cast of S97); p4–m1 dex (2008z0049/0040, cast of S33); d4 dex (2008z0049/0018, cast of S53); p4 sin (2008z0049/0027, cast of P17); m1–m2 sin (2008z0049/0022, cast of S30); m1–m2 dex (2008z0049/0030); m1 sin (2008z0049/0009, cast of S117; 2008z0049/0015, cast of S134; 2008z0049/0028, S67); m1 dex (S115, 2008z0049/0029); m2 sin (S114); m2 dex (2008z0049/0008, cast of S116; 2008z0049/0021, cast of S31); m3 dex (2008z0049/0003, cast of S15; 2008z0049/0019, cast of S86; 2008z0049/0026, cast of P15); fragmentary m? (S81); fragmentary m3 sin (2008z0049/0004, cast of S16, P54); D4–M3 sin (2008z0049/0023, cast of S138); D4 sin (2008z0049/0017, cast of S62; 2008z0049/0025, cast of P14); D4 dex (2008z0049/0012, cast of S123; 2008z0049/0013, cast of S125; 2008z0049/0016, cast of S64); M1 dex (2008z0049/0011, cast of S120; S63); M2 sin (2008z0049/0002, cast of S9); M2 dex (2008z0049/0001, cast of S6; 2008z0049/0010, cast of S119); M3 dex (2008z0051/0013, cast of S133); M1/2/3 sin (S121; 2008z0049/0024, cast of P13); M1/2/3 dex (2008z0049/0005, cast of S17); fragmentary M2/3 dex (P55);

Postcranial material: distal end of humerus sin (2008z0049/0033, cast of P51); distal end of humerus dex (2008z0049/0032, cast of P50); distal end of radius sin (2008z0054/0008); distal end of tibia dex (2008z0049/0034); proximal end of calcaneus dex (P58); fragmentary calcaneus sin (P59); astragalus sin (2008z0049/0035-0037, casts of S148); astragalus dex (2008z0049/0039, cast of P37, 2008z0049/0038, cast of S148); three phalanges proximales (2008z0049/0000, casts of S146 and P42), phalanx medialis (P61).

D e s c r i p t i o n : The dentition is well preserved and represented by several tooth positions. The teeth are low crowned, the enamel is wrinkled. The morphology of the premolars and molars is selenodont with slim stylids and styls.

In the rectangular lower molars (pl. 1, figs 1, 2, 8) the Σ-shaped *Dorcatherium*-fold is well defined. Anteriorly and posteriorly, cingulids are always present. The exostylid is variable from well defined (2008z0049/0019) to nearly absent (2008z0049/0003), being most strongly developed in m1.

The preprotocristid is less curved in m1 and most curved in m3. Lingoposteriorly in m3 the entoconulid is small and not in contact with the postentocristid or the posthypoconulidcristid. The m3-appendage is lobe-formed with a slender, labioposteriorly pointed (hypoconulid) shape (pl. 1, fig. 8). In all tooth rows the m1 is shorter and narrower than the m2 (pl. 1, fig. 1).

The subquadratic upper molars become larger from M1 to M3 within a tooth row (pl. 1, figs 6, 7, 9). At the labial side, parastyle and mesostyle as well as the columns of paraconus and metaconus are prominent from the tip to the base of the crown. Parastyle and mesostyle are coniform. Parastyle and paraconus as well as mesostyle and

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metaconus converge at the base but do not connect. The metastyle is weak. In labial view, the columns of para- and metaconus are rhombic. Lingually at the base of the crown, a cingulum extends from the anterior side of the protoconus to the posterior side of the hypoconus. A weak entostyle is developed at 2008z0049/0011. Postprotocrista and prehypocrista do not connect. The crowns in the only slightly worn tooth row 2008z0049/0023 (pl. 1, figs 9a, b) are comparably high among upper molars of Miocene European tragulids.

The p1, p2, and p3 are only represented in the heavily worn tooth row 2008z0049/0031 (pl. 2, fig. 9). All of them are longish and lack lingual tooth crown elements – a tragulid feature. p2 and p3 have 3 cusps (protoconulid, protoconid, hypoconid), p4 has two cusps (protoconulid, protoconid), and p1 one cusp. p2 has more or less the same length as p4 and both are shorter than p3. Due to a lingually located postprotocristid, the p4 is the widest of the premolars. At p4 the preprotocristid is anteriorly curved to lingual. The preprotoconulidcristid either runs straight anterolingually (2008z0049/0027) or forms a slight hook lingually (2008z0049/0040). The anterior valley is opened lingually. The lacking entoconid complex is characteristic for tragulids. The presence of a short labioposterior crista at the hypoconid is variable (present in 2008z0049/0027 and 2008z0049/0031, not developed in 2008z0049/0040). p1 is single-rooted, p2 and p4 are two-rooted, p3 is three-rooted.

The lower lacteal premolars are only represented by one d4 (pl. 1, fig. 3) with a missing posterior part, but unworn. Only the paraconid, protoconulid, metaconid, protoconid and the *Dorcatherium*-fold are preserved. The anteriolabial cingulid is weak. The anterior and the posterior lobus are completely connected. Posterior of the end of the *Dorcatherium*-fold, a metastylid is developed at the base of the crown. Roots are not preserved.

The upper lacteal premolars are represented by six D4 (pl. 1, figs 4, 5, 9). They are subquadratic and lower crowned than the upper molars. Their parastyle is proportionally stronger than in the upper molars. Like in the upper molars, the anterior lobe is more V-shaped, while the posterior lobe is more U-shaped. At the base of the anterior lobe, two small posterior cristae are developed. Labially, the styles and columns of coni are prominent from the top to the base. The parastyle and mesostyle are coniform. A cingulum extends over the complete anterior and lingual side to the posterior wall of the hypocone. The D4 is smaller than the M1 within one tooth row.

A subcomplete right half of a mandible (pl. 2, fig. 9) with a heavily worn tooth row from p1 to m3 is still imbedded in sediment and can only be studied from the lingual perspective. The pars incisiva and processus coracoideus are missing; the angulus mandibulae is partially broken. The margo ventralis of the corpus is weakly convex. Ventral to the caput mandibulae, the caudal margin of the ramus mandibulae is concave. The slightly damaged caput mandibulae is small and mediolaterally concave and craniocaudally convex. Within the tooth row, there is a gap of 2 mm between p1 and p2.

Two distal humerus fragments show characteristic tragulid features. In cranial view, the condylus humeri is trapezoidal, with the lateral diameter of the trochlea being smaller than the medial one. The sagittal crest, situated in the lateral part of the trochlea, is more prominent than in pecorans. The groove between the medial and lateral part of the trochlea is more concave than in pecoran humeri. The medial ligament grooves are weak. 2008z0049/0033 (pl. 1, fig. 11) is slightly smaller than 2008z0049/0032.

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The distal end of a left radius (2008z0054/0008) (pl. 1, fig. 13) carries a clear proximo-distal-oriented trench for a tendon on the dorsal and lateral surface. The medial side of the distal shaft is slightly concave. In distal view, the trochlea radii is dorsopalmarly less deep than in pecorans and curved, forming a concave palmar outline. The distomedial articular facet for the radiale is deeply concave, distinctly deeper than the shallow facet of pecorans and even deeper than in the extant tragulids *Hyemoschus* and *Tragulus* (GAILER 2007). The articular facets for the intermedium and the ulnare merge and are more or less at the same level, in contrast to the slightly palmarly inclined facet for the ulnare in pecorans. Like in other artiodactyls, the distopalmar facet for the ulna is almost vertical. Unlike pecorans, the facet for the intermedium is less extended in palmar direction. The trochlea radii is dorsally bordered by a distinctive transversal crista, which is more pronounced than in pecorans and extant tragulids.

The tibia is represented by a distal portion (2008z0049/0034). The distal shaft and distal end are trapezoid in outline, tapering laterally. The distal cochlea tibiae is dominated by two sagittal grooves for the articulation with the trochlea of the astragalus. The lateral groove is plantarly clearly shorter than the medial one, which is characteristic for tragulids (personal observation RÖSSNER). As typical for tragulids, the distalmost point of the distal tibia is a projection in the middle of the dorsal margin of the cochlea, whereas in pecorans the distalmost point is a medial projection (personal observation RÖSSNER). Tibia and fibula were distally not fused, which is indicated by a small distolateral, dorsoplantarly concave articulation facet for the malleolar (a distal remnant of the original fibula).

Two calcanei are fragmentary preserved. Unlike pecorans, the sustentaculum tali is oriented more plantarly in *D. naui*. The tuber calcanei is medioplantarly prominent, whereas in pecorans it is symmetrical. P59 is somewhat smaller than P58, which is in the range of variability, sexual dimorphism or late ontogeny.

Five astragali are more or less completely preserved (pl. 1, fig. 12). The mediolateral axes of the dorsoproximal trochlea tali and the distal caput tali converge to medial, like in suids. However, there is no step-like subdivision in the caput tali like in suids, which clearly indicates tragulids. In size they correspond well with those of the type material of *D. naui* figured in KAUP (1832-1839, pl. 23C, figs 6, 6a).

Three proximal phalanges (pl. 1, fig. 10) differ slightly in size but are identical morphologically. The median sagittal groove in the proximal articular facet does not reach the dorsal margin. The lateral side of the proximal end extends further proximally than in *Euprox* sp. from Atzelsdorf. Furthermore, the proximal phalanges are proportionally shorter and flatter than those of *Euprox* sp.

Measurements for all dental and postcranial remains of *D. naui* are listed in tables 1 to 3.

D i s c u s s i o n : The morphology of the described teeth and postcranials clearly suggests a tragulid origin as indicated above. In comparison with other Miocene tragulids from Europe, the Atzelsdorf tragulid differs from *Dorcatherium crassum* (LARTET, 1851) as well as central European *D. vindebonense* VON MEYER, 1846 and *D. peneckei* (HOFMANN, 1893) (THENIUS 1952; MOTTEL 1961; FAHLBUSCH 1985) by selenodont molars in contrast to bunoselenodont molars, and by higher molar crowns in contrast

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to truly brachyodont molars. Moreover, in *D. crassum* the malleolar is fused with the tibia (MILNE-EDWARDS 1864: pl. 12, fig. 1b, 1c; FILHOL 1891: pl. 13, fig. 4; RÖSSNER in press), which is not the case in *Dorcatherium* from Atzelsdorf. The western and central European *D. guntianum* MEYER, 1846 and *D. jourdani* (DÉPERET, 1887) from France and Austria are selenodont, as in the case of *Dorcatherium* from Atzelsdorf, but differs by smaller size and morphological details (e.g. two-cusped p3 in *D. guntianum* and weak *Dorcatherium*-fold in *D. jourdani* (MOTTL 1961; BONNEAU & GINSBURG 1974; FAHLBUSCH 1985; BOUVRAIN & DE BONIS 2007). The remains of *D. puyhauberti* ARAMBOURG & PIVETEAU, 1929 from Greece were not originally available during the investigation; the available figures (ARAMBOURG & PIVETEAU 1929) are unfortunately of poor quality and few in number. Nonetheless, the dentition of *D. puyhauberti* described in the latter study differs in several morphological features from all other European *Dorcatherium*; it is also smaller than that of *D. naui*. A further, previously unpublished difference is the size of the M3: it is larger than M1 and M2 in all other *Dorcatherium* species, but is smaller than M2 in *D. puyhauberti* (ARAMBOURG & PIVETEAU 1929: pl. 5, fig. 1).

In summary, the tragulid remains from Atzelsdorf correspond best – in size and morphology of teeth and bones – to the type material of *D. naui* (KAUP 1839; KAUP 1832-1839) and further material housed at the HLMD, unpublished data RÖSSNER). An affiliation to the latter species is therefore justified.

Table 1. Measurements (in mm) of lower premolars and molars of *Dorcatherium naui* from Atzelsdorf.

Invent.No.	p1		p2		p3		p4		m1		m2		m3	
NHMW 2008z...	l	w	l	w	l	w	l	w	l	aw	l	aw	l	aw
0049/0031	4.0	-	10.9	3.8	12.3	2.6	10.6	-	9.7	8.3	11.2	8.8	19.4	8.6
0049/0040							11.1	5.3	10.2	7.2				
0049/0027							12.5	5.0						
0049/0022									11.8	7.0	11.5	8.4		
0049/0030									11.6	7.1	11.8	8.2		
S67									11.7	7.8				
S115									11.8	7.6				
0049/0009									12.6	7.4				
0049/0015									11.9	7.3				
0049/0028									12.5	7.6				
0049/0029									-	8.1				
0049/0008											13.5	9.0		
0049/0021											13.0	7.9		
S114											13.0	8.9		
0049/0003													19.3	8.3
0049/0019													17.1	8.5
0049/0026													18.2	8.6

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Infraorder Pecora LINNAEUS, 1758

Family Moschidae GRAY, 1821

Subfamily Moschinae GRAY, 1821

Genus *Micromeryx* LARTET, 1851

T y p e s p e c i e s : *Micromeryx flourensianus* LARTET, 1851.

Micromeryx flourensianus LARTET, 1851
(pl. 2, figs 1-8)

H o l o t y p e : Hitherto not determined; type material from Sansan (France, MN6) under revision; partly figured in FILHOL (1891: pl. 24, figs 1-15; pl. 26, figs 1-11), stored at the MNHN.

M a t e r i a l : Teeth: p3–m2 dex (NHMW 2008z0050/0001, cast of S35); m1–m2 sin (2008z0050/0006, cast of P9); p4–m1 dex (P60); m1 dex (2008z0050/0003, cast of S55); m1 sin (S60); m2 dex (2008z0050/0009, cast of P12); m3 sin (2008z0050/0005, cast of S57; 2008z0050/0008, cast of P11); D4 dex (2008z0050/0004, cast of S56), P4 sin (2008z0050/0019), M 1/2/3? sin (2008z0050/0002, cast of S54; 2008z0050/0007, cast of P10; 2008z0050/0010, S61).

Table 2. Measurements (in mm) of lacteal premolars and upper molars of *Dorcatherium naui* from Atzelsdorf.

Invent.No.	d4		D4		M1		M2		M3		M1/2/3	
NHMW	l	w	l	aw	l	aw	l	aw	l	aw	l	aw
2008z0049/0018	-	5.3										
2008z0049/0023			11.1	10.4	11.4	12.9	13.0	14.3	13.5	15.0		
2008z0049/0017			11.8	11.3								
2008z0049/0025			11.6	10.0								
2008z0049/0012			10.8	10.0								
2008z0049/0013			12.1	11.8								
2008z0049/0016			11.1	11.1								
S63					11.1	12.4						
2008z0049/0011					11.4	13.5						
2008z0049/0002							12.4	14.4				
2008z0049/0001							12.2	13.6				
2008z0049/0010							13.3	13.8				
2008z0049/0005											13.4	15.1
2008z0049/0024											12.9	13.4
S121											10.7	-
2008z0051/0013									14.0	15.1		

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Postcranial material: astragalus sin (2008z0050/0012, cast of S84; 2008z0050/0014, cast of S90; 2008z0050/0017, cast of P35); astragalus dex (2008z0050/0013, cast of S89; 2008z0050/0015, cast of S92; 2008z0050/0016, cast of S95); distal end of humerus sin (s93); calcaneus dex (2008z0050/0011, cast of S147); phalanx medialis (2008z0050/0018, cast of P40).

D e s c r i p t i o n : Generally, all teeth assigned to *M. flourensianus* are slightly worn and do not display the original crown heights. However, their semihypsodont morphology is still visible. The enamel is smooth. For measurements see table 4.

In occlusal view, the lower molars (pl. 2, figs 1-3) are rectangular. A weak *Palaeomeryx*-fold as well as a prominent metastylid are developed in all lower molars. The exostylid is prominent, but weaker in m3 than in m1 and m2. The m2 is larger than m1. The m3 has the characteristic large-sized entoconulid as well as a postexostylid.

The P4 is horseshoe-shaped. Labially, the column for the paracone as well as the parastyle and mesostyle are prominent. The medial crista runs from the hypocone nearly to the postparacrista.

The upper molars are subquadratic; their anterior part is wider than the posterior one. Parastyle, mesostyle, metastyle and entostyle are prominent. The lingual and posterior cingulums are weak. The upper molars 2008z0050/0007 (pl. 2, fig. 4) and 2008z0050/0010 have a neocrista and a spur at the end of the posthypocrista.

At p3 and p4 (pl. 2, fig. 1) the postentocristid and the posthypocristid are close to one another. The elongated premetacristid, which closes the anterior valley of p4 and which is characteristic for *Micromeryx*, is well defined in the teeth from Atzelsdorf.

Table 3. Measurements (in mm) of postcranial material of *Dorcatherium naui* from Atzelsdorf.

humerus (dist.)			distal condylus				
		width	lat. depth	med. depth			
2008z0049/0033		21.1	9.8	15.3			
2008z0049/0032		24.7	8.9	17.0			
tibia (dist.)		lat. depth	dors. width	med. depth			
2008z0049/0034		11.2	21.7	17.1			
astragali	n=5	length	prox. width	dist. width	lat. depth	med. depth	mid. length
2008z0049/0035-	min.	28.8	15.1	14.9	14.6	14.7	23.5
0039	max.	32.1	16.7	17.2	16.7	16.1	26.1
phalanges proximales	n=3	length	prox. width	prox. depth	dist. width	dist. depth	
2008z0049/0000	min.	25.3	12.8	11.5	9.6	7.8	
	max.	30.0	13.2	12.3	9.9	8.4	
phalanx medialis							
P61		24	14.7	15	11.5	12	

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The D4 (pl. 2, fig. 5) morphologically differs from the upper molars by an anteriorly separated parastyle. The crown height is lower than in the upper molars. However, parastyle, mesostyle and metastyle are prominent. The tooth is three-rooted.

The astragali (pl. 2, fig. 7) are small; the maximum length is less than 16.9 mm. They have an elongated, slender shape, and the medial and the lateral side are parallel. The mediolateral axes of the trochlea tali and the caput tali are parallel. In a few specimens (2008z0050/0013, 2008z0050/0017) the medial roll of the trochlea tali carries proximoplantarly a pointed projection. The other astragali probably lost this feature by abrasion.

The calcaneus is almost complete (pl. 2, fig. 6). The plantar side of the tuber calcanei is in its proximal third marked by a groove. The sustentaculum tali is partially broken. The processus coracoideus is short and carries a facet which is, in its larger proximal part, dorsally convex and, in its smaller distal part, concave.

The humerus is only represented by a condylus humeri, which is abraded. Only the small size indicates that it probably belongs to the species. The lateral ligament groove is well marked.

The phalanx medialis (pl. 2, fig. 8) is strongly abraded and no specific morphological details are preserved. The attribution to *Micromeryx* is based on the general pecoran morphology with a smaller width than in tragulids and its small size.

D i s c u s s i o n : The combination of the following dental features in the teeth of the smallest-sized ruminant from Atzelsdorf is characteristic for the genus *Micromery*: a large-sized entoconulid at m3, a premetacristid more or less closing the anterior valley at p4, the subquadratic upper molars, and the slightly high crown with concomitant

Table 4. Tooth measurements (in mm) of *Micromeryx flourensianus* from Atzelsdorf.

Invent.No.	p3		p4		m1		m2		m3		D4		P4		M1/2/3	
NHMW	l	w	l	w	l	aw	l	aw	l	aw	l	aw	l	w	l	aw
2008z0050/0001	5.8	3.5	5.9	3.8	7.0	4.6	7.2	4.9								
P60			6.3	3.6	6.3	4.1										
2008z0050//0003					7.2	4.2										
2008z0050//0006					6.6	4.3	7.0	6.9								
S60					-	4.0										
2008z0050//0009							7.0	5.0								
2008z0050//0005									8.6	4.2						
2008z0050//0008									10.1	4.8						
2008z0050//0004											6.6	5.3				
2008z0050//0019													5.2	6.1		
2008z0050//0002															7.3	7.1
2008z0050//0007															6.5	7.3
2008z0050//0010															7.0	6.9
S61															-	7.3

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stretching of lingual (in upper molars) and labial (in lower molars) tooth crown elements (RÖSSNER 2006).

Beside the type species *M. flourensianus*, three more *Micromeryx* species have been described: *M. styriacus* THENIUS, 1950 from Göriach (Austria, MN5), *M. mirus* VISLOBOKOVA, 2007 from Kohfidisch (Austria, MN11), and recently *M. azanzae* SÁNCHEZ & MORALES, 2008 from Toril-3 (Spain, MN7/8). *Micromeryx* from Atzelsdorf, *M. flourensianus* from Sansan and *M. mirus* overlap in teeth dimensions (see THENIUS 1950: tab. 4; VISLOBOKOVA 2007; unpublished data of RÖSSNER). *M. styriacus* and *M. azanzae* have mostly larger molars (SÁNCHEZ & MORALES 2008). The tooth crown height of *Micromeryx* from Atzelsdorf corresponds to that of *M. styriacus* and of *M. flourensianus* from Sansan, which is slightly high crowned. *M. mirus* and *M. azanzae* have a somewhat larger tooth crown height linked with further morphological features like less prominent styles, stylids, and columns as well as flatter lingual conids. In the lower molars of *Micromeryx* from Atzelsdorf and the type locality Sansan (FILHOL 1891), the *Palaeomeryx*-fold is present but weak, whereas in *M. styriacus* it is prominent (THENIUS 1950), in *M. mirus* it is nearly absent (VISLOBOKOVA 2007), and in *M. azanzae* it is also absent (SÁNCHEZ & MORALES 2008). In the p4 of *M. flourensianus* from the type locality Sansan and Atzelsdorf, the posterior valley is anteriorly closed, shorter and narrower than in *M. styriacus*; in *M. styriacus* the posterior valley is opened anteriorly between preentocristid and prehypocristid. The p4 of *M. mirus* differs from *M. styriacus* and

Table 5. Measurements (in mm) of postcranial material of *Micromeryx flourensianus* from Atzelsdorf and of *Micromeryx mirus* from Kohfidisch (Austria, MN11, figured in VISLOBOKOVA 2007: pl. 13, fig. 5).

astragalus	**length**	**prox. width**	**dist. width**	**lat. depth**	**med. depth**	**mid. length**
NHMW			**Kohfidisch**			
2005z0021/0008	-	9.3	10.6	9.9	8.5	12.3
			Atzelsdorf			
2008z0050/0012	-	-	8.5	10.0	8.6	12.4
2008z0050/0014	16.1	9.5	9.1	8.7	8.7	13.8
2008z0050/0017	15.6	10.0	9.0	8.6	8.4	12.0
2008z0050/0013	15.4	9.6	9.1	8.7	8.5	12.4
2008z0050/0015	16.9	10.1	9.7	9.3	8.9	14.1
2008z0050/0016	15.5	9.9	8.4	8.5	7.8	13.4
calcaneus	**length**	**prox. width**	**prox. depth**	**depth at proc. coracoideus**	**length proc. coracoideus**	
2008z0050/0011	37.4	7.5	9.6	13.5	12.0	
humerus	**width of condyle**	**lat. depth of condyle**	**med. depth of condyle**			
S93	13.3	6.3	8.8			
phalanx medialis	**length**	**prox. width**	**dist. width**	**prox. depth**	**dist. depth**	
2008z0050/0018	14.7	7.6	6.9	8.0	7.2	

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M. flourensianus from Atzelsdorf in forming a crest at the labial wall of the hypoconid (VISLOBOKOVA 2007); this causes a labial prominence of the hypoconid and a deeper incision between hypoconid and protoconid. In summary, *Micromeryx* from Atzelsdorf has the same features as *M. flourensianus* and is therefore assigned to it.

Postcranials of *Micromeryx* are barely described, which hampers morphological comparisons. However, all postcranial elements from Atzelsdorf, which represent the smallest pecoran recorded, are referred to *Micromeryx.* Morphology and size correspond to the general morphology of *M. flourensianus* from Sansan (FILHOL 1891: tab. 5; VISLOBOKOVA 2007; SÁNCHEZ & MORALES 2008; unpublished data of RÖSSNER).

Family Cervidae GOLDFUSS, 1820

Genus *Euprox* STEHLIN, 1928

Type species: *Euprox furcatus* (HENSEL, 1859).

Euprox sp.
(pl. 3, figs 1-7)

Material: Teeth: p2 dex (NHMW 2008z0054/0006, cast of P16), m1/2 sin (2008z0052/0001, cast of S132). Cranial appendage: antler fragment (2008z0052/0002).

Postcranial material: distal ends of scapula sin and dex (2008z0052/0003, cast of S158a 2008z0052/0004, cast of S158b), distal half of metacarpale III+IV (cannonbone) (2008z0052/0007, cast of P33), astragalus dex (S149a), three phalanges proximales (2008z0052/0005, casts of S143), five phalanges mediales (2008z0052/0006, casts of S144).

Description: In the Atzelsdorf fauna, only a single cranial appendage of a cervid is recorded. It is a 35-mm-long fragmentary basal portion of an antler with its burr and remains of its pedicle. The bifurcation starts 3 cm above the burr (pl. 3, fig. 3). Although the antler portion is quite abraded, a longitudinal striation on the anterior and posterior surface is visible. The cross section at the level of the burr is oval. The anteroposterior diameters of the pedicle and burr are 13 mm and 25 mm, respectively.

The unworn lower cervid molar (m1 or m2) (pl. 3, fig. 1), with its seleno-brachyodont morphology and a prominent *Palaeomeryx*-fold, has strong labial columns of the metaconid and entoconid, and a strong metastylid. An exostylid is present. Anteriorly and posteriorly a weak cingulid is developed. The enamel is wrinkled. The tooth is 12.8 mm long and 8.1 mm wide.

The p2 has a strong postprotocristid, which makes the middle part of the tooth dominant. Posthypocristid and entocristid do not connect. Preprotoconulid and postprotoconulid connect anteriorly and form a central valley.

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The scapula is represented by two distal fragments (pl. 3, fig. 6). In both specimens the spina scapulae and the tuberculum supraglenoidale are broken. The cavitas glenoidale is almost circular.

A distal half of a metacarpal III+IV (cannonbone) (pl. 3, fig. 7) shows a median longitudinal furrow on the dorsal surface, which distally ends at the canalis metacarpi distalis; this indicates a cervid (HEINTZ 1970: 48). The canalis is situated about 1.5 cm proximal to the incisura intertrochlearis. The palmar surface is flat. The keels on the distal trochleae protrude further palmarly than dorsally, but they reach dorsally to the proximal end of the trochlea.

One astragalus is about the same size as those of *Miotragocerus* vel *Tethytragus* from Atzelsdorf, but differs in being slightly smaller and in having a distal trochlea whose median sulcus is slightly asymmetric; furthermore, the border between the lateral condyla of the distal trochlea and the median sulcus is marked by a moderate ridge. These features are characteristic for cervids and differ from the condition in bovids (HEINTZ 1970: fig. 31).

The three phalanges proximales (pl. 3, fig. 4) are about the same size. Proximally, the median sagittal groove in the fovea articularis metacarpea reaches the dorsal margin. The proximopalmar/plantar fossa is weak, which is characteristic for cervids, whereas it is stronger in bovids (HEINTZ 1970: 52–53, fig. 39). A further feature typical for cervids is the dorsoproximal bulge at the proximal end (dorsal view) (HEINTZ 1970: fig. 40). The size of the proximal phalanges fits well with the size of the medial phalanx 2008z0052/0006 as well as with the size of the metacarpus 2008z0052/0007.

The four phalanges mediales (pl. 3, fig. 5) are about the same size. The proximopalmar/plantar margin is concave, but the concavity does not reach the proximal surface like in bovids (HEINTZ 1970: 53, fig. 41).

D i s c u s s i o n : Among Late Miocene cervids the antlers of *Euprox furcatus* and *E. dicranocerus* (KAUP, 1839) are most similar to the antler fragment of Atzelsdorf; other Late Miocene cervid genera like *Lucentia* AZANZA & MONTOYA, 1995 or *Amphiprox* HAUPT, 1935 differ in a more distal bifurcation higher above the burr. The type material of both species of *Euprox* only comprises antlers, and the different level of bifurcation should be diagnostic also on the species level. However, there is a morphological overlapping of the types attributed to each species. In all antlers of *E. furcatus*, the bifurcation is always situated directly above the burr, which is also the case in the Atzelsdorf antler. The type material of *E. dicranocerus* from Eppelsheim, however, comprises several antlers with the bifurcation situated at different positions, either more distally than in the antler of *E. furcatus* and that from Atzelsdorf or at the same position (KAUP 1832-39: pl. 24, figs 3a-3e, GENTRY 2005: 285, fig. 3).

The Atzelsdorf antler fragment strongly resembles the antlers of *E. furcatus* from Sosnicowice (Poland, MN7/8, figured in HENSEL 1859: pl. 10, fig. 1), from Steinheim (Germany, MN7, figured in FRAAS 1870: pl. 7), from Mikulov (Czech Republic, MN9, collection of the NHMW 1907 No 72) as well as several cranial appendages determined as *E. furcatus* from diverse Austrian localities (e.g. Wien XVIII-Türkenschanze, Sarmat: NHMW 1879/0034/0002; Wien XXXIII-Atzgersdorf, MN8-9: NHMW A 4076). Unlike an antler specimen of *E. dicranocerus* from Wien III-St. Marxer Linie (Pannon:

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NHMW A 4245, figured in THENIUS 1948: 281, fig. 8), the bifurcation of the antler from Atzelsdorf is positioned somewhat more proximal.

A current revision of the Eppelsheim cervid material might shed light on this nomenclatorial problem and help to satisfactorily determine the cervid from Atzelsdorf in the future. For the time being, we have decided not to attribute the antler fragment of Atzelsdorf to *E. dicranocerus* or *E. furcatus.*

The morphology of both represented teeth is clearly cervid. Although the type material of *E. dicranocerus* and *E. furcatus* comprises only antlers, the size of the cervid teeth from Atzeldsorf might well correspond to the same cervid species represented by the antler fragment. Therefore, we refer the entire cervid material of Atzelsdorf to *Euprox* sp.

The described postcranial material also comprises some characteristic cervid features: circular shape of the distal articular facet of the scapula; distally closed dorsal median groove of the metacarpal; weak proximopalmar/plantar fossa at the phalanx proximalis; at the medial phalanx a small concavity restricted to the palmar/plantar side. Since the size of the bones correlates with the described antler fragment and teeth (see above), they probably belong to that taxon. Note, however, that *Euprox* sp. is represented by a relatively high number of postcranials but only two teeth, whereas in the other ruminantia taxa from Atzelsdorf this relation is reversed. There is no reasonable explanation for this inverse relation of quantity, but as the cervid postcranials are fragmentary or

Table 6. Measurements (in mm) of dental and postcranial material of *Euprox* sp. from Atzelsdorf.

p2	**l**	**w**				
2008z0054/0006	12.8	5.8				
m1/2	**l**	**aw**				
2008z0052/0001	13.0	9.5				
scapula			**ventr. length of artic. facet**	**ventr. width of artic. facet**		**ant.-post. length collum**
2008z0052/0003			29.1	25.0		23.5
2008z0052/0004			29.2	25.4		22.3
metacarpale III+IV			**dist. width**	**dist. depth trochlea**	**width single pulley**	**lat. depth lat. pulley**
2008z0052/0007			27.9	18.8	12.4	13.0
astragalus		**length**	**prox. width**	**dist. width**	**depth**	**mid. length**
S149a		37.0	23.0	22.3	19.2	29.7
phalanx prox.	**n=3**	**length**	**prox. width**	**prox. depth**	**dist. width**	**dist. depth**
2008z0052/0005	min.	39.6	13.4	16.4	11.0	10.8
	max.	41.0	14.2	17.4	12.3	12.0
phalanx med.	**n=5**	**lenght**	**prox. width**	**prox. depth**	**dist. width**	**dist. depth**
2008z0052/0006	min.	21.3	11.4	14.6	8.1	12.1
	max.	23.1	13.6	18.4	9.4	14.0

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represent undiagnostic elements (e.g. phalanges), it cannot be excluded with certainty that they contain a second cervid taxon of similar size.

Family Palaeomerycidae LYDEKKER, 1883

Genus *Palaeomeryx* VON MEYER, 1834

T y p e s p e c i e s : *Palaeomeryx kaupi* VON MEYER, 1834

***Palaeomeryx* cf. *eminens* VON MEYER, 1847**

(pl. 5, figs 1a, b)

H o l o t y p e : right half of a mandible in two parts with p2–p4 and m2–m3, from Oehningen (Germany, MN7), MN7 figured in VON MEYER (1852: pl. 14 fig. 5), formerly stored in the private collection of VON SEYFRIED (Constance, Germany), current whereabouts unkown.

M a t e r i a l : Phalanx medialis (NHMW 2008z0053/0002).

D e s c r i p t i o n : The phalanx represents the largest ruminant taxon represented in Atzelsdorf; it is 51.9 mm long (further measurements: prox width: 28.8 mm, prox depth: 25.4 mm, dist width: 36.4 mm, dist depth: 37.6 mm). It is relatively slender and dorsopalmarly/-plantarly deep. At the proximal end, the external palmar/plantar edge projects proximopalmarly/-plantarly (pl. 5, figs 1a, b). The distal trochlea is asymmetric; its external part extends far dorsoproximally, where it tapers. The palmar/plantar side of the proximal end bears a concavity that does not extend on the proximal surface.

D i s c u s s i o n : An affiliation of this phalanx to bovids can be excluded – in bovids the plantar/palmar concavity on the proximal end reaches more proximally (HEINTZ 1970: fig. 41). It also differs morphologically from the medial phalanges of Giraffidae. Thus, only the Palaeomerycidae, a large-sized ruminant family from the Late Miocene of central Europe, come into question. The medial phalanx *Palaeomeryx magnus* from Neudorf an der March (= Devínská Nová Ves, MN6, Slovakia) (NHMW without number, ZAPFE 1993) is clearly smaller. Size and morphology correspond best with the phalanx of *P. eminens* from Steinheim (Germany, MN7) (FRAAS 1870, fig. 23; unpublished data of RÖSSNER).

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Family Bovidae Gray, 1821

Subfamily Bovinae Gray, 1821 vel Caprinae Gray, 1821

Genus *Miotragocerus* Stromer, 1928 vel *Tethytragus* (Thenius, 1951)

***Miotragocerus* sp. vel *Tethytragus* sp.**
(pl. 4, figs 1-15)

M a t e r i a l : Teeth: p3 dex (2008z0051/0026; 2008z0049/0007, cast of S113), p4 sin (2008z0051/0005, cast of S32; 2008z0051/0006, cast of S65); p4 dex (2008z0054/0002; 2008z0051/0007, cast of S66; 2008z0049/0014 cast of S127); m1-m2 sin (S100a); m1 sin (2008z0051/0011, cast of S130); m1 dex (S71; 2008z0051/0016, cast of P19); m2 sin (S14; 2008z0051/0008 cast of S70; 2008z0051/0009, cast of S128; 2008z0051/0010, cast of S129); m2 dex (2008z0051/0004, cast of S18); fragmentary m 1/2 (S7); D2 sin (2008z0049/0020, cast of S82); D3 dex (2008z0051/0027, cast of P56), D4 sin (2008z0049/0006 cast of S20; 2008z0054/0007, cast of S122);. D4 dex (S21); M1 sin (2008z0051/0003, cast of S13); M1 dex (2008z0051/0012, cast of S131); M1/2 dex (S124); M1/2 sin (2008z0054/0015, cast of S126); M2 sin (2008z0051/0001, cast of S11; 2008z0051/0015, cast of P18); M2 dex (2008z0051/0002, cast of S12); M3 dex (2008z0051/0014, cast of S136); M1/2/3 sin (S5).

Cranial appendage: fragment of a horn core (2008z0051/0019, cast of P62).

Postcranial material: os carpi II+III sin (2008z0051/0021, cast of P45; 2008z0051/0028); os carpi ulnare dex (2008z0051/0022, cast of P47; 2008z0051/0029; 2008z0051/0030); proximal half of metacarpal III+IV sin (2008z0051/0018, cast od S157); caput femoris (P63), distal end of tibia sin (2008z0051/0031, cast of P64);); astragali sin (5x) and dex (2x) (6x 2008z0051/0000, casts of S149, P34); cubonavicular sin (2008z0051/0020, cast of P44).

D e s c r i p t i o n : In general, all teeth have relatively high crowns, as in contemporaneous ruminants. At the lower molars (pl. 4, figs 3, 4) all cristids fuse centrally. Meta- and entoconid are lingually convex and the metastylid is tiny. A cingulid is only anteriorly developed and protrudes lingually. It is high and integrated in the occlusal surface at an early wear stage. Labially, a high and slender exostylid is present. The slender anterior and posterior lobi make the teeth look labiolingually compressed. There is no *Palaeomeryx*-fold. The enamel is smoother lingually than labially.

At the upper molars (pl. 4, figs 7-9), the postparacrista and premetacrista are fused; postprotocrista and prehypocrista are neither fused to one another nor to postpara- or premetacrista. Labially, the column of the paracone, the parastyle, mesostyle and metastyle are prominent and slender. Lingually, the entostyle is small. Tooth width decreases from the base to the occlusal surface. Anteriorly, there is a moderate or weak cingulum; it is weakest in M3. Lingually, the enamel is wrinkled, labially it is smooth. The lobi are deep. The posterior part of the upper molars is wider than the anterior part. The anterior lobes become wider from M1 to M3. Preprotocrista and postprotocrista are straight in M1, more bent in M3. The fissure between postprotocrista and prehypocrista is most open in M1.

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The two-rooted slender D2 (pl. 4, fig. 5) shows slightly prominent parastyle and paracone columns. The triangular D3 (pl. 4, fig. 6) lacks its most anterior part. It is moderately worn and indicates a higher tooth crown than in *D. naui* and *Euprox.* Para-, meta- and mesostyle are weak. The labial column of the paracone is weak. The labial column of the metacone is clearly prominent and slender. Postparacrista and premetacrista are fused. The remains of a worn spur are visible at the posthypocrista. The width/length index of the D4 is < 1. A lingual cingulum runs from the anterior side of the protoconus to the posterior side of the hypoconus. At the end of the postprotocrista, a short spur protrudes from the posthypocrista.

The lower premolars (pl. 4, figs 1, 2) are represented by five p4 and two p3. At the p4, the posthypocristid and postentocristid are connected and border a slender, closed valley. Preprotoconulidcristid and postprotoconulidcristid diverge. Preprotocristid and postprotocristid are oriented to lingual. In specimens 2008z0051/0005 and 2008z0051/0007, a metaconid is present. The enamel is lingually smoother than labially. The labial wall forms an emargination anterior to the hypoconid. The two p3 lack the postentocristid, but show a metaconid and a postmetacristid connected to the posthypocristid.

Cranial appendages are represented solely by a small, tapering fragment of a porous horn core without torsion (pl. 4, fig. 10) and with oval diameter. Based on the small diameter, the fragment is clearly part of the distal half of a horn core. Besides the weak longitudinal striae, no sculpture is developed.

At the carpale secundum et tertium (CII+III) the proximal articulation facet for the radiale is palmarly concave. The distal articulation facet for the metacarpal III is flat and horseshoe-shaped with the opening directed to lateral. The small lateral facet for the carpale quartum (CIV) is situated dorsally and extends to proximal.

The os carpi ulnare (pl. 4, fig. 12) is high, dorsoplantarly thin, and with a laterodistal hook-like projection. The proximal articular facet for the radius forms a mediolaterally strongly convex roll. The distal facet for the CIV is transversally oval and concave and reaches onto the hook-like process. Lateroproximal on the hook-like projection is an oval concave facet for the os accessorium; this facet is oriented palmar in tragulids. The medial facet for the articulation with the carpi intermedium is triangular and positioned proximally on the medial surface.

As typical for bovids, the preserved proximal half of the metacarpal cannonbone (Mc III+IV) (pl. 4, fig. 11) shows a deep but narrow incision in the middle of the palmar margin of the proximal articular facet (HEINTZ 1970: 47-48, fig. 26). The proximal medial articular facet for the CII+III is medially horseshoe-shaped; the lateral articular facet for the CIV is triangular. Dorsally, the proximal end of the metacarpal III forms a bump. The shaft of the cannonbone is semicircular in cross section, with the palmar side being slightly concave. The sulcus longitudinalis dorsalis is weak.

A femur is recorded only by a spherical caput femoris with a weak fovea capitis.

The distal epiphysis of a tibia is present (pl. 4, figs 14a, b). Its dorsal surface is flat, its plantar surface centrally concave. The cochlea tibiae is relatively symmetric. The sagittal crest of the cochlea tibiae dorsally forms a strong distal projection. The latter is slightly distally surpassed by the long distal process of the medial malleolus.

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Seven astragali are identified as belonging to the bovid from Atzelsdorf (pl. 4, fig. 15). They are about the same size as the astragalus of *Euprox* sp. from Atzelsdorf, but they differ in being slightly broader and having a more symmetric median sulcus of the distal caput tali. The width/length index is smaller than that of *D. naui*, making the astragali more quadratic.

The cubonavicular (pl. 4, figs 13a, b) is distoplantarly slightly damaged. The lateral part of the proximal concave cochlea (for the astragalus) is wider than the medial one and bears a central dent, which is characteristic for bovids (HEINTZ 1970: 50-51, fig. 35). The lateral and medial facets are plantarly separated by a notch. Proximally, along the lateral margin, a narrow, only sightly convex facet declines for the articulation with the calcaneus. The medioplantar margin of the cubonavicular forms a proximal projection. Distally, the lateral facet surpasses the medial one in distal direction. The two facets surround a central dent. Because of abrasion, the facet outlines are indistinct, but the lateral facet is separated by a distinct transverse furrow in its plantar half.

D i s c u s s i o n : The horn core fragment, the morphology of the listed teeth, and the postcranial elements clearly support the affiliation to bovids. Furthermore, the size of all represented fossil elements indicates a single bovid taxon. Hitherto, the following bovid genera are described from the late Middle to early Late Miocene (MN7/8 to MN9) of central Europe: *Protragocerus* DEPÉRET, 1887, *Austroportax* (SICKENBERG, 1929), *Miotragocerus* STROMER, 1928 and *Tethytragus* (THENIUS, 1951) (GENTRY et al. 1999). However, an assignment to *Austroportax* can be excluded: the horn cross section of that genus is flattened and lense-shaped (SICKENBERG 1929: figs 1-4), whereas the horn core fragment from Atzelsdorf is oval. *Protragocerus* differs from the Atzelsdorf bovid in the morphology of its lower molars; in *Protragocerus* they are more slender and lower crowned, the metastylid is more prominent, and the exostylid is weaker (DEPÉRET 1887: pl. 12, fig. 2).

The remaining genera *Miotragocerus* and *Tethytragus*, however, are difficult to diagnose and to compare with, because their type species are based solely on characters of their horn core holotypes (*Miotragocerus monacensis*: fragment of a skull with left and right horn from Oberföhring (BSPG 1923 I 9), Germany, MN8 or 9 (see STROMER 1928), *Tethytragus stehlini*: left horn fragment from Mikulov, Czech Republic, MN9 (see THENIUS 1951)). The type materials of the type species of *Tethytragus* and *Miotragocerus* do not provide any teeth; thus, comparisons are restricted to the cores. Unfortunately, the horn core portion from Atzelsdorf is too fragmentary to allow a definite attribution. It corresponds with that of *Miotragocerus* in its oval distal profile, but in the holotype core of *Tethytragus stehlini*, the distal part is missing; no correspondence can therefore be determined. Currently, the bovid material from Atzelsdorf does not allow a decision about whether it belongs to *Miotragocerus* or *Tethytragus*.

Based on horn remains, both genera seem to have had the same body size. The postcranial material also corresponds in size with the postcranial type material from *M. monacensis* (humerus fragment BSPG 1921 I 501 from Aumeister near Munich, Germany). Morphologically, we found general correspondence with humerus fragments of *M. pannoniae* NHMW A 4249 from Brunn (Austria) and *M. monacensis* from Aumeister. The cubonavicular, the tibia and the femur caput are in a size range that can be attributed to the Atzelsdorf bovid.

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Table 7. Tooth measurements (in mm) of *Miotragocerus* sp. vel *Tethytragus* sp. from Atzelsdorf.

	D2		D3		D4					
NMHW	l	w	l	w	l	aw				
2008z0049/0020	12.7	7.8								
2008z0051/0027			13.0	9.8						
2008z0054/0007					14.1	12.7				
2008z0049/0006					14.5	13.0				
S21					12.5	11.4				
			p3		p4					
			l	w	l	w				
2008z0051/0026			12.2	7.3						
2008z0049/0007			12.2	7.6						
2008z0049/0014					12.6	7.2				
2008z0054/0002					14.6	7.5				
2008z0051/0005					13.5	7.0				
2008z0051/0006					12.2	7.2				
2008z0051/0007					13.6	7.6				
	m1		m2		M1		M2		M3	
	l	aw	l	aw	l	aw	l	aw	l	aw
2008z0051/0016	14.5	9.6								
2008z0051/0011	-	8.2								
S100a	12.6	9.8								
S71	13.3	10.0								
2008z0051/0004			16.2	11.3						
2008z0051/0008			15.4	10.2						
2008z0051/0009			16.3	11.2						
2008z0051/0010			15.1	9.6						
S14			15.4	9.5						
S100a			15.5	11.2						
2008z0051/0003					16.1	16.1				
2008z0051/0012					15.5	15.9				
2008z0051/0015							16.4	16.1		
2008z0051/0001							17.1	16.9		
2008z0051/0002							17.0	17.1		
2008z0051/0014									18.0	17.4
					M1/2				M1/2/3	
					l	aw			l	aw
S124					14.9	14.6				
2008z0054/0015					13.5	14.8				
S5									(15.0)	18.3

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Since none of the type materials of the type species of *Miotragocerus* or *Tethytragus* come with teeth or postcranial bones, they cannot be compared with the Atzelsdorf material. However, as the above-described teeth and postcarnial bones from Atzelsdorf belong to a larger-sized bovid, they are referred to the taxon *Miotragocerus* sp. vel. *Tethytragus* sp.

Pecora indet.

(pl. 5, figs 2-6)

M a t e r i a l : atlas (colln PENZ, P73); distal trochlea of humerus sin (NHMW 2008z0051/0017, cast of P49); patella (2008z0054/0009); cubonaviculare sin (2008z0053/0003); phalanges proximales (P65, P66), phalanges mediales (P67, P68, P69), phalanges distales (2008z0051/0025, cast of S155; 2008z0051/0024, cast of P41)

D e s c r i p t i o n & D i s c u s s i o n : One atlas (pl. 5, fig. 6) is preserved, which largely lacks its ala atlanti. It has a trapezoid shape (in dorsal/ventral view), widening caudally. It is 60 mm in total length, 35 mm in median dorsal length, and approximately 70 mm in total width. The entire shape of the deeply concave foveae articulares craniales is wide but low; its dorsal margin forms a median, square incision, which is

Table 8. Measurements (in mm) of postcranial material of *Miotragocerus* sp. vel *Tethytragus* sp. from Atzelsdorf.

os carpale II+III	**width**	**depth**	**max. height**			
2008z0051/0021	17.7	14.5	11.5			
2008z0051/0028	16.7	14.7	10.7			
os carpi ulnare	**width**	**depth**	**height**			
2008z0051/0022	16.6	9.7	23.8			
2008z0051/0029	18.0	9.5	23.7			
2008z0051/0030	17.3	9.0	21.6			
metacarpale III+IV (prox.)			**prox. width**		**prox. depth**	
2008z0051/0018			27.3		19.5	
femur (caput)			**ant.-post. diameter caput**		**transverse diameter caput**	
P63			27.3		27.1	
tibia		**lat. depth**	**dors. width**		**med. depth**	
P64		20.2	30.5		24.3	
cubonaviculare	**width**	**depth**	**max. height**		**ant. height**	
2008z0051/0020	30.2	28.6	24.8		17.4	
astragali	**n=8**	**length**	**prox. width**	**dist. width**	**lat. depth**	**med. depth**	**mid. length**
2008z0051/0000	min.	36.0	19.9	21.6	18.7	18.4	28.2
	max.	38.8	24.0	24.0	21.3	22.3	32.0

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wider and concave in the ventral margin. The foveae articulares caudales are rounded triangular and flat. The tuberculum dorsale is large but blunt, whereas the turberculum ventrale is more prominent. The ventral surface on both sides of the tuberculum ventrale is slightly concave. Foramen alare and foramen vertebrale laterale are fragmentary. This general shape corresponds with that of ruminants, but the specimen is too fragmentary to distinguish between cervids and bovids. In size, the atlas might correspond with *Miotragocerus* sp. vel *Tethytragus* sp. or *Euprox* sp. However, the atlas of tragulids is proportionally shorter (personal observation).

Only a distal abraded condylus of a left humerus (pl. 5, fig. 4) is preserved. The diameter of the condylus humeri tapers laterally. A sagittal bulge divides the condylus in the ratio 2:1 (medial:lateral) and runs slightly diagonal to proximal lateral. The medial trochlea humeri is almost circular in medial view, the lateral capitulum more oval in lateral view. The fossa olecrani is deeply concave. The shape of the condylus corresponds with those of higher ruminants, because in tragulids the lateral diameter of the capitulum is proportionally smaller (the condylus is proportionally more tapering in tragulids). Detailed morphological comparisons are impossible because of an advanced grade of abrasion of the distal humerus portion from Atzelsdorf. Measurements: width of distal condylus 34.9 mm, depth of lateral capitulum 16.8 mm, depth of medial trochlea 24.2 mm.

The patella (pl. 5, fig. 3) has an inverse drop-shaped outline. The apex is blunt, in contrast to tragulids, where the patella is much more slender and the distal apex is longer and more pointed. The two parts of the articular facet form an angle of about 120°; the larger part is slightly concave. Measurements: 33.0 mm length, 20 mm width, 15 mm depth.

The proximal ends of two proximal phalanges are preserved. The sagittal furrow, which divides the proximal articular facet, is not closed dorsally as in tragulids.

One subcomplete and two proximal halves of medial phalanges are represented; they represent pecorans because in tragulids the medial phalanges and their proximal ends are proportionally broader.

There are two distal phalanges (claws) (pl. 5, fig. 5). Slight differences in morphology suggest that they might represent a lateral and a medial one and/or belong to the front or hind limb. The proximal facets are strongly concave; the abaxial one is longer than the axial one and runs diagonally. The dorsal edge is slightly concave and proximally ends in a bump-like processus extensorius. The axial surface is slightly concave; its sulcus parietalis ends proximally in a large foramen; additionally, there is a foramen axiale dorsal on the axial surface. The tuberculum flexorium is moderately thickened. The morphology of the distal phalanges is neither clearly bovid nor cervid (following the given characters by HEINTZ 1970: 53–55, fig. 42). Accordingly, the specimens are determined as pecora indet. (Measurements: 2008z0051/0024: length: 34.2; prox width: 11.7; prox depth: 20.4; 2008z0051/0025: length: 35.4; prox width: 10.7; prox depth: 18.7)

A cubonavicular (pl. 5, figs 2a, b) represents a very large-sized Pecora, which, however, differs from that of *Palaeomeryx eminens* from Steinheim (personal observation). The cubonavicular is strongly abraded and distally damaged. Unlike in bovids (HEINTZ 1970: 50–51, fig. 35), the lateral part of the proximal concave cochlea does not show any central dent. Although distally damaged and abraded, there is no indication for a transverse

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sulcus between the dorsal and plantar part of the lateral facet for the metatarsal, and no indication for a two-parted medial facet for the os carpale II+III on the bone from Atzelsdorf. Both features, however, are present in bovids and cervids (HEINTZ 1970: fig. 34). The possibility that this cubonavicular represents a fossil giraffid needs much further investigation and comparisons and cannot be decided in this study.

Ruminantia indet.

M a t e r i a l : Teeth: i (NHMW 2008z0054/0001); fragments of teeth (2008z0054/0003, 2008z0054/0004, 2008z0054/0005, 2008z0050/0000, colln. PENZ no numbers).

Postcranial material: astragalus sin (2008z0054/0010, cast of P36; 2008z0054/0011, cast of P38; 2008z0054/0012, cast of P39); fragments of calcanei sin (P70, P71, P72).

D e s c r i p t i o n : The lower incisive is asymmetrically spatula-shaped but does not bear diagnostic features that allow a more precise affiliation. The same holds true for several tiny teeth fragments.

The astragali are too abraded to allow exact measurements or to show diagnostic features. The proximal fragments of three calcanei are too badly preserved to allow more detailed determinations than Ruminantia indet.

Conclusions

Due to its stratigraphic position at the very beginning of the early Late Miocene (MN9, earliest Vallesian) (confirmed by marine-terrestrial stratigraphic correlation and absolute dating), the ruminant fauna from Atzelsdorf is composed of one typical MN9 species, the tragulid *Dorcatherium naui*, as well as of species with earlier appearance datums, such as the palaeomerycid *Palaeomeryx* cf. *eminens*, a bovid taxon that can be systematically restricted to *Miotragocerus* sp. vel *Tethytragus* sp., the moschid *Micromeryx flourensianus*, and the cervid *Euprox* sp. Additionally, a very large-sized pecoran taxon, represented by an incomplete cubonavicular, is recognized to be different from palaeomerycids, bovids and cervids; it is larger than any ruminant in central Europe before MN9, but needs further comparison for a more precise taxonomic determination. Accordingly, the ruminant fauna from Atzelsdorf represents a typical composition that is familiar from central European sites of late Middle Miocene or Late Miocene age.

In specimen numbers, *Dorcatherium naui* is the most common ruminant taxon. The material recorded is the most extensive available for that species, making it especially valuable for our knowledge of this taxon. The second most frequent ruminant is *Miotragocerus* sp. vel *Tethytragus* sp., with one horn core fragment, several postcranials and teeth. Unfortunately, both type species are based only on horn core portions, and the Atzelsdorf material is too fragmentary to allow an attribution to one taxon or the other. Based on comparisons with Late Miocene bovids, however, the determination can be restricted to *Miotragocerus* sp. or *Tethytragus* sp. *Micromeryx flourensianus* is the smallest ruminant in Atzelsdorf and is represented by several teeth and some postcranial material. The cervid *Euprox* sp. is documented by just two teeth, some postcranials, and

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a small portion of an antler. *Palaeomeryx* cf. *eminens* is recorded only by one large-sized phalanx.

D. naui, *P.* cf. *eminens*, *Miotragocerus* sp. vel *Tethytragus* sp., *Euprox* sp. and *M. flourensianus* are familiar from late Middle Miocene and Late Miocene faunas from central Europe that featured more or less closed and humid habitats (e.g. KÖHLER 1993; GENTRY 2005; ERONEN & RÖSSNER 2007). This supports the assumption of an earliest Late Miocene central European humid habitat with abundant cover. This is further supported by dental micro- and mesowear analyses including the ruminants from Atzelsdorf by MERCERON (2009, this volume), which confirm only browsing taxa and the total absence of grazers in this assemblage. This strongly indicates the dominance of forested landscapes along the Pannon lake shores during Vallesian times.

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Plate 1

***Dorcatherium naui* KAUP & SCHOLL, 1834**

Figs 1a-c: tooth row with m1–m2 dex (NHMW 2008z0049/0030), a: labial view, b: occlusal view, c: lingual view.

Fig. 2: m1 sin (NHMW 2008z0049/0009), occlusal view.

Fig. 3: fragmentary d4 dex (NHMW 2008z0049/0018), occlusal view.

Fig. 4: D4 sin (NHMW 2008z0049/0025), occlusal view.

Fig. 5: D4 dex (NHMW 2008z0049/0013), occlusal view.

Fig. 6: M2 dex (NHMW 2008z0049/0010), occlusal view.

Fig. 7: M3 dex (NHMW 2008z0051/0013), occlusal view.

Figs 8a, b: m3 dex (NHMW 2008z0049/0003), a: occlusal view, b: labial view.

Figs 9a, b: tooth row with D4-M3 sin (NHMW 2008z0049/0023), a: labial view, b: occlusal view.

Figs 10a, b: phalanx proximalis (NHMW 2008z0049/0000), a: palmar/plantar view, b: side view.

Fig. 11: humerus sin, distal end (NHMW 2008z0049/0033), cranial view

Figs 12a-c: astragalus sin (NHMW 2008z0049/0035), a: dorsal view, b: medial view, c: lateral view.

Figs 13a, b: radius sin, distal end (NMHW 2008z0054/0008), a: dorsal view, b: distal view.

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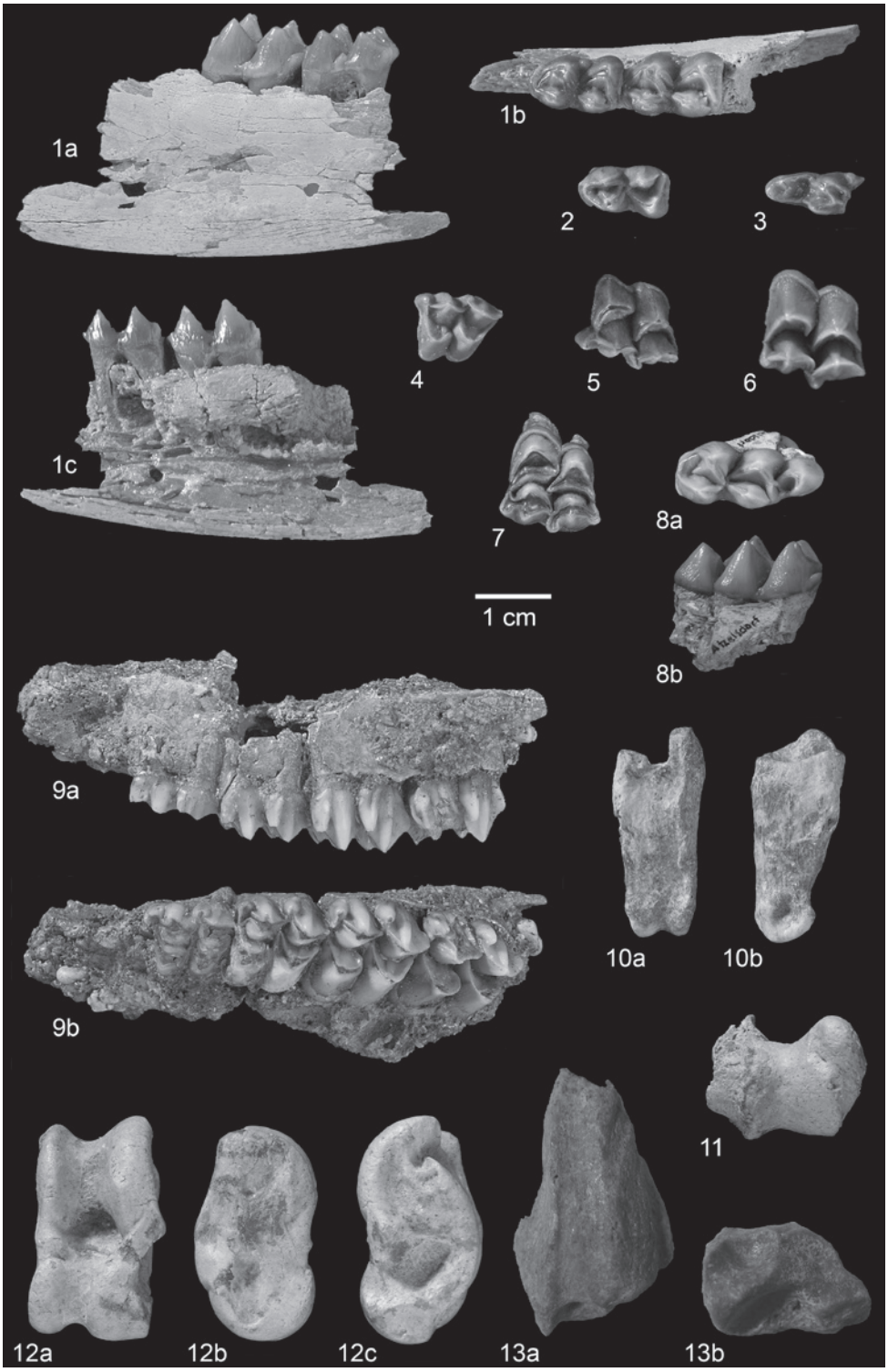

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Plate 2

***Micromeryx flourensianus* Lartet, 1851**

Figs 1a-b: tooth row with p3-m2 dex (NHMW 2008z0050/0001), a: occlusal view, b: labial view.

Figs 2a-c: m3 sin (NHMW 2008z0050/0008), a: occlusal view, b: lingual view, c: labial view.

Fig. 3: tooth row with m1-m2 sin (NHMW 2008z0050/0006), labial view.

Fig. 4: M1/2/3 sin (NHMW 2008z0050/0007), occlusal view.

Fig. 5: D4 dex (NHMW 2008z0050/0004), occlusal view.

Fig. 6: calcaneus dex (NHMW 2008z0050/0011), dorsal view.

Fig. 7: astragalus dex (NHMW 2008z0050/0013), dorsal view.

Fig. 8a, b: phalanx medialis (2008z0050/0018), a: side view, b: palmar/plantar view.

***Dorcatherium naui* Kaup & Scholl, 1834**

Fig. 9: mandible, right half with p1-m3 (NHMW 2008z0049/0031), lingual view.

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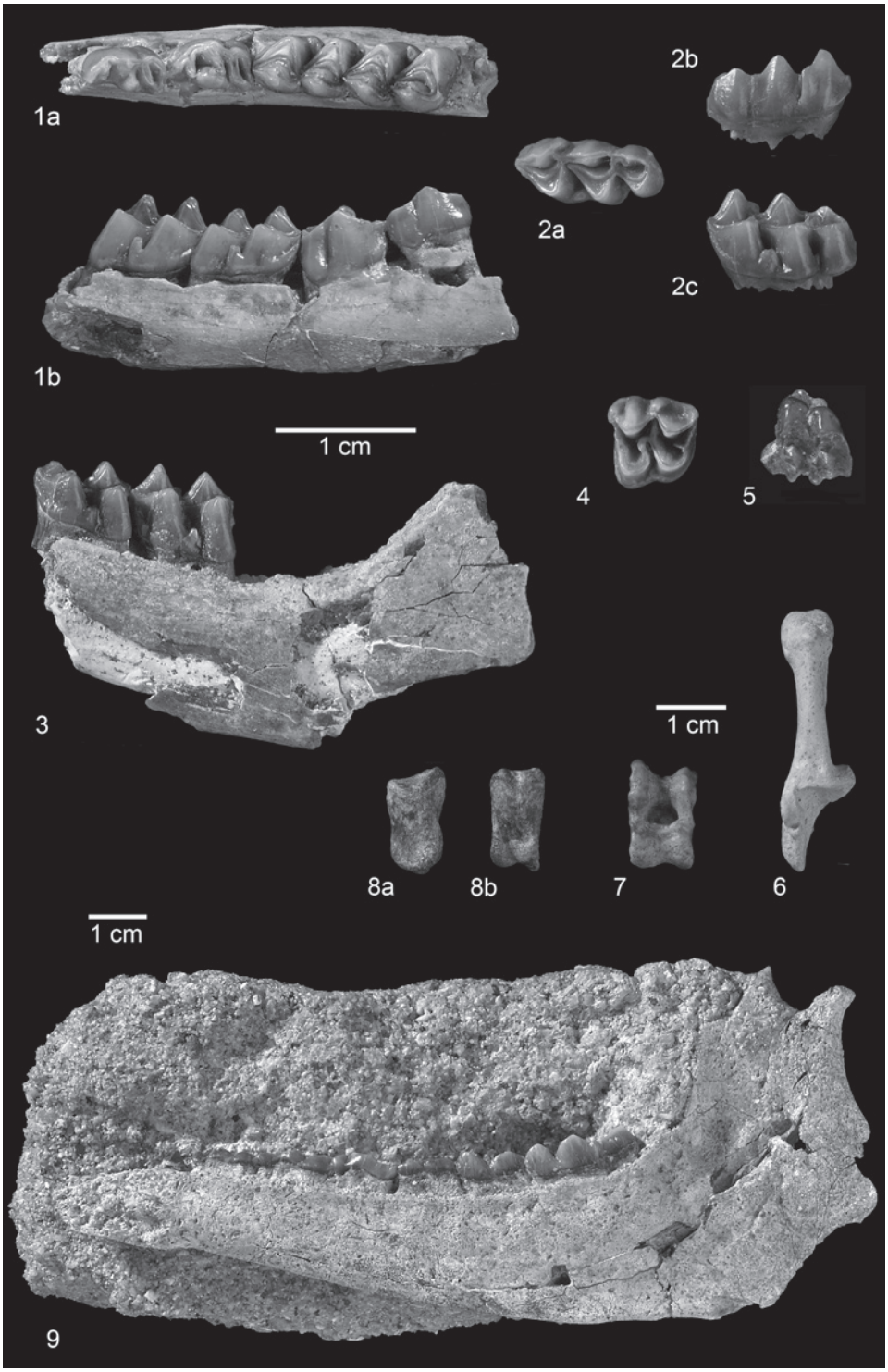

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Plate 3

***Euprox* sp.**

Fig. 1: m 1/2 ? sin (NHMW 2008z0052/0001), occlusal view.

Fig. 2: p4 dex (NHMW 2008z0054/0006), occlusal view.

Fig. 3: fragmentary antler (NHMW 2008z0052/0002), side view.

Figs 4a, b: phalanx proximalis (NHMW 2008z0052/0005), a: side view, b: palmar/plantar view.

Figs 5a, b: phalanx medialis (NHMW 2008z0052/0006) a: palmar/plantar view, b: side view.

Figs 6a, b: scapula dex, distal end (NHMW 2008z0052/0003), a: cranial view, b: distal view.

Figs 7a, b: metacarpale III+IV, distal half (NHMW 2008z0052/0007), a: dorsal view, b: plantar view.

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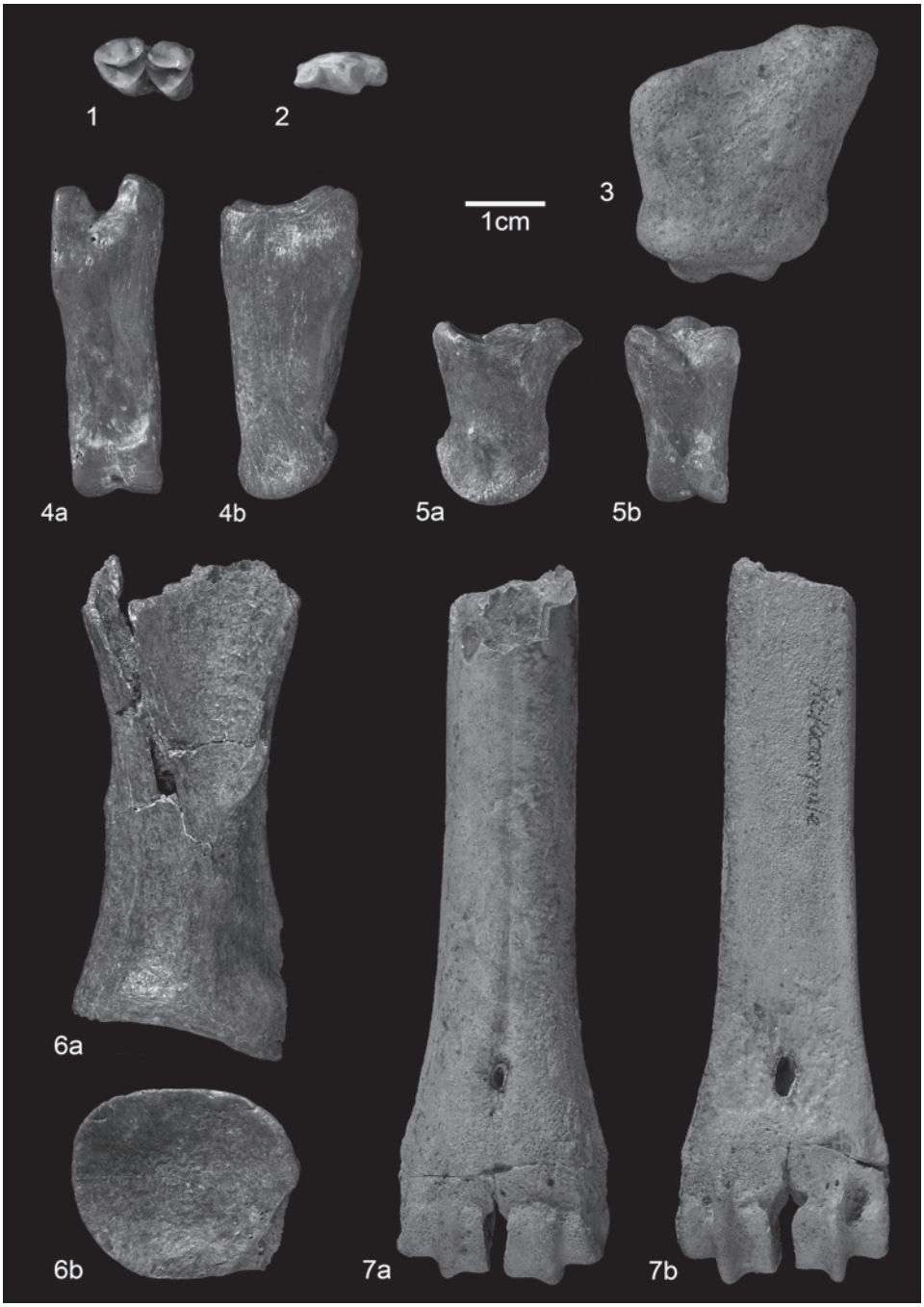

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Plate 4

***Miotragocerus* sp. vel *Tethytragus* sp.**

Fig. 1: p4 sin, (NHMW 2008z0051/0005), occlusal view.

Fig. 2: p4 dex (NHMW 2008z0054/0002), occlusal view.

Figs 3a-c: m2 sin (NHMW 2008z0051/0009), a: occlusal view, b: lingual view, c: labial view.

Fig. 4: m2 dex (NHMW 2008z0051/0004), occlusal view.

Fig. 5: D2 sin (NHMW 2008z0049/0020), occlusal view.

Fig. 6: d3 dex (NHMW 2008z0051/0027), occlusal view.

Fig. 7: M1 sin (NHMW 2008z0051/0003), occlusal view.

Fig. 8: M2 dex (NHMW 2008z0051/0002), occlusal view.

Fig. 9: M3 dex (NHMW 2008z0051/0014), occlusal view.

Fig. 10: horn core fragment (NHMW 2008z0051/0019) side view.

Figs 11a, b: metacarpale III+IV sin (cannonbone), proximal half (NHMW 2008z0051/0018), a: proximal view, b: dorsal view.

Fig. 12: os carpi ulnare dex (NHMW 2008z0051/0022), medial view

Figs 13a, b: cubonaviculare sin (NHMW 2008z0051/0020), a: proximal view, b: dorsal view.

Figs 14a, b: tibia sin, dist end (NHMW 2008z0051/0031), a: dorsal view. b: distal view

Fig. 15: astragalus sin (NHMW 2008z0051/0000), a: dorsal view.

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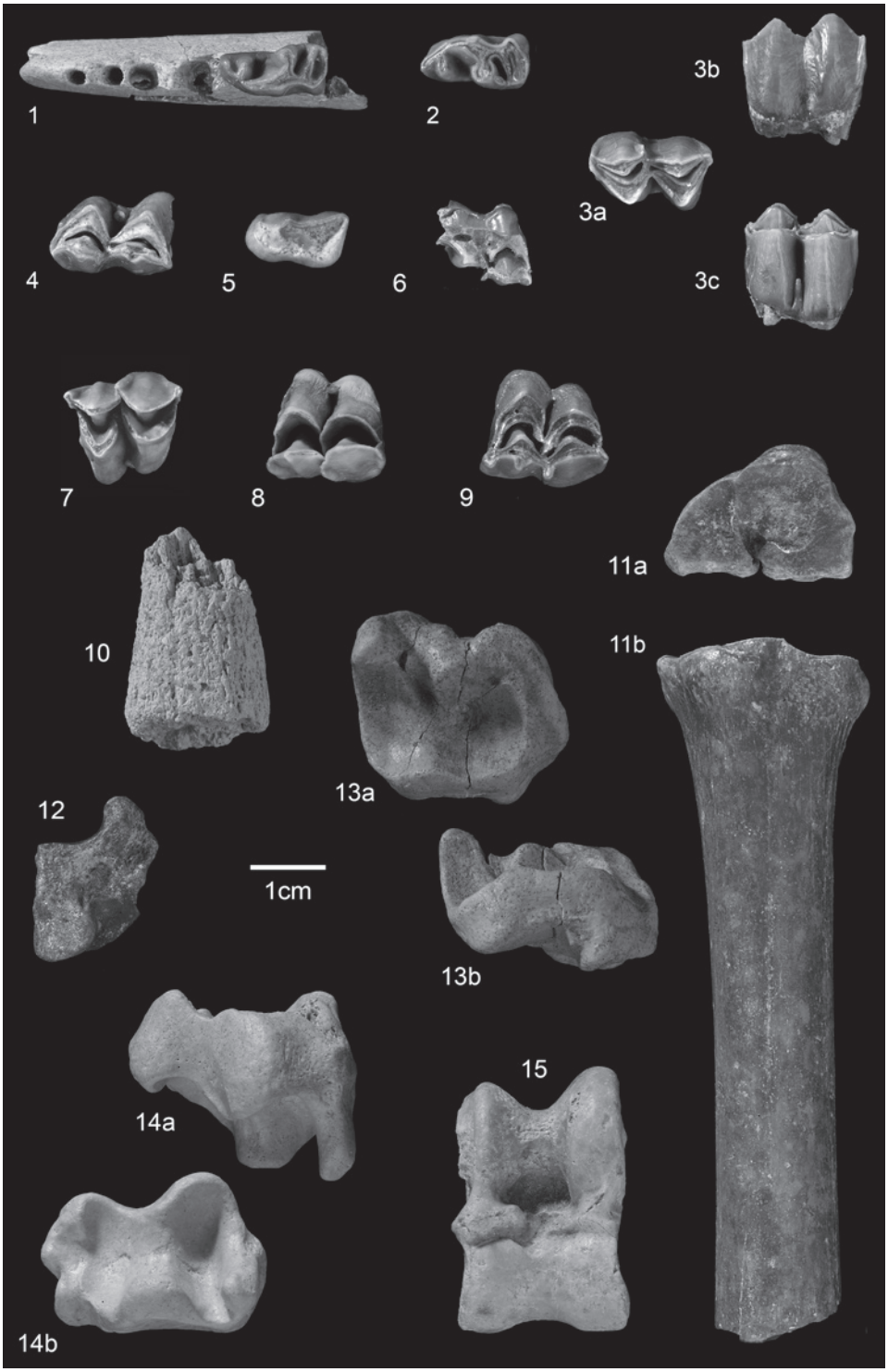

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Plate 5

***Palaeomeryx* cf. *eminens* von Meyer, 1847**

Figs 1a, b: phalanx medialis of *Palaeomeryx* cf. *eminens* (NHMW 2008z0053/0002), a: side view, b: palmar view

Pecora indet.

Figs 2a, b: cubonaviculare sin (NHMW 2008z0053/0003), a: proximal view, b: dorsal view.

Fig. 3: patella (NHMW 2008z0054/0009), dorsal view.

Fig. 4: humerus sin, distal end (NHMW 2008z0051/0017), cranial view.

Fig. 5: claw (phalanx distalis) (NHMW 2008z0051/0024), lateral view.

Fig. 6: atlas (colln Penz, P73), dorsal view

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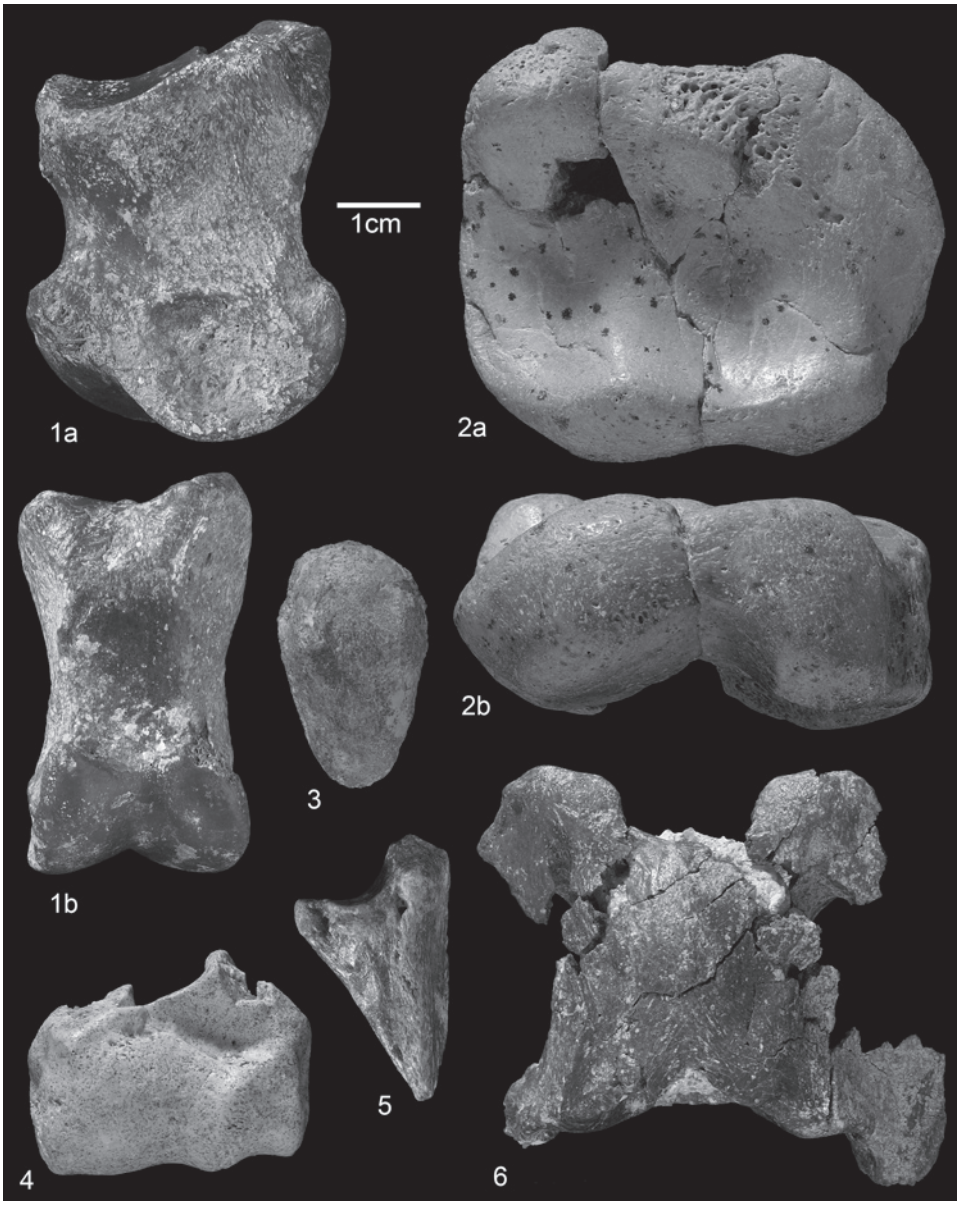

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