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Article *in* Palaeobiodiversity and Palaeoenvironments · March 2014

DOI: 10.1007/s12549-013-0141-9

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DOI 10.1007/s12549-013-0141-9

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ORIGINAL PAPER

Dorcatherium naui and pecoran ruminants from the late Middle Miocene Gratkorn locality (Austria)

Manuela Aiglstorfer · Gertrud E. Rössner · Madelaine Böhme

Received: 30 September 2013 / Revised: 1 December 2013 / Accepted: 12 December 2013 / Published online: 21 February 2014

Abstract One of the rare records of a rich ruminant fauna of late Middle Miocene age (Sarmatian sensu stricto; 12.2–12.0 Ma) was discovered at the Gratkorn locality (Styria, Austria). It comprises, besides *Micromeryx flourensianus*, ?*Hispanomeryx* sp., *Euprox furcatus*, Palaeomerycidae gen. et sp. indet., and *Tethytragus* sp., one of the oldest records of *Dorcatherium naui*. Gratkorn specimens of the latter species are in metric and morphologic accordance (e.g. selenodont teeth, bicuspid p2, non-fusion of malleolus lateralis and tibia) with type material from Eppelsheim (Germany) and conspecific material from Atzelsdorf (Austria), and do not show an intermediate morphology between Late Miocene *Dorcatherium naui* and Middle Miocene *Dorcatherium crassum*, thus enforcing the clear separation of the two species. It furthermore confirms the assignation of *Dorcatherium naui* to a selenodont lineage (together with *Dorcatherium guntianum*) distinct from a bunoselenodont lineage (including *Dorcatherium crassum*). The record of ?*Hispanomeryx* sp. is the first of this genus in Central Europe. While *Tethytragus* sp. could also be a new bovid representative for the Sarmatian of Central Europe, *Micromeryx flourensianus* and *Euprox furcatus* are well-known taxa in the Middle Miocene of Central Europe, but comprise their first records from Styria. Morphological data from this work in combination with isotopic measurements ($\delta^{18}O_{CO3}$, $\delta^{13}C$; Aiglstorfer et al. 2014a, this issue) indicate a niche partitioning for the ruminants from Gratkorn with subcanopy browsing (*Euprox furcatus*), top canopy browsing (*Tethytragus* sp.) and even a certain amount of frugivory (*Dorcatherium naui* and *Micromeryx flourensianus*).

Keywords *Euprox furcatus* · *Micromeryx flourensianus* · *Tethytragus* · *Hispanomeryx* · Palaeomerycidae · Sarmatian · Central Europe · Styrian Basin · Paratethys

This article is a contribution to the special issue "The Sarmatian vertebrate locality Gratkorn, Styrian Basin."

Electronic supplementary material The online version of this article (doi:10.1007/s12549-013-0141-9) contains supplementary material, which is available to authorized users.

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Introduction

The Gratkorn locality (claypit St. Stefan; 10 km NNW of Graz, Styria, Austria) is one of the richest vertebrate localities of the late Middle Miocene (late Sarmatian sensu stricto; 12.2–12.0 Ma) in the Central Paratethys realm (Gross et al. 2011, 2014, this issue). Besides a rich and diverse ectothermic vertebrate (Böhme and Vasilyan 2014, this issue) and small mammal fauna (Prieto et al. 2014, this issue), and some birds (Göhlich and Gross 2014, this issue), a diverse large mammal fauna was excavated, comprising the proboscidean *Deinotherium levius* vel *giganteum* (Aiglstorfer et al. 2014b, this issue), the rhinocerotids *Brachypotherium brachypus, Aceratherium* sp., and *Lartetotherium sansaniense*, the chalicothere

Chalicotherium goldfussi, the equid *Anchitherium* sp. (Aiglstorfer et al. 2014c, this issue), the suids *Listriodon splendens* and *Parachleuastochoerus steinheimensis* (van der Made et al. 2014), several carnivores (not yet described), and a rich ruminant fauna, described here.

All vertebrate fossils originate from a single fine-clastic soil layer (55 cm in total thickness; Gross et al. 2011, 2014, this issue), interpreted as a floodplain palaeosol (Gross et al. 2011, 2014, this issue). The uniformity of the palaeosol, the good preservation of the fossils, as well as the preservation of coprolites and pellets, point to a rather rapid accumulation and short time of soil formation (10^1–10^2 years; Gross et al. 2011, 2014, this issue; Havlik et al. 2014, this issue) and therefore confirm the assumption of a contemporaneous and stratigraphically not mixed mammal assemblage. The environment of the wider area around Gratkorn at the time of its deposition was reconstructed as a mosaic of a wide range of habitats, comprising, e.g. active and abandoned river channels, riparian woodland, floodplains, and ephemeral ponds as well as drier and more open areas (Gross et al. 2011).

During the Early and earlier Middle Miocene, a great number of Central European localities (see, e.g. Fig. 1) provided rich and diverse ruminant faunas (e.g. five contemporaneous cervid species at about 14.2 Ma; Böhme et al. 2012). Of course, sampling biases, such as fluviatile reworking, have to be taken into consideration, but it is still remarkable that late Middle Miocene ruminant findings are rare in Central Europe and usually only provide isolated dental material or cranial appendages (only one cervid species recorded at about 12 Ma; Böhme et al. 2012). Ruminant assemblages from the Late Miocene (though not as rich in total numbers as the Middle Miocene) again comprise a more diverse fauna (with at least four contemporaneous cervid species at about 10.5 Ma, Böhme et al. 2012; or three sympatric species at the locality of Dorn-Dürkheim 1, Azanza et al. 2013), but differ from the Middle Miocene assemblages in their different taxonomic composition. The rich ruminant assemblage from Gratkorn closes a gap in Central Europe between the well-documented record from the Early to middle Middle Miocene and the Late Miocene.

Especially remarkable in this context is the record of *Dorcatherium naui* Kaup 1833, which represents one of the oldest records of this species so far described. Usually, the species is a rare faunal element in fossil assemblages (see, e.g. Alba et al. 2011). In contrast to this, *D. naui* is the second most frequent large mammal species at Gratkorn, and one of the most extensive materials recorded besides Eppelsheim (Kaup 1839) and Atzelsdorf (early Late Miocene; Hillenbrand et al. 2009).

Therefore, it adds to a more complete insight into the skeletodental morphology and intraspecific variability of this insufficiently known species. With the first rich record for the early representatives of the species, it gives new insights into its phylogenetic relationships.

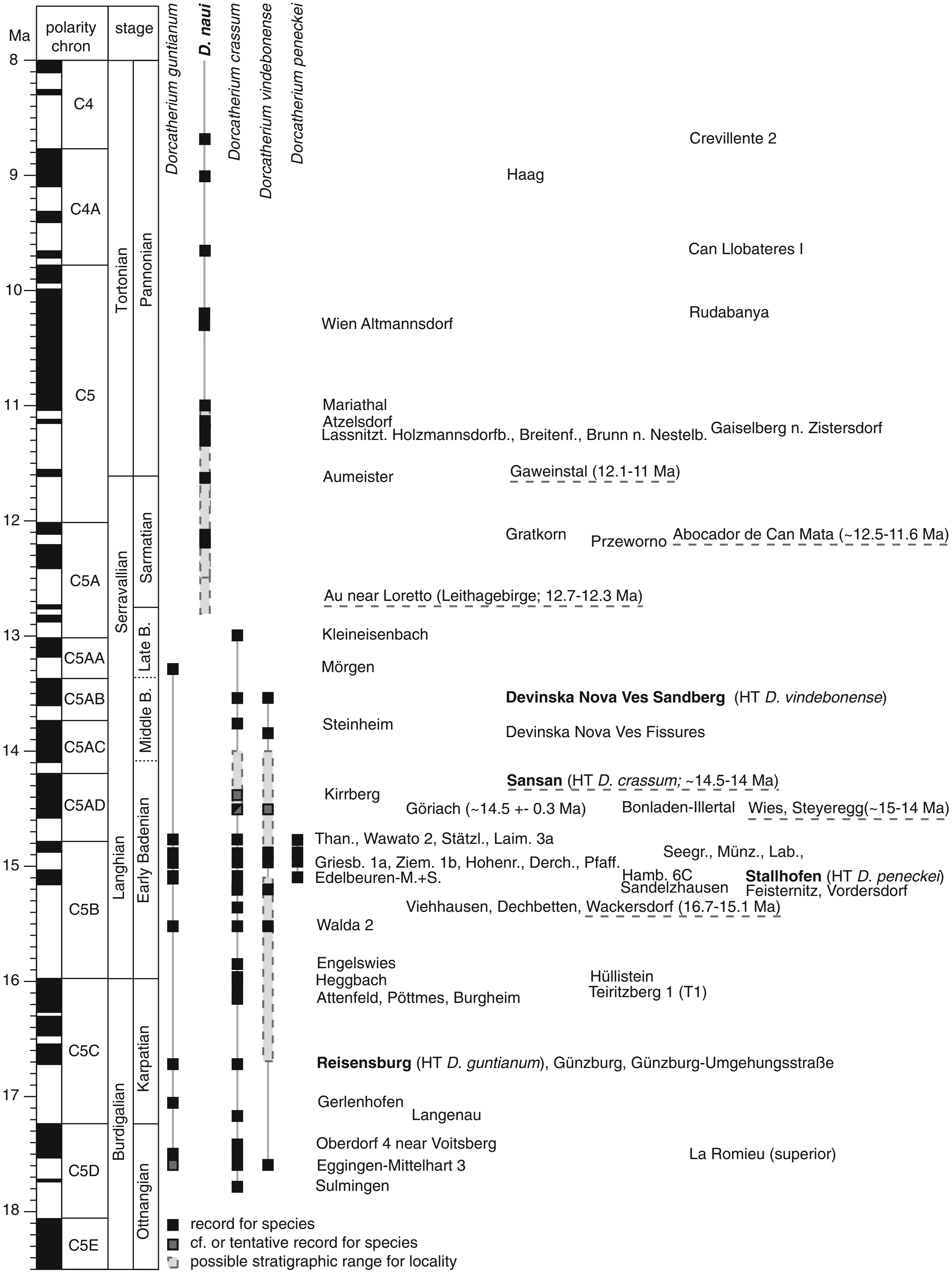
Fig. 1 Stratigraphic range for different *Dorcatherium* species in Central ▶ Europe (focus is on localities from the North Alpine Foreland Basin (NAFB) and Austria; only localities with reliable species identification have been taken into consideration). Type localities for species highlighted in *black*. For some localities, only stratigraphic ranges can be given due to lack of good dating or a considerable amount of stratigraphic mixing (e.g. Gaweinstal; Harzhauser et al. 2011). The Eppelsheim Formation (Fm) housing the type locality of *D. naui* has been recently shown to cover a wide stratigraphic range from Middle Miocene to Late Miocene and is therefore not taken into consideration here (Böhme et al. 2012). *Lassnitzt.* Lassnitztunnel, *Holzmannsdorfb.* Holzmannsdorfberg, *Breitenf.* Breitenfeld, *Brunn n. Nestelb.* Brunn near Nestelbach, *Than.* Thannhausen, *Wawato 2* Wannenwaldtobel 2, *Stätzl.* Stätzling, *Laim. 3a* Laimering 3a, *Griesb. 1a* Griesbeckerzell 1a, *Ziem. 1b* Ziemetshausen 1b, *Hohenr.* Hohenraunau, *Derch.* Derching, *Pfaff.* Pfaffenzell, *Seegr.* Seegraben, *Lab.* Labitschberg near Gamlitz, *Münz.* Münzenberg near Leoben, *Edelbeuren-M.+S.* Edelbeuren-Maurerkopf and Schlachtberg, *Hamb. 6c* Hambach 6c (references for records; online resource 1).

Materials and methods

The material described here was excavated in cooperation of the Universalmuseum Joanneum, Graz (Graz, Austria), the Eberhard Karls Universität Tübingen (Tübingen, Germany) and the Ludwig-Maximilians-Universität München (München, Germany) from 2005 to 2013. It is housed at the Universalmuseum Joanneum (UMJGP) and at the Paläontologische Sammlung der Universität Tübingen (GPIT).

Due to the general taphonomic situation (for further details, see Havlik et al. 2014, this issue), teeth and mandibular fragments are more abundant than postcranial elements in the ruminant material from Gratkorn. Postcrania often only comprise distal or proximal epiphyses, while diaphysis have suffered from intense scavenging (Havlik et al. 2014, this issue).

Metric and morphologic comparison of the material was accomplished by personal observation on collection material (BMNH, SNSB-BSPG, GPIT, IGM, IPS, MNHN, NMB, NHMM, NHMW, NMNHS, IPUW, SMNS, UMJGP) and literature data.
Measurements were done with digital calipers and follow modified van der Made (1996) (for postcrania), Azanza et al. (2013) (for antlers) and Rössner (1995) (for dental material).
Material personally observed for comparison comprises:
Dorcatherium naui: *D. naui* from Eppelsheim (NHMM, BMNH, SNSB-BSPG, GPIT), Atzelsdorf (NHMW), Abocador de CanMata (IPS), Holzmannsdorfberg (UMJGP), Lassnitztunnel (UMJGP), Brunn near Nestelbach (UMJGP), Strumyani (NMNHS); *D. guntianum* from Wannewaldtobel 2 (SMNS), Günzburg/Reisensburg (SNSB-BSPG), Stätzling (SNSB-BSPG, NMA), Thannhausen (SNS-BSPG), Walda 2


Ma
polarity chron
stage
Dorcatherium guntianum
D. naui
Dorcatherium crassum
Dorcatherium vindebonense
Dorcatherium peneckei
8
9
10
11
12
13
14
15
16
17
18
C4
C4A
C5
C5A
C5AA
C5AB
C5AC
C5AD
C5B
C5C
C5D
C5E
Tortonian
Serravallian
Langhian
Burdigalian
Pannonian
Sarmatian
Late B.
Middle B.
Early Badenian
Karpatian
Ottnangian
Crevillente 2
Haag
Can Llobateres I
Rudabanya
Wien Altmannsdorf
Mariathal
Atzelsdorf
Lassnitzt. Holzmannsdorfb., Breitenf., Brunn n. Nestelb.
Gaiselberg n. Zistersdorf
Aumeister
Gaweinstal (12.1-11 Ma)
Gratkorn
Przeworno
Abocador de Can Mata (~12.5-11.6 Ma)
Au near Loretto (Leithagebirge; 12.7-12.3 Ma)
Kleineisenbach
Mörgen
Devinska Nova Ves Sandberg (HT *D. vindebonense*)
Steinheim
Devinska Nova Ves Fissures
Sansan (HT *D. crassum;* ~14.5-14 Ma)
Kirrberg
Göriach (~14.5 +- 0.3 Ma)
Bonladen-Illertal
Wies, Steyeregg(~15-14 Ma)
Than., Wawato 2, Stätzl., Laim. 3a
Seegr., Münz., Lab.,
Griesb. 1a, Ziem. 1b, Hohenr., Derch., Pfaff.
Edelbeuren-M.+S.
Hamb. 6C
Sandelzhausen
Stallhofen (HT *D. peneckei*)
Feisternitz, Vordersdorf
Viehhausen, Dechbetten, Wackersdorf (16.7-15.1 Ma)
Walda 2
Engelswies
Heggbach
Attenfeld, Pöttmes, Burgheim
Hüllistein
Teiritzberg 1 (T1)
Reisensburg (HT *D. guntianum*), Günzburg, Günzburg-Umgehungsstraße
Gerlenhofen
Langenau
Oberdorf 4 near Voitsberg
Eggingen-Mittelhart 3
La Romieu (superior)
Sulmingen
■ record for species
▣ cf. or tentative record for species
▨ possible stratigraphic range for locality

(SNSB-BSPG); *D. crassum* from Sansan (MNHN, SNSB-BSPG), Sandelzhausen (SNSB-BSPG), Engelswies (GPIT), Viehhausen (SNSB-BSPG), Göriach (UMJGP, IGM), Vordersdorf (UMJGP, IGM), Feisternitz near Eibiswald (UMJGP), Steyeregg (UMJGP), Piberstein (UMJGP), Steinheim a. A. (am Albuch; SMNS), Münzenberg near Leoben (UMJGP), Labitschberg near Gamlitz (UMGP), Walda 2 (SNSB-BSPG); *D. vindebonense* from Labitschberg near Gamlitz (UMJGP), Wackersdorf (SNSB-BSPG), Seegraben (UMJGP, IGM); *D. peneckei* from Stallhofen near Voitsberg (UMJGP;), Stätzling (SNSB-BSPG, NMA), Seegraben (UMJGP, IGM), Walda 2 (SNSB-BSPG);

Micromeryx flourensianus: *M. flourensianus* from Sansan (MNHN), Steinheim a. A. (GPIT, NMB, SMNS), Atzelsdorf (NHMW); *M. styriacus* from Göriach (UMJGP); *M. mirus* from Kohfidisch (NHMW); *M.* sp. from Dorn-Dürkheim 1 (SMF); *Lagomeryx ruetimeyeri* from Langenau 1 (SMNS); *Lagomeryx parvulus* from Göriach (UMJGP), Sandelzhausen (SNSB-BSPG); *Lagomeryx pumilio* from Sandelzhausen (SNSB-BSPG);

Euprox furcatus: *Euprox furcatus* from Steinheim a. A. (GPIT, NMB, SMNS); *Euprox minimus* from Göriach (UMJGP); *Euprox* sp. from Atzelsdorf (NHMS); *Euprox* vel *Heteroprox* from Steinheim a. A. (GPIT, NMB, SMNS); *Heteroprox larteti* from Sansan (MNHN), Steinheim a. A. (GPIT, NMB, SMNS), Göriach (UMJGP), Seegraben (UMJGP); *Heteroprox eggeri* from Sandelzhausen (SNSB-BSPG); *Dicrocerus elegans* from Sansan (MNHN), Göriach (UMJGP, IGM), Seegraben (UMJGP), Stätzling (NMA), Sprendlingen 2 (NHMM, SSN); *Procervulus dichotomus* from Viehhausen (SNSB-BSPG); *Paradicrocerus elegantulus* from Stätzling (NMA), Sprendlingen 2 (NHMM, SSN);

Palaeomerycidae gen. et sp. indet.: *Palaeomeryx eminens* from Steinheim a. A. (GPIT, SMNS); *Germanomeryx* from Sandelzhausen (SNSB-BSPG);

***Tethytragus* sp.**: *Miotragocerus monacensis* from Aumeister (SNSB-BSPG); *Miotragocerus* vel *Tethytragus* from Atzelsdorf (NHMW); *Eotragus clavatus* from Sansan (MNHN) and Göriach (UMJGP); *Eotragus artenensis* from Artenay (MNHN); *Pseudoeotragus seegrabensis* from Seegraben (UMJGP); as well as other records/isolated findings from the North Alpine Foreland Basin (NAFB) and Austria.

For plots material described by Kaup (1833, 1839), von Meyer (1846), Hofmann (1893), Schlosser (1886), Thenius (1950), Rinnert (1956), Mottl (1954, 1961, 1966, 1970), Ginsburg and Crouzel (1976), Fahlbusch (1985), van der Made (1989), Ginsburg and Azanza (1991), Sach (1999), Azanza (2000), Vislobokova (2007), Hillenbrand et al. (2009), Rössner (2010), Alba et al. (2011), Morales et al. (2012), van der Made (2012), Aiglstorfer and Costeur (2013) was personally measured, to minimise bias due to different measurement standards. Furthermore, literature data were included (see figure captions for references).

Nomenclature for dental material follows Bärmann and Rössner (2011). To avoid confusion, the term '*Dorcatherium*-fold' is not used in this work, as proposed by Bärmann and Rössner. The term has been under discussion since Mottl (1961; Alba et al. 2011). While some authors prefer to apply the term '*Dorcatherium*-fold' to the whole ∑-like structure (e.g. Janis and Scott 1987; Hillenbrand et al. 2009; Rössner 2010), according to the definition by Mottl (1961), others use the term only for the folded structure posterior of the metaconid (Métais et al. 2001; Sánchez et al. 2010b; Alba et al. 2011; see also discussions in Métais et al. 2001 and Alba et al. 2011). In this publication, the terms 'internal' and 'external postmetacristid' and 'internal' and 'external postprotocristid' (sensu Bärmann and Rössner 2011) or the term '∑-structure' are used. Postcranial terminology mainly follows Nickel et al. (1968) and König and Liebich (2008), and for antler terminology, Azanza et al. (2013).

Body mass estimations (kg) given here follow, if possible, the equations of Janis (1990), and are based on length of m2 (SLML, mm) and length of the lower molar row (LMRL, mm): *Dorcatherium naui*: equation "ruminants only" [$\log(BM)=3.337\times\log(SLML/10)+1.118$], [$\log(BM)=3.352\times\log(LMRL/10)-0.604$]; *Micromeryx flourensianus*: equations "ruminants only" (for equation, see above) and "bovids only" [$\log(BM)=3.375\times\log(SLML/10)+1.119$], [$\log(BM)=3.335\times\log(LMRL/10)-0.581$]; *Euprox furcatus*: equations "cervids only" [$\log(BM)=3.106\times\log(SLML/10)+1.119$], [$\log(BM)=3.209\times\log(LMRL/10)-0.524$].

Due to limited dental material, the equations of Damuth (1990) based on the length of M2 (mm) "all selenodonts" {[$\log(BM)=3.15\times\log(M2\ \text{length})-0.94$]/1,000}, "selenodont browsers" {[$\log(BM)=3.34\times\log(M2\ \text{length})-0.73$]/1,000} are used for *Tethytragus* sp. and one of Scott (1990) based on the length of the metacarpal (Mc1, mm) "ruminants" [$\log(BM)=2.4722\times\log(Mc1)-1.237$] for the Palaeomerycidae gen. et sp. indet. Body mass estimations based on dental measurements are considered less reliable than those based on postcranial material (Mendoza et al. 2006). However, taking into consideration the tragulid *D. naui*, the equations of Janis (1990) based on dental material of extant ruminants are preferred here to the equations based on postcranial material of extant ruminants by Scott (1990). On the one hand, Janis (1990) also included Tragulidae in her "ruminants only" data matrix, and on the other hand, for tragulids with their peculiar "intermediate suid/ruminant postcranial anatomy", the equations of Scott (1990) cannot be applied properly.

Anatomical abbreviations

C	upper canine
P 2, -3, -4	second, third, fourth upper premolar
M1, -2, -3	first, second, third upper molar
i1, -2, -3	first, second, third lower incisor
p 1, -2, -3, -4	first, second, third, fourth lower premolar
m1, -2, -3	first, second, third lower molar
sin.	sinistral/left
dex.	dextral/right
l (max)	maximal length of tooth
w (max)	maximal width of tooth
want (max)	maximal anterior width of tooth
h (max)	maximal height
L	length
Lint	internal length in astragalus
Lext	external length in astragalus
wint	internal dorsoplantar width of astragalus
wext	external dorsoplantar width of astragalus
DAPp	proximal anteroposterior/dorsovolar diameter
DAPps	maximal proximal dorsovolar diameter of phalanx
DTp	proximal transversal diameter
DAPd	distal anteroposterior/dorsovolar diameter
DTd	distal transversal diameter
DTn	minimal transversal width in calcaneum
Dtdf	transversal diameter of the trochlea humeri

Institutional abbreviations

BMNH	British Museum of Natural History, London, UK
GPIT	Paläontologische Sammlung der Universität Tübingen, Tübingen, Germany
IGM	Montanuniversität Leoben, Leoben, Austria
IPS	Collections of the Institut Català de Paleontologia, Barcelona, Spain
IPUW	Institut für Paläontologie Universität Wien, Wien, Austria
MB.Ma	Museum für Naturkunde—Leibniz-Institut für Evolutions-und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Mammal Collection, Berlin, Germany
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NMA	Naturmuseum Augsburg, Augsburg, Germany
NMB	Naturhistorisches Museum Basel, Basel, Switzerland
NHMM	Naturhistorisches Museum Mainz, Mainz, Germany
NHMW	Naturhistorisches Museum Wien, Wien, Austria
NMNHS	National Museum of Natural History, Sofia, Bulgaria
SMF	Senckenberg Museum Frankfurt, Frankfurt, Germany
SMNS	Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany
SNSB-BSPG	Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany
SSN	Paläontologisches Museum Nierstein, Nierstein, Germany
UMJGP	Universalmuseum Joanneum, Graz, Austria

Systematic Palaeontology

Class Mammalia Linnaeus, 1758
Order Artiodactyla Owen, 1848
Suborder Ruminantia Scopoli, 1777
Infraorder Tragulina Flower, 1883
Family Tragulidae Milne Edwards, 1864
Genus *Dorcatherium* Kaup, 1833

Type species: *Dorcatherium naui* Kaup, 1833
Further European species: *Dorcatherium crassum* (Lartet, 1851); *Dorcatherium vindebonense* von Meyer, 1846; *Dorcatherium guntianum,* von Meyer, 1846; *Dorcatherium peneckei* (Hofmann, 1893); *Dorcatherium jourdani* Depéret, 1887; and *Dorcatherium puyhauberti* Arambourg and Piveteau, 1929.

The genus *Dorcatherium*, erected by Kaup in 1833, comprises five species generally accepted from the Miocene of Europe, differing in dimensions, dental and postcranial morphology and stratigraphic range (Fig. 1): the small-sized *D. guntianum*, the medium-sized *D. naui* and *D. crassum*, the larger-sized *D. vindebonense*, and the large-sized *D. peneckei.*

D. puyhauberti and *D. jourdani* are rarely documented, with only a few specimens, which possess no unambiguous features distinguishing them from other European species and could be synonymous to *D. guntianum* and *D. naui* respectively. Morales et al. (2012), also referring to Geraads et al. (2005), accordingly propose that both species could be included in *D. naui*, but need to be revised in more detail. *D. puyhauberti* is smaller in dimensions than *D. naui*, being in the size variability of *D. guntianum* (Hillenbrand et al. 2009; Rössner and Heissig 2013). Hillenbrand et al. (2009) found a character distinguishing the species from all other *Dorcatherium* species: smaller M3 in comparison to M2. The *D. puyhauberti* type material was not available for study during comparative investigations for this paper, but, as could be recognised on photographs recently taken from the type material at the MNHN, the feature, correctly extracted by Hillenbrand et al. (2009) from the original description of Arambourg and Piveteau (1929), cannot be verified on the original material. M2 and M3 are not articulated in the maxilla but fixed together with a gypsum bed, and the two teeth are now fixed in inverse order compared with the original description. The different colours of the enamel furthermore indicate that the two teeth might originate from different individuals (for further information on the historical context of the genus and discussion on species validity, see Appendix 1).

The Miocene tragulid genus *Dorcabune* Pilgrim, 1910, is known with several species but so far only from Asia (Rössner 2007). As *Dorcabune* and *Dorcatherium* overlap in morphological key features, a revision of the two genera would probably result in two morphotypes/lineages of Miocene tragulids with a differentiation into more bunodont (including *D. crassum, vindebonense* and *peneckei*) and more selenodont forms (including *D. naui* and *guntianum*) (Rössner 2007, referring also to Mottl 1961, Fahlbusch 1985, Qui and Gu 1991).

To get a better idea about relationships of and faunal exchanges between Asian, African and European Miocene tragulids, a revision of the different taxa and lineages, as also proposed by Sánchez et al. 2010b, is surely needed.

Dorcatherium naui Kaup, 1833

Holotype: Mandibula with p3–m3 and alveolae of p1 and p2 described in Kaup (1833) and figured in Kaup (1839, pl. XXIII, fig. 1, 1a, 1b), lost, cast available (BMNH M3714, SNSB-BSPG 1961 XIX 37).
Type locality: Eppelsheim (Germany)

Dentition and mandibulae (Fig. 2a–n)

Material: UMJGP 204059 (C dex.), GPIT/MA/2377 (D2 dex.), UMJGP 204675 (D3 dex.), UMJGP 204064 (D3 dex.), GPIT/MA/2375 (D4–M1 sin.), GPIT/MA/2379 (P4 dex.), GPIT/MA/2376 (M1? dex.), UMJGP 210956 (d2 sin.), UMJGP 210694 (fractured mandibula with i1, p2–m3 sin. and dex.), GPIT/MA/2734 [mandibula sin. with i2 or 3 sin. (isolated), alveolae for p1–p3, and p4–m3], GPIT/MA/2401 (m1 sin.), UMJGP 204109 (fragment of mandibula sin. with fragments of m2–3), GPIT/MA/2756 (m2 sin.), UMJGP 203714 (fragment of labial side of mx).

Finding position, preservation, and degree of dental wear allow for deducing GPIT/MA/2741 (i1 dex.), GPIT/MA/2741 (i2or3 dex.), GPIT/MA/2741 (i2 or 3 sin.), GPIT/MA/02741 (p2 sin.) and GPIT/MA/2741 (mandibula sin. with p3–m3) as belonging to one individual, as do UMJGP 204667 (mandibula sin. with p2–3), UMJGP 204661 (mandibula dex. with p2–3), UMJGP 204664 (fragment of mandibula sin. with p4–m1), UMJGP 204663 (fragment of mandibula dex. with m1–2), UMJGP 204662 (fragments of mandibulae with m2 sin., m3 dex.) and UMJGP 204665 (m3 sin. with fragment of mandibula). UMJGP 210696 (d3 sin.), UMJGP 210692 (d4 sin.), and UMJGP 210693 (m1 sin.) most likely belong to one individual.

UMJGP 204067 (D3–4 sin.) and UMJGP 209952 (M1 sin.) also fit together. From finding position and degree of wear, GPIT/MA/2732 (M1? dex.), UMJGP 210698 (M2 sin.), and UMJGP 210697 (M3 sin.) are also assigned to one individual.

Description and comparison

From dimensions, all teeth are well within the variability of the medium-sized *Dorcatherium naui* and *D. crassum* (Fig. 3; for detailed information and measurements, see online resource 2).

Only isolated teeth and incomplete deciduous tooth rows are preserved of the **upper dentition**. Therefore, characters based on tooth row length, or size increases from M1 to M3, etc., cannot be verified. Only one fragmentary sabrelike **C dex.** (UMJGP 204059; Fig. 2a) is preserved. It is curved with the tip directed to posteriad and a drop-shaped cross-section (rounded anteriorly and with a sharp angle posterior). The anteroposterior diameter of the tooth does not decrease continuously from base to tip as is the case in canines of *Euprox* and *Micromeryx*, but is more constant and the sharp tip has been produced by lingual wear on the tooth. Enamel covers only the labial side. Strong wear during lifetime is indicated by a large wear surface on the lingual side of the tip. The growth striation is more distinct than it is in Cervidae or Moschidae. In size and shape, the canine is in accordance with those of *D. crassum* and *D. naui*. The only **D2** (GPIT/MA/2377; Fig. 2b) preserved is fragmented and missing the posterolabial cone. The tooth is anteroposteriorly elongated and has a strong lingual cingulum, comparable to specimens of *D. crassum* from Sansan. The anterolabial cone is larger than the anterior style. So far, a D2 of *D. naui* has only been described from the localities Ballestar and Can Petit in Spain by Moyà-Solà (1979), but not figured. His description is

Fig. 2 Dental and postcranial material of *Dorcatherium naui.* **a** C dex. ▶ (UMJGP 204059; *1* labial view, *2* lingual view), **b** D2 dex. (GPIT/MA/2377; *1* lingual view, *2* occlusal view), **c** D3 dex. (UMJGP 204675; occlusal view), **d** D3–4 sin. (UMJGP 204067; occlusal view), **e** d2 sin. (UMJGP 210956; labial view), **f** d3 sin. (UMJGP 210696; occlusal view), **g** d4 sin. (UMJGP 210692; occlusal view), **h** P4 dex. (GPIT/MA/2379; occlusal view), **i** M1 sin. (UMJGP 209952; occlusal view), **j** M2 sin. (UMJGP 210698; occlusal view), **k** M3 sin. (UMJGP 210697; occlusal view), **l** mandibula sin. with p4–m3 and alveolae for p1–p3 (GPIT/MA/2734; *1* occlusal view, *2* labial view, *3* m3 in occlusal view), **m** mandibula sin. with p2–3 (UMJGP 204667; *1* labial view, *2* occlusal view), **n** fractured mandibula with i1, p2–m3 sin. and dex. (UMJGP 210694; *1* mandibula dex. in lingual view and sin. in labial view, *2* p4–m3 sin. in labial view, *3* p4–m3 sin. in lingual view, *4* p4–m3 sin. in occlusal view, *5* m3 sin. in occlusal view), **o** humerus sin. (GPIT/MA/2389; *1* cranial view, *2* distal view), **p** radius sin. (GPIT/MA/2391; *1* dorsal view, *2* proximal view), **q** cubonavicular sin. (UMJGP 203419; dorsal view), **r** tibia sin. (UMJGP 203419; *1* dorsal view, *2* lateral view of distal end, *3* distal view), **s** astragalus dex. (GPIT/MA/2409; *1* dorsal view, *2* palmar view), **t** fragmented calcaneum dex. (GPIT/MA/2409; medial view); *scale bar* 10 mm (except **n***1*, 50 mm)


a1
a2
b1
b2
c
d
e
f
g
h
i
j
k
l1
l2
l3
m1
m2
n1
n2
n3
n4
n5
o1
o2
p1
p2
q
r1
r2
r3
s1
s2
t

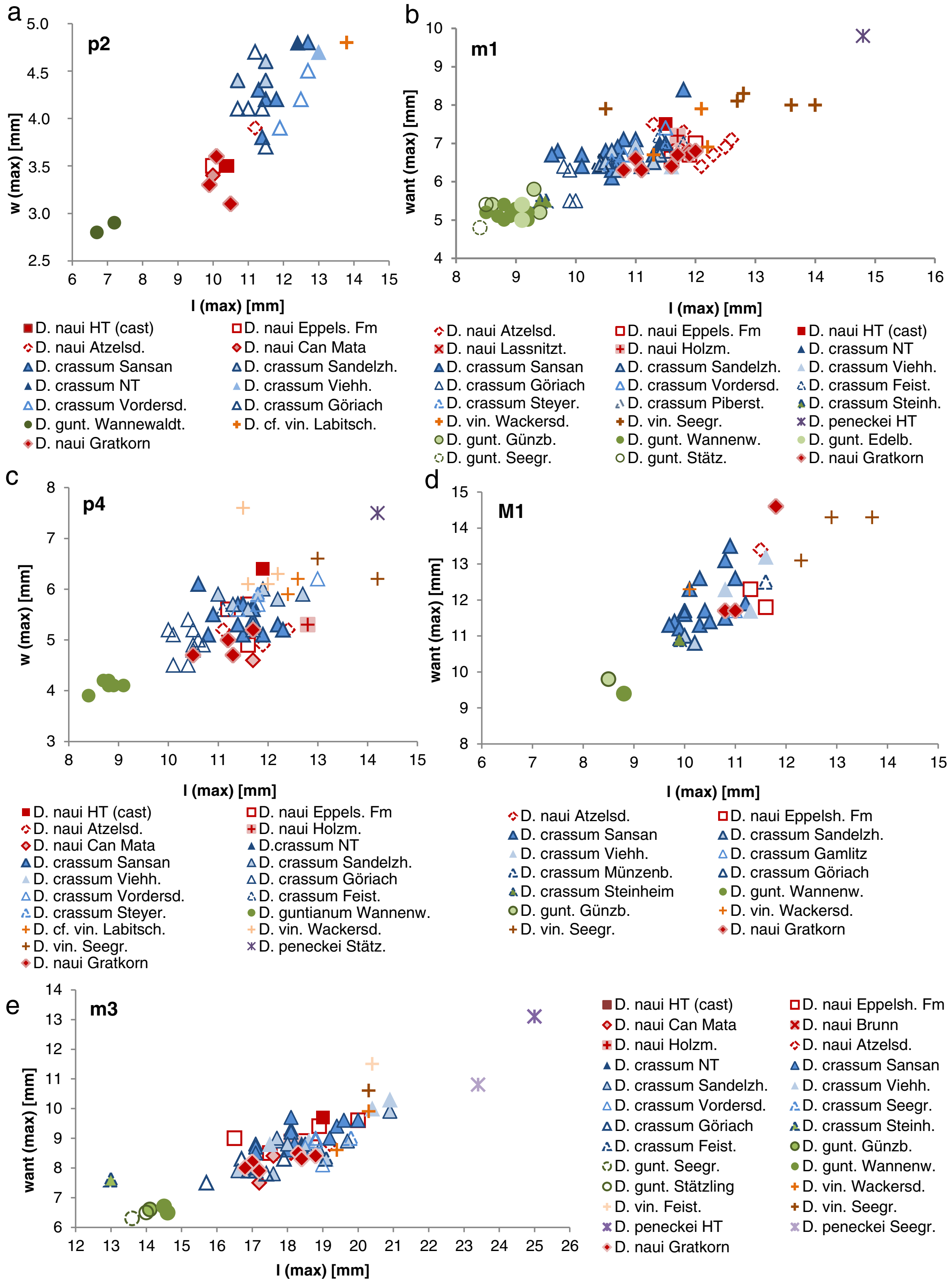


Fig. 3 Bivariate plots for p2 (**a**), p4 (**c**), m1 (**b**), m3 (**e**) and M1 (**d**) of *Dorcatherium naui* from Gratkorn in comparison to other Central European *Dorcatherium* species (all own measurements, mm), with the focus on type material and Styrian localities; *HT* holotype, *NT* neotype, *gunt.* guntianum, *vin.* vindebonense, *Eppelsh. Fm* Eppelsheim Fm, *Atzelsd.* Atzelsdorf, *Sandelzh.* Sandelzhausen, *Viehh.* Viehhausen, *Vordersd.* Vordersdorf, *Wannenwaldt.* Wannenwaldtobel 2, *Labitsch.* Labitschberg, *Lassnitzt.* Lassnitztunnel near Graz, *Holzm.* Holzmannsdorfberg, *Feist.* Feisternitz near Eibiswald, *Steyer.* Steyeregg, *Piberst.* Piberstein, *Steinh.* Steinheim a. A., *Edelb.* Edelbeuren-Schlachtberg, *Wackersd.* Wackersdorf, *Seegr.* Seegraben, *Günzb.* Günzburg/Reisensburg, *Stätz.* Stätzling, *Münzenb.* Münzenberg

generally in congruence with the specimen from Gratkorn. In occlusal view, the **D3** (Fig. 2c) exhibits a triangular shape and an anterior cone with a well-pronounced anterior crista. Para- and metacone are the dominant cones. The metaconule is well developed, while the protocone is small and positioned at a more anterior level than the paracone. The premetaconulecrista is split into one external and two internal premetacunulecristae; of the latter, the posterior one terminates in a small tubercle. The postmetaconulecrista fuses posterolabially with the posterior cingulum. While the parastyle is weak and attached to a small labial cingulum, the mesostyle is strong and clearly set off from the metacone. The metastyle is tiny. With a weaker cingulum, the specimens from Gratkorn differ from *D. crassum* from Sansan. A D3 of *D. naui* has so far only been described by Moyà-Solà (1979), but not figured. He states a similar size for D3 in *D. naui* and *D. crassum*. The **D4** shows a trapezoid molar-like shape (Fig. 2d) with enlarged and anteriad protruding parastyle and well-pronounced mesostyle. Both D4 specimens from Gratkorn show a crest at the posterolingual wall of the paracone, comparable to a small tubercle lingual to the postprotocrista in *D. naui* from Can Mata and from Atzelsdorf. Comparable to *D. guntianum* and *D. naui,* the mesostyle is not as bulky in the Gratkorn specimens as it is in *D. crassum* from Sansan and Sandelzhausen. Typical for Tragulidae (Milne Edwards 1864, pl. IX fig. 9, pl. X fig. 3; Rössner 2007, fig. 16.3 B), the **P4** (GPIT/MA/2379; Fig. 2h) is triangular in shape and thus differs from Pecora, which have a lingually rounded P4. The labial cone is dominant, and anterior and posterior styles are well developed. The first is more set off than the latter. There is no central fold, but the posterolingual crista is instead shifted anteriorly and not fused with the posterolingual cingulum, but terminates inbetween the lingual cone and posterior style. The anterolingual cingulum is short and weak.

As common in the genus, the five subrectangular to trapezoid **upper molars** (Fig. 2i–k) show no clearly developed splitting of the postprotocrista (Fahlbusch 1985). Only in one specimen (UMJGP 210698) a splitting is developed, resulting in short external and internal postprotocristae. This can also be observed in some specimens of the type series of *D. crassum* from Sansan and was recently described for Early Miocene *D. crassum* from Spain (Alba et al. 2013), indicating that this feature, even if rarer, can occur. As is typical in tragulids, the premetaconulecrista is longer in all specimens than the postprotocrista and reaches the posterolingual wall of the paracone. Only one specimen (UMJGP 210698) exhibits a more complex morphology with small tubercles at its anterior end. All specimens have prominent para- and mesostyles, a clear lingual rib at the paracone and a pronounced lingual cingulum reaching from the anterior side of the protocone to the posterior side of the hypocone. A distinct entostyle is not present in any of the specimens; only in GPIT/MA/2375 is it indicated by a thickening of the cingulum. While in all M1 (UMJGP 210698, GPIT/MA/2375, GPIT/MA/2376; Fig. 3d) the metastyle is very small, it increases in size in the M2 (UMJGP 210698), and is further enlarged in the M3 (UMJGP 210697). Although M2 and M3 are less slender in habitus than M1 and possess a clearly more inflated mesostyle, all teeth are selenodont and differ clearly from the bunoselenodont *D. crassum* from Sansan and Sandelzhausen with its more bulky styles (Morales et al. 2012; Rössner 2010).

The **mandibulae** from Gratkorn show a slender corpus mandibulae (Fig. 2e–g, l–n), nesting in the lower part of the morphological variability of *D. crassum* from Sansan and Sandelzhausen (Morales et al. 2012; Rössner 2010), and are in accordance with dimensions of *D. naui* from Atzelsdorf (Hillenbrand et al. 2009), Abocador de Can Mata (Alba et al. 2011), Eppelsheim (skull with both mandibulae, BMNH M 40632; cast GPIT/MA/3653), and the cast of the holotype (BMNH M 3714, BSPG 1961 XIX 37). In all specimens with a preserved rostral part of the mandibula, an alveola for the p1 is present (Fig. 2l, n). There are two foramina mentalis on the lateral side of the corpus mandibulae (Fig. 2l, n), of which the rostral one is enlarged and elongated reaching from the caudal rim of the symphysis to the alveola of the p1. The interspace between anterior premolars and caudal rim of the symphysis is short, as it is also in *D. naui* from Atzelsdorf (Hillenbrand et al. 2009, pl. 2, fig. 9) and Abocador de Can Mata. In the cast of the holotype of *D. naui* (BMNH M 3714, BSPG 1961 XIX 37), the caudal rim of the symphysis is even at the level of the rostral alveola for the p2. The interspace is also small in *D. crassum* from Sansan. The length of premolar and molar tooth rows from Gratkorn (online resource 2) are within the variability of *D. naui* from Eppelsheim, Atzelsdorf and Abocador de Can Mata*,* *D. crassum* from Sansan and Sandelzhausen, and *D.* “cf. *puyhauberti”* from Strumyani (Bulgaria; Geraads et al. 2011; which could very likely be *D. naui*). They are clearly larger than in *D. guntianum* (e.g. from Wannenwaldtobel 2; see also Sach 1999). The holotype of *D. peneckei* from Stallhofen (UMJGP 1601; length of m1–3: 54 mm) is larger. In UMJGP 210694, the angulus mandibulae is clearly set off from the corpus mandibulae by a ventral depression (Fig. 2n), which is weak in *D. naui* from Atzelsdorf (Hillenbrand et al. 2009, pl. 2, fig. 9) and not present in a *D. naui* from Eppelsheim (BMNH M 40632). In *D. crassum* from Sansan (e.g. MNHN Sa 10852), it is generally less pronounced. While the processus coronoideus is not preserved in any specimen from Gratkorn, a rounded incisura mandibulae (50 mm dorsal of the ventral rim of the angulus mandibulae) and the caput mandibulae of the processus condylaris, are documented in UMJGP 210694 (Fig. 2n). The caput mandibulae is slightly less high than in the mandibula of *D. naui* from Atzelsdorf (Hillenbrand et al. 2009, pl. 2, fig. 9). The reconstructed length of the symphsis at roughly about 20 mm and the height at about 10 mm

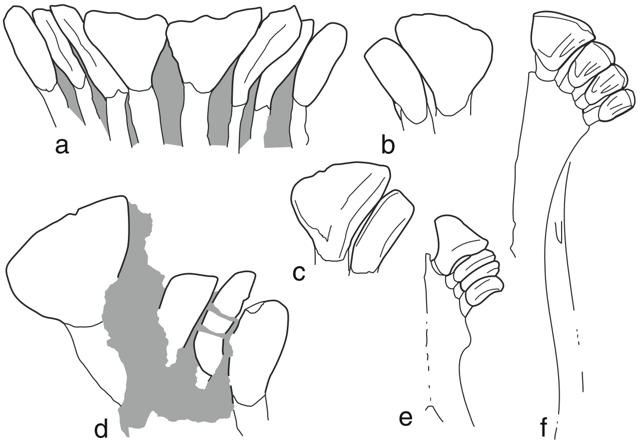


Fig. 4 Schematic drawing of different ruminant incisor arcades: **a** *Dorcatherium naui* (redrawn from Kaup 1839), **b** i1 (UMJGP 210694) and i2 (GPIT/MA/2741) of *D. naui* from Gratkorn in labial view, **c** i1 (UMJGP 210694) and i2 (GPIT/MA/2741) of *D. naui* from Gratkorn in lingual view, **d** i1–c1 of *Dorcatherium* cf. *puyhauberti* in labial view (presumably *naui*) from Strumyani, Bulgaria (NMNHS FM-2741), **e** i1–c1 of *Tragulus javanicus* (modified from Thenius 1989), **f** *Cervus elaphus* (modified from Thenius 1989)

correspond well to the medium-sized *Dorcatherium* species, *D. crassum* and *D. naui*. The **i1** is of spade-like shape (Fig. 4b), widening from base to tip more than in cervids (Fig. 4f). The tooth shape is lingually concave and occlusally bent to the posterior. On the lingual plane, it shows a thin anterior vertical crest and a strong groove at the posterior rim. Three isolated **i2 or 3** are preserved from Gratkorn. They are pen-like, lingually concave, bent to the posterior, and bear a small anterior crest on the lingual plane and a deep groove close to the posterior rim, like in the i1. In contrast to the latter, the anteroposterior diameter is more constant from base to tip, and the posterior groove is not as distinct. Modern tragulids show a similar morphology pattern with an extensively occlusoposteriorly widened i1 and more pen-like i2-c (Fig. 4e).), as do *D. naui* from Eppelsheim (BMNH M 40632 and Kaup (1839, tab 23B, fig. 4); Fig. 4a) and *D.* “cf. *puyhauberti”* from Strumyani, Bulgaria (Geraads et al. 2011; Fig. 4d). The only preserved **d2** (UMJGP 210956; Fig. 2e) is posteriorly strongly worn, biradiculate, and bicuspid. Its general morphology does not differ from the p2, except for the lower tooth crown height. Only one **d3** (UMJGP 210696; Fig. 2f), with a missing labial half of the posterolabial conid, is recorded. It has an elongate, anterolingually bent shape with anterior, mesolabial and posterolabial conids and a more or less isolated posterolingual conid. The mesolabial conid is the dominant cusp. There is a weak anterior cingulid. From the mesolabial conid, the transverse cristid and posterolabial cristid proceed posteriorly enclosing an acute angle, the latter turning to lingual posteriorly. In *D. crassum*, especially from the type locality Sansan, an anterior stylid is often present, while it is absent in the specimen from Gratkorn as well as in *D. guntianum* (e.g. from Thannhausen and Wannenwaldtobel 2). One fragmented **d4** (UMJGP 210692 Fig. 2g) is preserved, missing the labial part. It is triradiculate, and has three lingual conids, higher than the labial elements. The anterolingual conid is positioned more anterior than the anterolabial conid, similar to a d4-fragment from Atzelsdorf. This seems to be less common in *D. crassum* (personal observation, Sansan), in contrast to *D. guntianum,* where it can be observed more often (e.g. Günzburg-Umgehungsstrasse and Wannenwaldtobel 2), but is usually not as pronounced as in the specimen from Gratkorn. On the grounds that there is quite a range of intraspecific variability, that only one d4 from Gratkorn has been recorded so far, and that the comparison material for this tooth position of *D. naui* is also limited, the value of this character as a taxonomic feature cannot be estimated. The entostylid is well pronounced. Postmeta- and postprotocristid are split into external and internal cristids, forming the ∑-structure characteristic for the family, while the preentocristid is short and fused with internal postmeta- and postprotocristids basally. The postentocristid is short and connects with the entostylid at its base, while the posthypocristid is longer and fused with the entostylid. Anterior and posterior cingulid are well pronounced. Although no **p1** is preserved, in both specimens where the rostral part of the mandibula is preserved, one alveola for the p1 was observed. This applies to all specimens of *D. naui* with the rostral part of a mandibula preserved, except for one specimen from Can Petit, where the p1 is lacking (Spain; Moyà-Solà 1979). Though rare in *D. crassum* from the type locality Sansan, a p1 more frequently occurs in *D. crassum* and *D. vindebonense* from the NAFB and Austria and in the Early Miocene record from Spain (Mottl 1961; Rössner 2010; Alba et al. 2013). The presence of a p1 is thus optional in *D. crassum* and *D. vindebonense* and cannot be used as a distinct diagnostic feature for *D. naui*, as proposed, e.g. by Ginsburg (1967; see also discussion in Moyà-Solà 1979; Fahlbusch 1985; Alba et al. 2011). All **p2** from Gratkorn are bicuspid and biradiculate (Fig. 2m). The mesolabial conid is dominant, while the posterolabial conid is smaller. While the anterolabial cristid turns slightly lingually at the anterior part and forms a weakly pronounced anterior stylid, the posterolabial cristid bends stronger lingually, forming the posterior wall of the back valley. A posterior cingulid is present. Although the p2 is not preserved in the holotype of *D. naui*, in other specimens from Eppelsheim (e.g. MNHM PW2012/9-LS; BMNH M 40632; cast GPIT/MA/3653), the p2 is bicuspid, as it is in *D. naui* from Can Mata (Alba et al. 2011). In Hillenbrand et al. (2009), the p2 of *D. naui* from Atzelsdorf was described as tricuspid, and is longer than the specimens from Gratkorn. But due to strong wear in the specimen, the morphology of the tooth is difficult to describe and the anterior stylid might give the impression of an anterior conid. In *D. crassum*, the p2 shows a clearly developed anterior conid and a more pointed mesolabial conid. It is clearly tricuspid in this species (Rössner 2010; Morales et al. 2012; Alba et al. 2013) as it is in *D. vindebonense* (Mottl 1961). *D. guntianum* also possesses a biscuspid p2 (e.g. Sach 1999; Mottl 1961; Rössner and Heissig 2013), but clearly differs by its smaller size from *D. naui* and the Gratkorn *Dorcatherium*. Dimensions of the Gratkorn specimens fall within the variability of *D. naui* from Eppelsheim and Spain and are clearly distinct from *D. crassum*, while the specimen from Atzelsdorf lies within the variability of the latter (Fig. 3). With a small anterior conid, the **p3** is tricuspid and longer than the p2. The mesolabial conid is clearly dominant, while the anterior conid is slightly turned lingually, and the posterolabial cristid forms the posterior wall of the back valley and is rectangular to the length axis of the tooth. The back valley is narrow and incises clearly in the posterior wall of the posterolabial conid. A weak anterior and a strong posterior cingulid are present. The preserved shape in the casts of the holotype of *D. naui* (BMNH M 3714, BSPG 1961 XIX 37) indicates a tricuspid p3. It is tricuspid and similar in shape to the Gratkorn specimens and *D. naui* from Eppelsheim (e.g. MNHM PW2012/9-LS; BMNH M 40632), from Atzelsdorf, and from Can Mata (Hillenbrand et al. 2009; see figs. in Alba et al. 2011). In *D. crassum*, the p3 is also tricuspid, but possesses a more dominant mesolabial conid, and a less strongly incised posterior valley (Rössner 2010; Morales et al. 2012). The smaller *D. guntianum* also shows a tricuspid p3 with a less dominant mesolabial conid (e.g. Wannenwaldtobel 2), but differs by a smaller size from *D. naui* and the Gratkorn specimens. The **p4** is shorter than the p3, and quite variable in morphology. The mesolabial conid is always dominant. The anterior valley strongly cuts in the anterolabial cristid forming a sharp groove. Anterior and posterior cingulid are present. In contrast to Pecora, only two cristids branch of the posterior part of the mesolabial conid, the lingual one comprising the fusion of transverse cristid, mesolingual conid and posterolingual conid (Rössner 2010), the labial one the posteriolabial cristid to posterior stylid. The two cristids enclose the posterior valley, which has a quite complex morphology as it comprises small additional transverse crests, which are varying in size and morphology. Development of the mesolingual, posterolabial and posterolingual conid, as well as of the posterior stylid, is variable (Figs. 2l, n, 5). In the casts of the holotype of *D. naui* (BMNH M 3714, BSPG 1961 XIX 37), as well as in the specimen from Abocador de Can Mata, the p4 possesses a complex posterior valley (see also Alba et al. 2011; Fig. 5). In Atzelsdorf the morphology is more variable. The more bunodont *D. crassum* and *D. vindebonense* are usually simpler in structures (Fig. 5), which is also described by Moyà-Solà (1979) when comparing *D. crassum* and *naui*. *D. guntianum* (e.g. from Wannenwaldtobel 2; Sach 1999) shows the same tendency towards a complex structure in the posterior valley, but is smaller than the specimens from Gratkorn (Fig. 3c).

The **lower molars** in the specimens from Gratkorn are less wide and slightly higher crowned than in the similar sized *D. crassum* but well in accordance with the more slender and higher crowned *D. naui* and *D. guntianum* (Figs. 2l, n, 3b, e). The lower molars from Gratkorn differ by a larger size from *D. guntianum*, and by a smaller size (Fig. 3b, e) and a more selenodont, slender and higher crowned morphology from *D. vindebonense* and *peneckei*. The size increases from m1 to m2. The postmetacristid and postprotocristid are both split into internal and external cristids, giving the posterior aspect of the anterior lobus the typical ∑-structure. No lingual stylids are present. The ectostylid is largest in m1 and decreases in size to m3, as in *D.naui* from Atzelsdorf and Abocador de Can Mata (Hillenbrand et al. 2009; Alba et al. 2011). In *D. crassum*, although also decreasing in size from m1 to m3, usually the ectostylid is still more pronounced in m2 and m3 (see, e.g. Morales et al. 2012, fig. 23). The length of the external postmetacristid in ratio to the internal is variable in the specimens from Gratkorn, as it is in other assemblages of *D. naui* (e.g. Eppelsheim and Atzelsdorf) and *D. crassum* from Sansan and Sandelzhausen. The postentocristid in specimens from Gratkorn is short and accentuated and does not reach the posterior cingulid, as is typical for *D. naui* (Morales et al. 2012), whereas the posthypocristid is longer and turns lingually enclosing posterior fossa and postentocristid posteriorly. Although there is also some variability in this feature, generally the postentocristid is blunter and less accentuated in *D. crassum* than in *D. naui* (Morales et al. 2012) and in the specimens observed for this study. A very small additional enamel fold is present at the posterior wall of the posthypocristid in some specimens (GPIT/MA/2741, GPIT/MA/2756, UMJGP 210694, 210693; probably also in GPIT/MA/2734 and UMJGP 204109), which cannot be verified or rejected as a crest due to preservation, while it is lacking in others (UMJGP 204662, 204663, 204664, and GPIT/MA/2401). Anterior and posterior cingulid are present, but less distinct and weaker than in *D. crassum.*

In **m3**, trigonid and talonid are similar to m1 and m2. At the posterior wall of the entoconid, a small crest-like entostylid is aligned to the postentocristid. In all specimens, the posthypocristid is split into a longer internal posthypocristid fusing with the entostylid closing the posterior fossa and a very short accessory external posthypocristid fusing with preentoconulidcristid and prehypoconulidcristid closing the back fossa of m3 anteriorly almost completely. The hypoconulid is the dominant conid in the third lobe. The postentoconulidcristid is reduced, while the posthypoconulidcristid is very dominant and closes the back fossa posteriorly by fusion with the entoconulid. Some specimens possess a very small posterior ectostylid (UMJGP 204662, 204665 and 210694). In all specimens, the third lobe is clearly set off from the talonid, and turned to labial by a shift of the hypoconulid to anterolabial (Fig. 2l3, n5). This feature is characteristic for the more selenodont *D. guntianum*

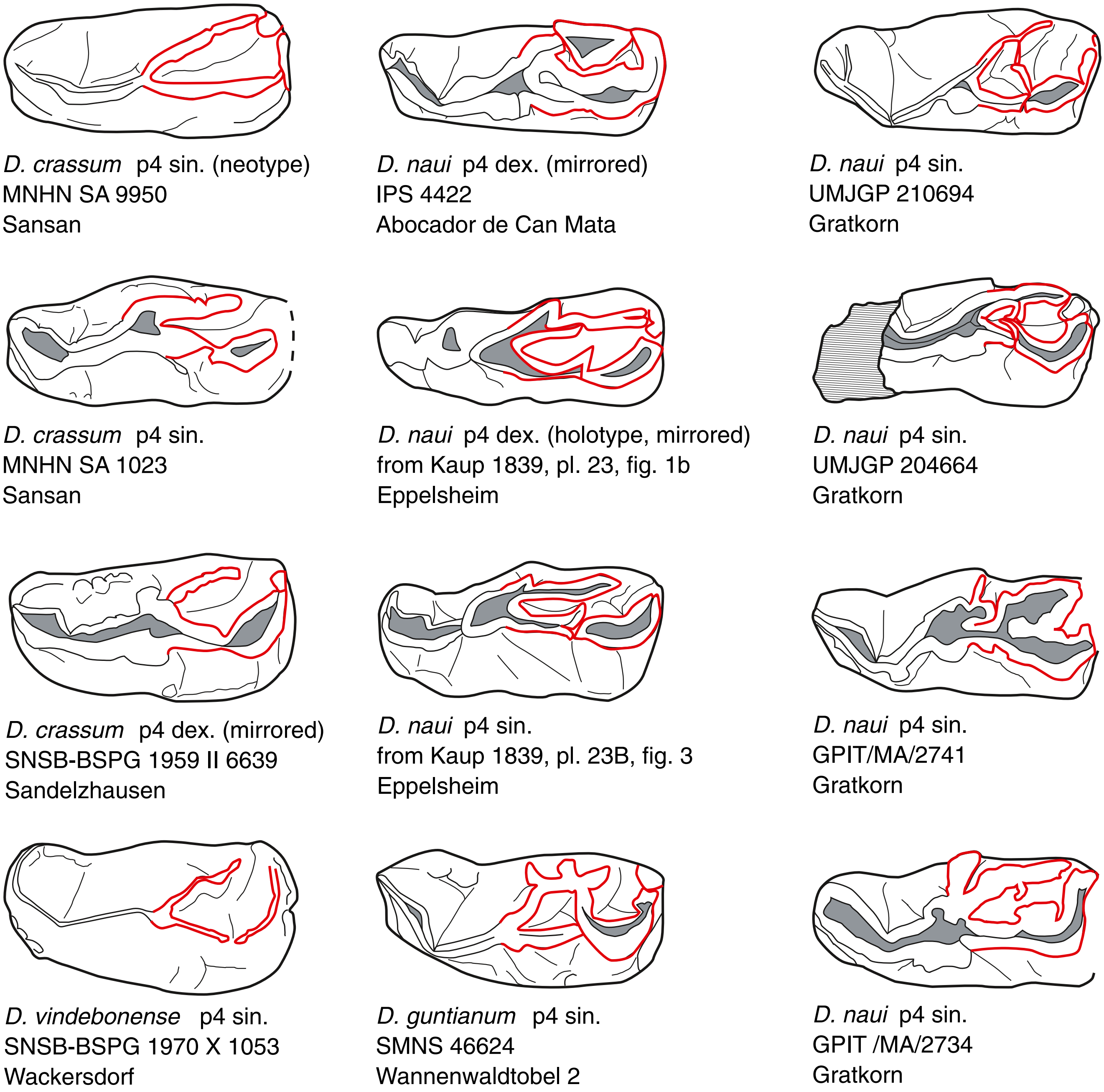


Fig. 5 Different p4 morphotypes for the genus *Dorcatherium*: More bunodont lineage (including *D. crassum* and *D. vindebonense*) with simple posterior valley, more selenodont lineage (including *D. guntianum* and *D. naui*) with more complex posterior valley, in terms of additional crests (red lines indicate crests of interest; dimensions not to scale; drawings based on original material or reference given)

and *D. naui*, while in the more bunodont species *D. crassum*, *D. vindebonense*, and *D. peneckei*, the third lobe is not turned to labial (Mottl 1961; Rössner 2010; Alba et al. 2013.

Postcrania (Fig. 2o–t)

Material: UMJGP 210792 (proximal part of radius dex.), GPIT/MA/2391 (proximal part of radius sin.), UMJGP 203419 (tibia sin. missing proximal part and cubonavicular sin.), UMJGP 203718 (distal half of tibia sin.), GPIT/MA/2759 (distal epiphysis of tibia sin.), UMJGP 210205 (cubonavicular dex. and os indet.), GPIT/MA/2745 (phalanx medialis).

As an astragalus dex. and a fragmented calcaneum dex. (GPIT/MA/2409) were found in close vicinity and articulate well, they are considered as part of the same individual.

A radius sin. (GPIT/MA/2420) articulates well with the distal fragment of a humerus sin. (GPIT/MA/2389) and, considering the finding position and general taphonomy of the locality, the affiliation to the same individual seems most reasonable.

Description and comparison

Only a few postcranial ruminant remains found at Gratkorn can be assigned to Tragulidae. Measurements correspond well to the medium-sized *Dorcatherium crassum* and *D. naui* (for measurements, see online resource 2). The distal articulation facet of a **humerus** sin. (GPIT/MA/2389; Fig. 2o) is similar in morphology to extant and extinct tragulids. The epicondylus medialis is short and knob-like, similar to *D. crassum* from Sansan (Morales et al. 2012, figs. 32–36; personal observation), to *D. naui* from Atzelsdorf (Hillenbrand et al. 2009, pl. I, fig. 11), and to modern genera, *Tragulus* and *Hyemoschus* (Gailer 2007, Abb. 4 AII, BII). In contrast, in Pecora, it is caudally more extended. The fossa olecrani is closed. In cranial view, the trochlea humeri is trapezoid in shape with a proximodistal diameter decreasing more strongly from medial to lateral than in Pecora and according to what is described for *D. naui* from Atzelsdorf by Hillenbrand et al. (2009). The distal surface of the trochlea humeri ascends from medial to lateral. The lateral crest is less distinct than in Pecora. In cranial view, the trochlea is less rounded than in Cervidae. In shape, it resembles *D. naui* (Kaup 1839, pl. 23C, fig. 2). Three fragmented **radii** (Fig. 2p) with proximal articulation surfaces are preserved. Although they are slightly varying in size (online resource 2), their morphology and dimensions are within the variability of *D. crassum* from Sansan (Morales et al. 2012), being slightly wider dorsopalmarily than *D. naui* from Abocador de Can Mata (Alba et al. 2011). A plane articulation facet on the palmar plane is present in all specimens for the articulation with the ulna. In proximal view, the proximal articulation surface is biconcave with a roughly trapezoid shape, with the lateral fossa in dorsopalmar extension less wide than the medial fossa in accordance with the shape of the trochlea humeri. The lateral part of the articulation surface reaches further proximally than in cervids and bovids. Two distal **tibia** fragments (Fig. 2r) show a transition from a proximal triangular cross-section to a more trapezoid distal one. A pronounced malleolus medialis is characteristic for Artiodactyla (Schmid 1972; not observable in UMJGP 203178 as mostly lost due to rodent gnawing). Typical for tragulids, it is not the longest distal projection, as it would be in Pecora (Hillenbrand et al. 2009). Medially, the sulcus malleolaris is clearly developed. The biconcave cochlea tibiae reflects the shape of the proximal trochlea of the astragalus. It comprises a narrow, dorsoplantarily extended and stronger plantarily tapering medial concavity and a wider, but less deep and dorsoplantarily clearly shorter, lateral concavity. Following Hillenbrand et al. (2009), this is characteristic for tragulids. The distal fibula, reduced to the malleolus lateralis, is not fused with the laterodistal surface of the tibia in the Gratkorn specimen, as is the case in *D. naui* from Eppelsheim (Kaup 1839, pl. 23 C, fig. 4) and Atzelsdorf (Hillenbrand et al. 2009), in *D. guntianum* from Günzburg (personal observation), and also in the modern genus *Hyemoschus* (Milne Edwards 1864, pl.11, fig. 1c; Gailer 2007). The tibia of *D. guntianum* differs by its smaller size from the Gratkorn specimens. In *D. crassum*, the malleolus lateralis is fused with the tibia (Milne Edwards 1864, pl.12, fig. 1b, 1c; Filhol 1891, pl. 13, fig. 4; Carlsson 1926; Hillenbrand et al. 2009; Rössner 2010). Two **cubonaviculars** are well within the size variability of the medium-sized *Dorcatherium* species (Fig. 2q). As in all ruminants (Janis and Scott 1987; Vislobokova 2001), they represent fused cuboids and naviculars. Typically for tragulids, they show a fusion with the ectocuneiform (Gentry et al. 1999; Rössner 2007). In comparison to cervids, the articulation surface to the calcaneum is steeper and lacks a central canal at the plantar plane (Gailer 2007; Sánchez et al. 2010a). Furthermore, the proximoplantomedial process is short, while it is more developed in Pecora (Sánchez et al. 2010a). In the **astragalus** dex. (Fig. 2s), the plantar trochlea covers most of the plantar plane, and is not longish triangular as in suids (Schmid 1972), as typical for ruminants (Morales et al. 2012). Like in modern Tragulidae and in *D. crassum*, the proximal trochlea, trochlea tali, encloses medially an obtuse angle with the caput tali, comparable to suids, but different to Pecora, where the two axes are parallel (Schlosser 1916; Gailer 2007; Morales et al. 2012). The lateral condyle of the caput tali is set off and mediolaterally wider than the medial condyle. The lateral border of the lateral condyle possesses a strong notch, as in *D. crassum*, distinguishing it from cervids and bovids, which possess a straight lateral border in the lateral condyle of the distal trochlea. In shape, it agrees with the astragulus of *D. naui* figured in Kaup (1839, pl. 23C, fig. 6). The fragment of a **calcaneum** dex. (GPIT/MA/2409; Fig. 2t) comprises more or less just the sustentaculum tali and a part of the processus calcanei. In comparison to cervids, the sustentaculum tali in the calcaneum is more strongly inclined plantarily (see, e.g,. fig. 25 in Gailer 2007; *Euprox* vel *Heterorpox* from Steinheim a. A., GPIT/MA/2984). A badly preserved **phalanx medialis** could be assigned to *D. naui* (GPIT/MA/2745). In dimensions it is smaller than specimens of *Euprox* vel *Heteroprox* (diverse specimens SMNS and GPIT) but within the variability of *Dorcatherium* (Sansan, Sandelzhausen and Viehhausen; see also Rinnert 1956). Due to preservation, the morphology cannot be clearly defined, but the shape of the proximal articulation surface is mediolateral wide, shallow and triangular, similar to *D. crassum* from Sansan (Morales et al. 2012; personal observation) and Sandelzhausen, while it is dorsovolarly elongated and dorsally more rounded in *Euprox* vel *Heteroprox* from Steinheim a. A. (specimens in SMNS and GPIT). Furthermore, the distal articulation is not as large and distinct as it is in *Euprox* vel *Heteroprox* from Steinheim a. A., but more similar in shape to *Dorcatherium* (specimens in SMNS and GPIT). In contrast to modern Tragulidae, where the proximal tuberosity for the attachment of the tendon is not as marked as in Cervidae (Gailer 2007), it is well pronounced in the specimen form Gratkorn, as it is in other *Dorcatherium* specimens.

Discussion

In size, *Dorcatherium* teeth from Gratkorn nest well within the dimensions (Fig. 3) given by Mottl (1961), Moyà-Solà (1979), Fahlbusch (1985), Rössner (2010), Alba et al. (2011), Morales et al. (2012), and Alba et al. (2013) for the medium-sized *Dorcatherium crassum* and *naui* (Fig. 3). They are larger than *D. guntianum* (Mottl 1961; Alba et al. 2011) and smaller than *D. vindebonense* (Mottl 1961; Fahlbusch 1985; Rössner 2010; Alba et al. 2011) and *D. peneckei* (Mottl 1961; Rössner and Heissig 2013).

In morphology, *Dorcatherium* from Gratkorn is in accordance with *D. naui* and *D. guntianum* (Hillenbrand et al. 2009; Rössner 2010; Alba et al. 2011; Rössner and Heissig 2013) because of: (1) a bicuspid p2/d2, (2) a tricuspid p3 with a less dominant mesolabial conid than in *D. crassum*, (3) a p4 with a more complex posterior valley, (4) more selenodont, more slender and higher crowned lower molars, (5) a labially turned third lobe in the lower m3, (6) upper molars with less bulky styles than in *D. crassum*, and (7) a non-fusion of tibia and malleolus lateralis (Kaup 1839; Mottl 1961; Sach 1999; Hillenbrand et al. 2009; Rössner 2010; Alba et al. 2011; Rössner and Heissig 2013). In contrast to this, *D. crassum*, *D. vindebonense*, and *D. peneckei* possess (1) a tricuspid p2/d2, (2) a more dominant mesolabial conid in the tricuspid p3, (3) a p4 with a more simple morphology of the posterior valley, (4) more bunodont, wider and less high crowned lower molars with a more prominent ectostylid, (5) a more middle position of the third lobe in the lower m3, (6) upper molars more bulky in habitus, and (7) a tibia fused with the malleolus lateralis (not all characters described in *D. vindebonense* and *D. peneckei*, as they are more rare and not all dental and skeletal elements have so far been recorded; Fahlbusch 1985; Rössner 2010; Morales et al. 2012; Alba et al. 2013).

Furthermore, the Gratkorn specimens share with *D. naui* the proportionally short and accentuated postentocristid (Morales et al. 2012). Although this character is variable in *D. crassum*, it seems to be more common in *D. naui* and is given as a diagnostic feature by Morales et al. (2012) to distinguish the two species. Following Morales et al. (2012), a remarkably shorter external than internal postmetacristid should be characteristic for *D. naui*, while in *D. crassum* the external postmetacristid should be more equal in length to the internal postmetacristid (see also figs. 81–82 in Morales et al. 2012). As in Gratkorn and in the rich *D. crassum* material from Sandelzhausen and other localities, a certain variability concerning this feature can be observed, it is not taken into consideration here. The erection of the subspecies *D. naui meini* on the basis of characters common in *D. crassum* and distinct from *D. naui* (Alba et al. 2011) cannot be followed, as the characters given (external postmetacristid shorter than internal one and shorter and less developed entocristid) are either more characteristic for *D. naui* than for *D. crassum*, and/or, as mentioned, variable to a certain degree (Morales et al. 2012; personal obsevation).

As mentioned above, all specimens with a preserved anterior part of the mandibula possess an alveola for p1, as is the case in all representatives of *D. naui* except for one specimen from Can Petit (Spain; Moyà-Solà 1979). Although the presence of a p1 cannot be used as a diagnostic feature to differentiate *D. crassum* and *D. naui*, as it is variable (see also discussion in Moyà-Solà 1979; Alba et al. 2011, 2013; Morales et al. 2012), it seems to be far more common in *D. naui* than in *D. crassum* from the type locality Sansan (Morales et al. 2012). In recently described *D. crassum* specimens from Lower Miocene sediments of Spain, the p1 is present in all specimens, which are complete enough to show this feature (Alba et al. 2013), while in *D. crassum* from Sandelzhausen, the presence of a p1 is also more common than in the type locality Sansan. As the results of Alba et al. (2013) were published during the review process of our publication, we could not fully take them into consideration. However, we think that the presence of a p1 in early representatives of *D. crassum* and the loss of it in later records should be included in our discussion. The observation by Alba et al. (2013) furthermore underlines that *D. crassum* and *D. naui* should be considered as belonging to different phylogenetic lineages, as the loss of the p1 is a derived feature in a lineage (see, e.g. discussions in Janis and Scott 1987). Thus, the withholding of p1 in *D. naui* is one of the arguments that it cannot be considered a direct descendant from *D. crassum* and supports, as mentioned, the suggestion of Moyà-Solà (1979) that the two species should be considered members of two different evolutionary lineages.

Stratigraphic range and phylogenetic relationship of *Dorcatherium naui*

As pointed out by Alba et al. (2011) and Rössner and Heissig (2013), the supposed synonomy of *D. crassum* and *D. naui* has produced confusion on the stratigraphic ranges of the different species for more than 100 years. Nevertheless, *D. naui* has also been considered a valid species distinct from *D. crassum* (Mottl 1961; Moyà-Solà 1979; Morales et al. 2003, 2012; Montoya and Morales 2004; Rössner 2007, 2010; Hillenbrand et al. 2009; Alba et al. 2011; Sánchez et al. 2011b). Its stratigraphic range has so far been considered to be restricted to the Late Miocene (Rössner 2007, 2010; Hillenbrand et al. 2009), while reliable records of *D. peneckei*, *D. vindebonense*, *D. crassum* and *D. guntianum* are only known from the Early and Middle Miocene (Fig. 1; Rössner 2007, 2010; Alba et al. 2011).

With the description of *D. naui* from Abocador de Can Mata (Spain, MN8), and the assignment of the tragulid material from Przeworno (Poland, MN7/8) to the same species, Alba et al. (2011) have already documented the first records for the occurrence of *D. naui* in the late Middle Miocene. For our work, we reevaluated the taxonomic affiliation and the stratigraphic ages for Central and Western European localities with records of *Dorcatherium* to gain a more detailed view of stratigraphic ranges of the different species (Fig. 1; note that this list is far from complete, that the focus is on localities from the NAFB and Austria, and that only localities with reliable species identification have been taken into consideration). Besides the integration of *D. naui* from Gratkorn in the stratigraphic range, we could date back the oldest record of the species at least as far as the early Sarmatian (12.7–12.3 Ma; Fig. 1).

In general, late Middle Miocene *Dorcatherium* material is quite scarce. It thus gives only limited insight into character variability of Middle Miocene *D. naui* and possible differences from the Late Miocene representatives of the species. With *D. naui* from Gratkorn, we present abundant material from the late Middle Miocene and can thus for the first time estimate variability among the early representatives of this species. The specimens from Gratkorn clearly show that there is no significant difference between the Middle Miocene representatives of *D. naui* and the abundant *D. naui* material from the Late Miocene Atzelsdorf locality (Hillenbrand et al. 2009). Furthermore, it is well in accordance with the type material from Eppelsheim (Kaup 1839). Thus, morphology of the Gratkorn *D. naui* does not indicate an intermediate position inbetween *D. crassum* and *D. naui*, and does not support the idea (e.g. Fahlbusch 1985) of *D. naui* evolving out of *D. crassum*. On the contrary, *D. naui* has to be considered part of a selenodont lineage, together with *D. guntianum*, but distinct from the bunoselenodont lineage including *D. crassum*, *D. peneckei*, and *D. vindebonense* (see also Rössner and Heissig 2013 and others) due to the characteristic features described above. As no common ancestor has so far been recorded, and as both lineages appear at about the same time (Fig. 1) and are already distinctly different in morphology in the first records, a divergence of both lineages after the immigration of a common ancestor to Europe is evaluated as unlikely, while an immigration of representatives of both lineages during the Early Miocene (Fig. 1) seems more plausible.

Palaeoecological characterisation

Dorcatherium naui had a shoulder height of about 40–50 cm. Body mass estimates for the Gratkorn specimens are about 28–29 kg (min: 26 kg, max 30.6 kg; $n=6$) and are well in accordance with body mass estimates for *D. naui* from Abocador de Can Mata by Alba et al. (2011). In weight, the species is therefore comparable to the modern roe deer, though smaller in height. Modern tragulids are exclusively small-sized ruminants, with a shoulder height of about 20–40 cm (Rössner 2007) and body masses of 7–16 kg for *Hyemoschus aquatius*, and of 1.5–2.5 kg for *Tragulus kanchil* (Meijaard 2011).

The ecology of Miocene Tragulidae, especially habitat and feeding strategy adaptations, is often discussed but still not fully understood, and presumably was more diverse than in modern members of the family (see, e.g. Kaiser and Rössner 2007; Ungar et al. 2012). In contrast to modern Tragulidae, which are restricted to disjunct areas in tropical Asia and Africa (Meijaard 2011), tragulids were a common faunal element in Europe, Asia and Africa during the Miocene (Vislobokova 2001; Rössner 2010; Rössner and Heissig 2013). Due to an overall morphological similarity of *Dorcatherium* with modern Tragulidae, a wet, forested habitat with dense underwood has always been assumed for the genus (Köhler 1993; Rössner 2010; Alba et al. 2011). The short metapodials and the morphology of the phalanges indicate low-gear locomotion (Leinders 1979; Köhler 1993; Morales et al. 2012). The rigidity in the hindlimb caused by the fusion of ectocuneiform and cubonavicular indicates an inability of a zigzag flight behaviour (Alba et al. 2011). Based on the latter, Moyà-Solà (1979) assumed a similar escaping behaviour in *Dorcatherium* as in the living African *Hyemoschus*, which is documented by Dubost (1978) as fleeing straight into the next open water when threatened. Whether the fusion of malleolus lateralis and tibia in *Tragulus* and *D. crassum* or the nonfusion in *D. naui* and *Hyemoschus* are convergent adaptions to the same habitat or environment, respectively, can only be verified by ecological investigations of the modern taxa. Morales et al. (2012) observed that *D. naui* and *crassum* differ furthermore in the articulation of MC III and IV (from Gratkorn this element is not recorded so far). While *D. crassum* may have been enabled to a greater mobility, *D. naui* would have had more stability in the joint due to an interlocking mechanism, comparable to but not as derived as in the modern *Hyemoschus aquaticus* (Alba et al. 2011; Morales et al. 2003). Whether this feature is indicative of an adaptation in *D. crassum* to soft and humid ground cannot be verified due to only a little material and lack of further investigations, but it is questioned by the similar morphology in *D. naui* and *Hyemoschus*. The latter is adapted to very humid environments (Dubost 1965).

Although Matsubayashi et al. (2003) observed daytime activity in *Tragulus javanicus*, a nocturnal or crepuscular way of life has been documented for *Hyemoschus* (Dubost 1975). The large size of the orbits in the *D. naui* skull from Eppelsheim (Kaup 1839, pl. 23A) might also be an indication for a possible nocturnal behaviour of this extinct species (Rössner 2010).

By lancing the sabre-like elongate upper canines at each other, primitive territorial fighting among males can be observed in recent Tragulidae (Dubost 1965), which most likely was not different in the Miocene species, with upper canines being proportionally even larger.

Modern Tragulidae feed on fallen fruit, seeds, flowers, leaves, shoots, petioles, stems, and mushrooms in the forest undergrowth (Dubost 1984). *Hyemoschus* is even known to casually feed on invertebrates, fishes, small mammals and carrion (Dubost 1964). Although diet reconstruction is limited for fossil taxa, different feeding strategies could be observed in fossil tragulids, ranging from browsing to grazing (for further discussion, see Aiglstorfer et al. 2014a, this issue). The only available isotopic measurements ($\delta^{13}C$ and $\delta^{18}O$) for *D. naui* published so far were done on the specimens from Gratkorn described here and point to the ingestion of a considerable amount of fruit or grass besides a browsing diet (Aiglstorfer et al. 2014a, this issue). The reconstruction of a diet with a certain amount of fruits is also supported by the incisor arcade of *D. naui* from Gratkorn. In accordance with Janis and Ehrhardt (1988) and Clauss et al. (2008), the architecture of the incisor arcade in *Dorcatherium naui* and modern Tragulidae (Fig. 4; strongly widened i1 in comparison to i2 and i3) points to a more selective feeding strategy. Although limited in its predictions (Fraser and Theodor 2011), disparity in incisor widths is significantly higher in browsers than in grazers, assumedly due to a more selective picking (Janis and Ehrhardt 1988; Clauss et al. 2008). Applying these ecomorphological considerations to the Gratkorn locality, *Euprox furcatus* (Hensel, 1859) with a typical isotopic composition of a subcanopy browser (feeding in the more closed, lower part of the vegetation; Aiglstorfer et al. 2014a, this issue) should have a higher ratio in i1 width to i2 or i3 width than *D. naui*, if the latter were more grazing. This is not the case. Assuming a more selective picking of perhaps fruits, the higher ratio of i1 width to i2 or i3 width of *Dorcatherium* in comparison to the subcanopy browsing cervid could be explained. Thus, combining tooth morphology and isotopic measurements, a significant amount of fruits is most likely to have been part of the diet of *D. naui*.

Although ecological differences between the different *Dorcatherium* species are indicated, a general adaptation to a forested environment or at least one with enough undergrowth, can be assumed for the fossil genus. In general, it is associated with dominantly browsing taxa in the fossil record (Kaiser and Rössner 2007; Hillenbrand et al. 2009; Rössner 2010; Alba et al. 2011; Gross et al. 2011). A dependency of *D. naui* on a forested environment and at least not fully arid conditions is suggested by the restricted occurrence during the late Middle Miocene in Spain. So far, it has only been described from Abocador de Can Mata (Vallès-Penedès Basin, Catalonia, Spain; co-occurring with beavers and arboreal primates there; Alba et al. 2011), which was less arid and more forested than the localities from the inner Iberian basins (less than 400 mm MAP for the Calatayud-Daroca and the Teruel basin between 12.5 and 11.5 Ma; Böhme et al. 2011). However, the abundance of *D. naui* at Gratkorn (MAP of 486±252 mm according to Gross et al. 2011) indicates a tolerance to less humid environments in comparison to *D. crassum*. The presence of the “genus” as an indicator for humid environments has thus to be considered with care. Isotopic measurements ($^{87}Sr/^{86}Sr$) indicate that *D. naui* was a permanent resident of the locality, and thus could cope with seasonal variations in its diet (for further discussion, see Aiglstorfer et al. 2014a, this issue).

Infraorder Pecora Linnaeus, 1758
Family Moschidae Gray, 1821
Genus *Micromeryx* Lartet, 1851
Type species: *Micromeryx flourensianus* Lartet, 1851

Micromeryx flourensianus Lartet, 1851

Holotype: hitherto not determined (Ginsburg proposed (letter from 1974): MNHN Sa 2957); type material from Sansan (France, MN6) under revision; partly figured in Filhol (1891, pls. 24, 25); stored at MNHN.

For the genus *Micromeryx*, five European species are considered valid at the moment: *Micromeryx flourensianus* Lartet, 1851, *Micromeryx styriacus* Thenius, 1950, *Micromeryx azanzae* Sánchez and Morales, 2008, *Micromeryx soriae* Sánchez, Domingo and Morales, 2009, and *Micromeryx mirus* Vislobokova, 2007.

Material: UMJGP 204058 (C sin.), UMJGP 204678 (sin. maxilla fragment with D2–M3), GPIT/MA/02387 (sin. maxilla fragment with D4–M1), UMJGP 204688 (dex. maxilla fragment with P3–M1, fragment of M2; P2 dex.), GPIT/MA/02388 (sin. maxilla fragment with P2–M3), UMJGP 204718 (M1? sin.), UMJGP 210972 (P4 sin.), UMJGP 210971 (mandibula sin. with d4–m1), UMJGP 204685 (mandibula sin. with m1–3), GPIT/MA/2751 (fragmented mandibula sin. with d3, d4–m3), UMJGP 204068 (mandibula dex. with p2–m3), UMJGP 204710 (mandibula dex. with p3–4; alveola for p2), UMJGP 204709 (mandibula dex. with p4–m3), UMJGP 204715 (m3 sin.; indet. tooth fragment).

Description (for detailed information and measurements, see online resource 3)

Upper toothrow: (Fig. 6a–d): On the sabre-like **C** sin. (UMJGP 204058; Fig. 6a), enamel covers the labial part of the anterior side and the labial side. The tooth is curved to posteriad and is linguolabially flattened with a triangular to drop-shaped cross-section (posterior edge sharp) and decreases gradually in anteroposterior width from base to tip like in Cervidae but distinct from Tragulidae (Rössner 2010). A slight undulation due to growth striation can be observed on the enamel. The tooth possesses no wear pattern lingually as can be observed in Tragulidae (Rössner 2010). Only one **D2** has so far been excavated (UMJGP 204678; Fig. 6b). Due to

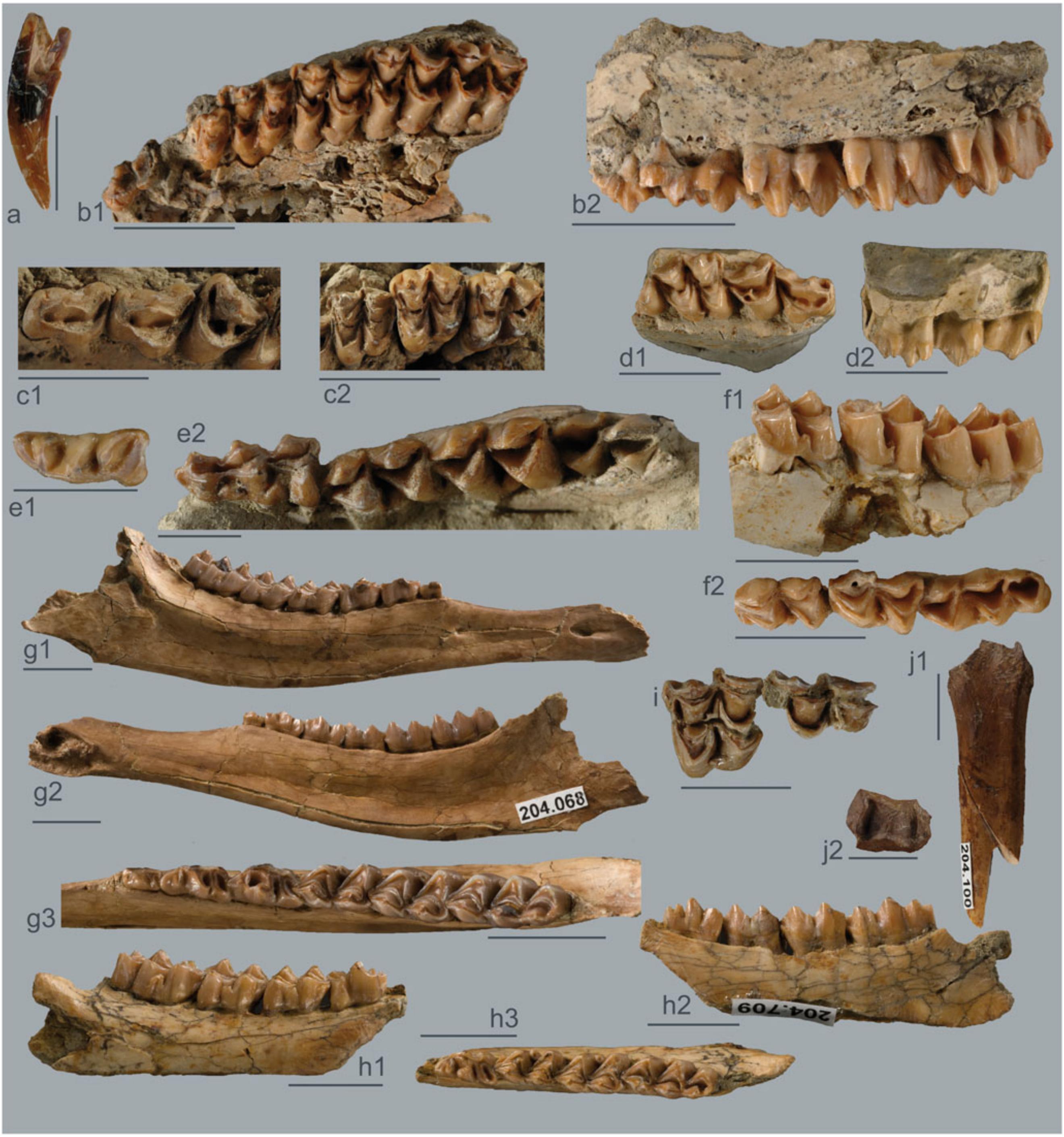


Fig. 6 Dental and postcranial material of Moschidae: **a** *Micromeryx flourensianus* C sin. (UMJGP 204058), **b** *M. flourensianus* maxilla sin. with D2–M3 (UMJGP 204678; *1* occlusal view, *2* labial view), **c** *M. flourensianus* maxilla sin. with P2–M3 (GPIT/MA/2388; *1* P2–P4, *2* M1–M3), **d** *M. flourensianus* maxilla dex. with P3–M1 (UMJGP 204688; *1* occlusal view, *2* labial view), **e** *M. flourensianus* mandibula sin. with d3–m3 (GPIT/MA/2751; *1* d3 sin., *2* d4–m3 sin.), **f** *M. flourensianus* mandibula sin. with m1–3 sin. (UMJGP 204685; *1* labial view, *2* occlusal view), **g** *M. flourensianus* mandibula dex. with p2–m3 (UMJGP 204068; *1* labial view, *2* lingual view, *3* occlusal view), **h** *M. flourensianus* mandibula dex. with p4–m3 (UMJGP 204709; *1* labial view, *2* lingual view, *3* occlusal view), **i** ?*Hispanomeryx* sp. M1–2? sin. (UMJGP 204666), **j** Moschidae gen et. sp. indet. distal tibia sin. (UMJGP 204100; *1* dorsal view, *2* distal view); *scale bar* 10 mm (except **e**, 5 mm)

strong wear, only the elongated triangular shape can be described. The only **D3** (UMJGP 204678; Fig. 6b) is badly damaged. The **D4** (Fig. 6b) is trapezoid in shape with the typically enlarged parastyle, more pronounced than can be observed in the cervid from the same locality. The mesostyle is developed while the metastyle is reduced and wing-like. Internal postprotocrista and metaconule fold are present, as are the entostyle and the basal cingulum. The latter is more clearly developed at the protocone. The **P2** (Fig. 6c) is elongate triangular in shape and lingually more rounded. The lingual cone is located more posteriorly than the labial cone. Anterior and posterior styles are present, and the first encloses a narrow incision with a well-pronounced rib at the labial cone, while the posterolabial depression is wider. At the lingual wall, a depression is clearly developed anterior to the lingual cone. The tooth possesses no clearly developed cingulum. The **P3** (Fig. 6c) is similar in shape to the P2 but linguolabially wider due to a more pronounced lingual cone. A small central fold is present. In comparison to the anterior premolars, the **P4** (Fig. 6c) is anteroposteriorly shortened and linguolabially widened. The lingual side is rounded. The labial wall is concave with a moderately pronounced rib at the labial cone and a strong anterior style. The posterior style is reduced and more wing-like. The anterolingual crista is only slightly shorter than the posterolingual one. There is no cingulum, but a clearly developed central fold, in some cases even split. The **upper molars** (Fig. 6b–d) are trapezoid to subquadratic in shape with four main cusps. Size increases from M1 to M3. Para- and mesostyle are distinct, while the metastyle is reduced and wing-like in shape. The latter increases in size from M1 to M3. The rib at the paracone is well pronounced, enclosing a distinct but narrow incision with the parastyle. The entostyle is clearly developed, increasing in size from M1 to M3. All upper molars show an internal postprotocrista. The premetaconulecrista is developed more or less pronounced and sometimes split anteriorly with one or two small anterior branches fusing with the internal postprotocrista. The premetaconulecrista itself is long and intruding wide labially inbetween paracone and metacone. The metaconule fold is present but varying in size. Anterior and posterior basal lingual cingula are present, usually more strongly anteriorly. The M3 differs from the anterior molars by stronger linguolabially width decrease posteriorly and the more developed metastyle. The **mandibula** (for detailed information and measurements, see online resource 3; Fig. 6e–h) possesses a slender corpus mandibulae, a longer premolar row than observed in *Hispanomeryx* (online resource 3) and no indication for the presence of a p1. Two foramina mentalia are developed, a smaller caudal one and a larger rostral one. The caudal rim of the symphysis is more distant from the toothrow than in Tragulidae due to an elongated rostrum in comparison to the latter. The **d3** (GPIT/MA/2751; Fig. 6 e1) is elongated with well-pronounced anterior conid and stylid. The mesolabial conid is dominant. The posterolingual conid closes the back valley lingually by fusion with the posterior stylid. The transverse cristid is directed slightly posterolingually not reaching the posterolingual conid. There is no mesolingual conid. The posterior and back valleys are oriented obliquely to the length axis of tooth. The first is wider than the latter and open lingually. A slight depression anterior to the posterolabial conid on the labial wall is present but no cingulid. The **d4** (Fig. 6 e2) is elongated with three lingual and three labial conids. The lingual conids are higher than the labial ones. Anterior stylid and metastylid are slightly stronger than mesostylid and entostylid. Internal and external postprotocristid are well developed forming a v-structure, usually termed *Palaeomeryx*-fold. Preprotocristid and premetacristid are fused with posterior cristids of anterolingual and anterolabial conids, respectively. The internal postprotocristid and metaconid are connected with the preentocristid, while the prehypocristid does not reach the preentocristid. The posthypocristid tapers wide lingually and is fused with the entostylid. Anterior ectostylid and ectostylid are well pronounced, the latter very large. An anterior cingulid is clearly present. The only preserved **p2** (UMJGP 204068; Fig. 6g) is elongated rectangular, with a small anterior conid and no anterior stylid. The mesolabial conid is dominant, the transverse cristid shifted posteriorly and enlarged posteriorly forming the mesolingual conid. The posterior valley is oriented obliquely to the length axis of the tooth and posteriorly open. The back valley is enclosed by posterolabial and -lingual conid and posterior cristid and stylid. It is oriented more perpendicularly to the length axis of tooth, but also open lingually. The incision on the labial wall anterior of the posterolabial conid is small. The **p3** (Fig. 6g) is more elongated rectangular than the p2, with more pronounced anterior conid and stylid (fused lingually in UMJGP 204710). The mesolabial conid is dominant, the transverse cristid is shifted posteriorly to different degrees, while the mesolingual conid is not strongly developed. The posterior valley is oriented obliquely to the length axis of the tooth, while the back valley is oriented more rectangularly and nearly (UMJGP 204068) or fully closed (UMJGP 204710) due to the posterior elongation of the posterior cristid. The incision on the labial wall anterior of the posterolabial conid is very weak. There is no clearly developed cingulid. In the triangular **p4** (Fig. 6g, h), the anterior stylid and conid are clearly separated. By fusion with the well-pronounced mesolingual conid, the latter closes or nearly closes the anterior valley. In contrast to the anterior premolars, the mesolingual conid is the dominant conid and slightly higher than the mesolabial conid. The transverse cristid is slightly shifted posteriorly and fused with the posterolingual cristid. The posterior valley is therefore very narrow, oriented obliquely to the length axis of the tooth and nearly closed. The back valley is also oriented obliquely and closed or nearly closed by elongation of the posterior cristid. The incision between mesolabial and posterolabial conid and the rib at posterolabial conid are stronger than in the preceding premolars. The tooth possesses a weak anterior cingulid.

The **lower molars** are brachyoselenodont (Fig. 6e–h). The main axis of the lingual conids is slightly oblique to the length axis of tooth but not as strong as in Cervidae. The metastylid is well pronounced, while meso- and entostylid are not really distinct. The postprotocristid is split into internal and external cristid forming a moderately developed v-structure (*Palaeomeryx*-fold; less visible with higher degree of wear).

The preprotocristid is long, reaching the lingual side anteriorly and fused with the shorter premetacristid. The preentocristid is short and connected with the longer postprotocristid. The prehypocristid is not fused with preentocristid and postprotocristid. The ectostylid is strong and a strong anterior cingulid is present. From m1 to m2, the size increases, the ectostylid becomes more slender, and the external postprotocristid as well as the anterior cingulid decrease in strength. In the **m3** ectostylid, external postprotocristid and anterior cingulid are further decreased in size. The third lobe is two-coned with a clearly developed entoconulid as the dominant cone. The posthypocristid is connected with the long prehypoconulidcristid closing the back fossa of m3 anteriorly. By the fusion of posthypoconulidcristid with a shorter entoconulidcristid, the back fossa is closed posteriorly and lingually by a quite high entoconulid. The posterior ectostylid is very small to not present.

Comparison and discussion

The small moschid from Gratkorn shows characteristic dental features for the genus *Micromeryx*: (1) the closed or nearly closed anterior valley in the triangular p4, (2) lower molars with only anterior cingulid, (3) bicuspid third lobe with a high entoconulid in the m3, and (4) non-shortened lower premolar row (Gentry et al. 1999; Rössner 2006, 2010; Vislobokova 2007; Sánchez and Morales 2008). It thus differs from the similarly sized cervid *Lagomeryx* (stratigraphic occurrence: late Early Miocene to middle Middle Miocene; Rössner 2010) which has lower crowned teeth, a lower lingual wall/cuspid in the third lobe of the m3 and an open anterior valley in the p4 (Rössner 2010). From the other European Miocene moschid genus, *Hispanomeryx* Morales, Moyà-Solà and Soria, 1981, the specimens from Gratkorn differ by a longer lower premolar row in comparison to the molar row, by the presence of the external postprotocristid, and by a generally smaller size (small overlap in some tooth positions and some specimens; Fig. 7; online resource 3; Sánchez et al. 2010a).

Dimensions of the dentition are well within the range of the type species *M. flourensianus* and show the greatest overlap with *M. flourensianus* from the Middle Miocene of La Grive and Steinheim a. A. and the Late Miocene of Atzelsdorf (Fig. 7). They are in the upper size range of *M. flourensianus* from the type locality, Sansan. In morphology, *Micromeryx* from Gratkorn is similar to *M. flourensianus* from Steinheim a. A. and La Grive and shows the greatest resemblance with *M. flourensianus* from Atzelsdorf (Hillenbrand et al. 2009), e.g. in terms of tooth crown height and reduction of the external postprotocristid with some specimens still showing a more developed cristid and others a more reduced one. It thus differs from the specimens of the type locality, which generally display a more pronounced external postprotocristid and a slightly lower tooth crown height (Fig. 8).

The validity of *M. styriacus* is still unclear (Sánchez and Morales 2008; Aiglstorfer and Costeur 2013). However, the Gratkorn specimens differ from the only tooth row and holotype of *M. styriacus* by a generally smaller size, a not fully closed posterior valley in the p4, and a less strongly developed external postprotocristid in the lower molars. *Micromeryx* from Gratkorn differs from *M. azanzae* by a general smaller size, a more compressed p4, and the presence of an external postprotocristid in the lower molars (Sánchez and Morales 2008). *M. soriae* is similar in size to the Gratkorn *Micromeryx* but possesses a broader external postprotocristid, so far unique in the genus (Sánchez et al. 2009). With *M. mirus* and *Micromeryx* sp. from Dorn-Dürkheim 1, the Gratkorn specimens share the labial incision anterior of the posterolabial conid in the p4 (in one specimen, UMJGP 204709, even as strong as in *M. mirus* (Vislobokova 2007; Aiglstorfer and Costeur 2013). With a generally smaller size (especially in the molars; not in p4 of *Micromeryx* sp. from Dorn-Dürkheim 1), *M. mirus* from Kohfidisch and *Micromeryx* sp. from Dorn-Dürkheim 1 differ from the Gratkorn specimens, and also by a generally further increased tooth crown height in the lower molars and a strongly reduced to non-existent external postprotocristid (Vislobokova 2007; Aiglstorfer and Costeur 2013). For the species *M. flourensianus*, the observed gradual change in morphology, in terms of the increase in tooth crown height and reduction for the external postprotocristid, could thus be well extended to the stratigraphically much younger *M. mirus* (Vislobokova 2007; Aiglstorfer and Costeur 2013). This trend has also been observed in other ruminant lineages (Janis and Scott 1987). However, in the Iberian Peninsula, it cannot be observed taking into consideration the morphology of the mainly Middle Miocene *M. azanzae* (no external postprotocristid) and the Late Miocene *M. soriae* (strong external postprotocristid; Sánchez et al. 2009).

In summary, the specimens from Gratkorn are well within the morphological and dimensional variability of the species *Micromeryx flourensianus*. They differ from specimens from the type locality, Sansan (early Middle Miocene), by an increase in the tooth crown height and a reduction of the external postprotocristid, and are more similar to the specimens from Steinheim a. A. and La Grive (Middle Miocene) and show the greatest overlap with the early Late Miocene representatives from Atzelsdorf (Hillenbrand et al. 2009). The specimens from Gratkorn are therefore attributed to the species *Micromeryx flourensianus*.

Stratigraphic range

The type species *Micromeryx flourensianus* is recorded from the early Middle Miocene to the Late Miocene (MN 5–9 (11?); Gentry et al. 1999; Bernor et al. 2004; Sánchez and

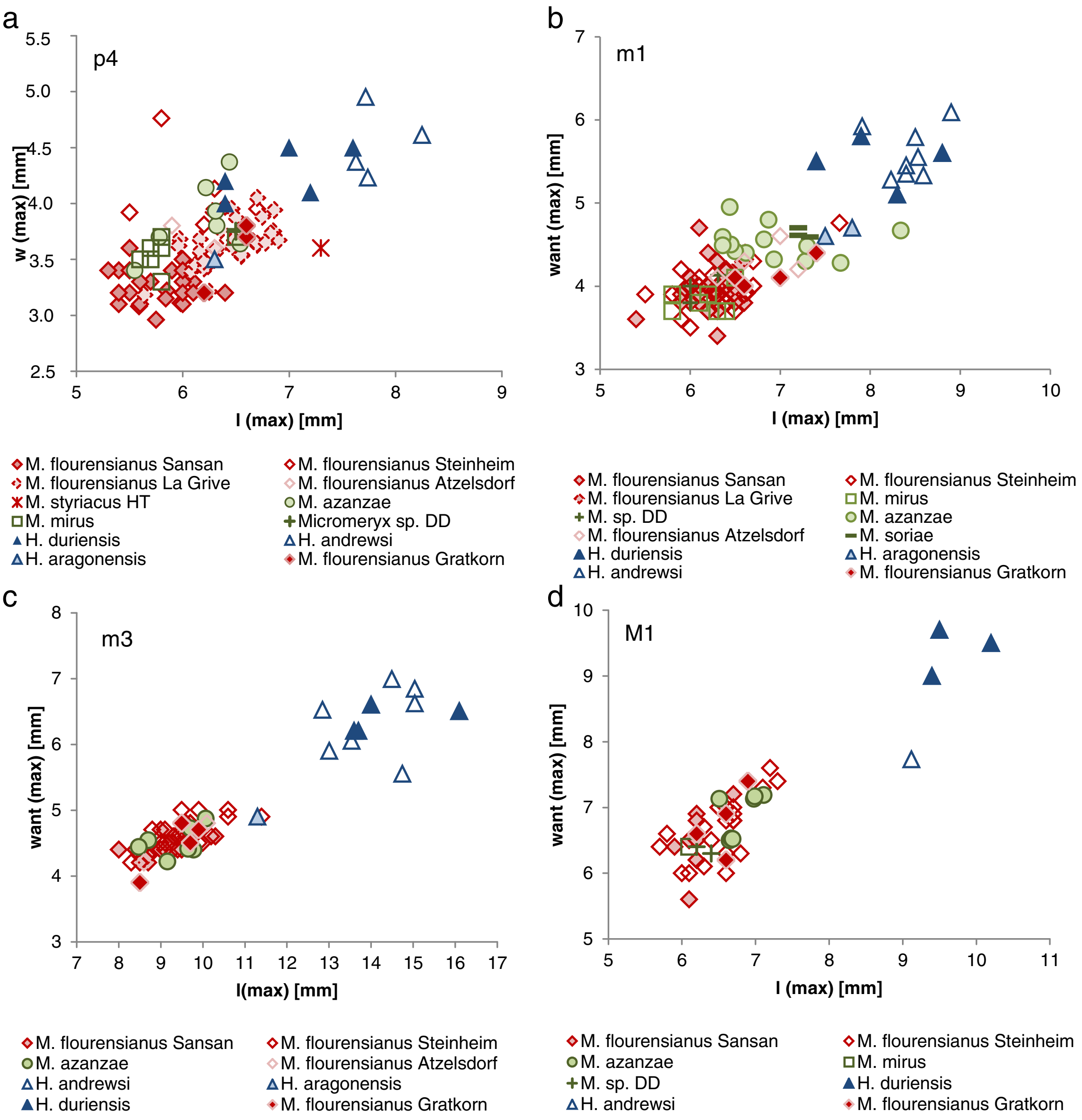


Fig. 7 Bivariate plots for p4 (**a**), m1 (**b**), m3 (**c**), and M1(**d**) of *Micromeryx flourensianus* from Gratkorn in comparison to other Miocene Moschidae (data for *M. styriacus* from Göriach, *M. flourensianus* from Gratkorn, Sansan, Steinheim a. A., La Grive, *M. mirus* and *M.* sp. from DD (Dorn-Dürkheim 1) personal observation and from Aiglstorfer and Costeur 2013; *M. flourensianus* from Atzelsdorf from Hillenbrand et al. 2009; *M. azanzae* from Sánchez and Morales 2008; *M. soriae* from Sánchez et al. 2009; *Hispanomeryx duriensis* from Morales et al. 1981; *H. andrewsi* from Sánchez et al. 2011a; *H. aragonensis* from Azanza 1986)

Morales 2008; Seehuber 2008). *Micromeryx styriacus* is so far only known from the locality Göriach (Austria; early Middle Miocene; MN 5/6; ~14.5 ± 0.3 Ma). *Micromeryx azanzae* (Middle Miocene to the early Late Miocene; MN6–9; Sánchez and Morales 2008) and *Micromeryx soriae* (Late Miocene; MN10; Sánchez et al. 2009) are recorded from Spain. Together with *Micromeryx* sp. from Dorn-Dürkheim 1 (DD; Germany; Late Miocene; Aiglstorfer and Costeur 2013), *Micromeryx mirus* from Kohfidisch (Austria; Late Miocene; MN11) represents the last occurrence of the genus in Europe.

The type species *M. flourensianus* shows a long species duration (at least 5 Ma) and gradual changes in morphology can be observed from the early representatives (e.g. Sansan; ~14.5–14.0 Ma) to later representatives [e.g. Gratkorn (12.2–12.0 Ma) and Atzelsdorf (11.1 Ma)], such as, e.g. an increase in tooth crown height (Fig. 8) and the reduction of the external postprotocristid. Well in accordance with a gradual morphological change, the locality Steinheim a. A. (~13.8–13.7 Ma; Böhme et al. 2012), stratigraphically intermediate between the first and the last records, also shows an intermediate position in morphology for *M. flourensianus*. As the type material from Sansan, as well as the rich material from Steinheim a. A., has

Fig. 8 Increase in general crown height and the height of the lingual wall at third lobe in m3 of *Micromeryx* of different ages: **a** m3 dex. of *M. flourensianus* from Sansan (MNHNS Sa 2962; mirrored), **b** m3 dex. of *M. flourensianus* from Steinheim a. A. (SMNS 46077; mirrored), **c** m3 sin. of *M. flourensianus* from Gratkorn (UMJGP 204685), **d** m3 sin of *M. mirus* from Kohfidisch (NHMW 2005z0021/0007)

never been described in detail, a challenging of the assignation of younger *Micromeryx* findings from Central Europe to the species *M. flourensianus* cannot be accomplished at the moment. However, it may be that a comprehensive description and comparison of records so far assigned to *Micromeryx flourensianus* might result in a revised specific diagnosis of the younger material. Furthermore, a mixing with the small-sized cervid *Lagomeryx* Roger, 1904 cannot yet be excluded for the undescribed material of *M. flourensianus* from the type locality Sansan. A possible mixing is indicated for example by an open anterior valley in the p4, and a lower tooth crown height in the m3 of one specimen of *M. flourensianus* from Sansan (MNHN Sa 2965), comparable with the morphology of *Lagomeryx pumilio* (Roger, 1896) (Rössner 2006, 2010). This might also bias the present-day species diagnosis of *M. flourensianus.*

Genus *Hispanomeryx* Morales, Moyà-Solà and Soria, 1981

Type species: *Hispanomeryx duriensis* Morales, Moyà-Solà and Soria, 1981.
Further species: *Hispanomeryx aragonensis* Azanza, 1986; *Hispanomeryx daamsi* Sánchez, Domingo and Morales, 2010; *Hispanomeryx andrewsi* Sánchez, DeMiguel, Quiralte and Morales, 2011

? *Hispanomeryx* sp.

Material: UMJGP 204666 (M1–2? sin.; Fig. 6i)

Description and comparison

Two fragmented upper molars from presumably one tooth row (UMJGP 204666) are intermediate in size between the medium-sized Pecora, *Euprox* and *Tethytragus*, and the small-sized *Micromeryx*, but fall well within the variability of the genus *Hispanomeryx* (Fig. 9). One tooth is more complete, lacking only the posterior wall, while only the labial wall is preserved of the second and larger molar. The first tooth is cautiously assigned an M1?, the larger an M2?, due to a weak metastyle in both (the M3 has a more pronounced metastyle in the other Moschidae from Gratkorn) and the moderately developed entostyle (which also increases from M1 to M3 in the other Moschidae from Gratkorn; as morphology is variable to a certain degree (see e.g. Sánchez et al. 2010a), the assignation is given with reservations only). In any case, a determination as M3 can be excluded for the more complete tooth due to the only slightly reduced labiolingual width of the posterior part of the tooth. Besides the moderately developed entostyle and the reduced metastyle, the more complete molar shows clearly developed internal and external postprotocrista, an anterior cingulum, and, as far as can be reconstructed, also a posterior one. With the lack of a strong lingual cingulum and the presence of well-developed internal and external postprotocrista, an affiliation to *Dorcatherium* can be excluded. The specimen also differs from Cervidae by the weak basal cingulum and by the weakly developed rib at the metacone. The latter is shared with Moschidae

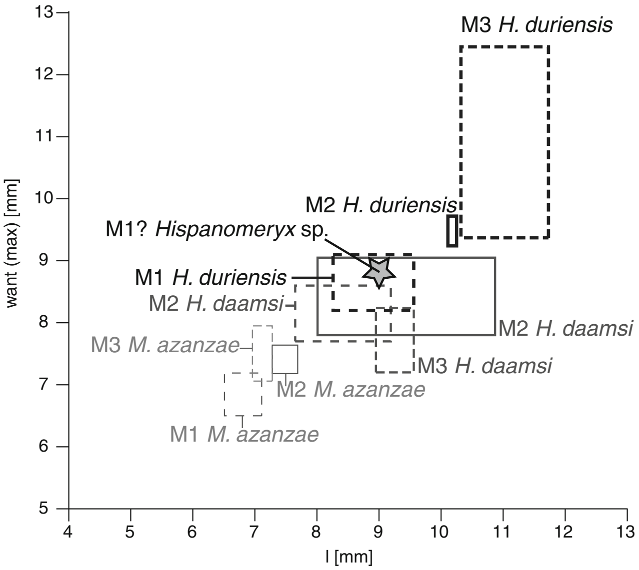


Fig. 9 Bivariate plot of M1? of *Hispanomeryx* sp. from Gratkorn (UMJGP 204666) in comparison to larger-sized Miocene Moschidae (data for *M. azanzae* from Sánchez and Morales 2008, for *H. daamsi* from Sánchez et al. 2010a, for *H. duriensis* from Morales et al. 1981)

and Bovidae, though. Due to strong wear, the degree of hypsodonty cannot be estimated.

As the teeth differ in size and morphology from the other ruminants recorded from the Gratkorn locality, but are well within dimensional and morphological range of the genus *Hispanomeryx*, they are tentatively assigned to this genus. As we are well aware that, due to limited material, the stage of wear and the preservation, a determination can only be given with reservations, we leave the specimens in open nomenclature as ? *Hispanomeryx* sp. The occurrence of *Hispanomeryx* in Gratkorn is the first record of the genus in Central Europe besides Steinheim a. A. (indicated in Heizmann and Reiff 2002, but not yet described) and indicates a wider geographic range than assumed so far.

Stratigraphic range

The genus *Hispanomeryx* first occurred in Europe in the middle Middle Miocene with *H. aragonensis* (MN6–7/8; Sánchez et al. 2010a) and *H. daamsi* (MN6–7/8; Sánchez et al. 2010a), while *H. duriensis* is only recorded from the Late Miocene (MN9–10; Sánchez et al. 2010a). To date, the last representative has been reported from the Late Miocene (one tooth of *Hispanomeryx* sp. from Puente Minero; 7.8 Ma; MN11; Sánchez et al. 2009). *Hispanomeryx andrewsi* has not been recorded from Europe so far (Sánchez et al. 2011a).

Moschidae gen. et sp. indet.

Material: UMJGP 204100 (tibia sin.; Fig. 6j)

Description and comparison

A fragmentary **tibia** sin. shows intense small mammal gnawing at the distal articulation. Its cross-section is trapezoid. There is no fusion of the malleolus lateralis and the tibia. A pronounced malleolus medialis can still be recognised, though its length in ratio to the central projection cannot be observed due to the small mammal gnawing. The sulcus malleolaris is clearly developed. The biconcave cochlea tibiae comprises a narrow, dorsoplantarily extended medial concavity and a wider, but a less deep and dorsoplantarily clearly shorter, lateral concavity. In contrast to Tragulidae, the first does not taper more widely plantarily than the latter. In size (preserved DAPd=10.7 mm and DTd=13.9 mm) the specimen is smaller than *D. naui* and *E. furcatus*, but larger than *M. flourensianus*. It overlaps in size with the larger moschids *M. azanzae* (Sánchez and Morales 2008) and *Hispanomeryx daamsi* (Sánchez et al. 2010a). Sánchez and Morales (2008) describe an anterodistal process of the tibia with a clear step in its lateral border in *Micromeryx*, distinguishing it from *Hispanomeryx*. Due to small mammal gnawing, the existence of such a step can neither be verified nor rejected for the Gratkorn material. Furthermore, a sexual size dimorphism for *Micromeryx* has been observed by Sánchez and Morales (2008) in *M. azanzae*, being more pronounced in dental material but also significant in the DAPd of the tibia. A certain size variation in the dental material of *M. flourensianus* from Gratkorn can be observed (Fig. 7). However, the small amount of material does not allow a reasonable differentiation into larger and smaller forms, or, following Sánchez and Morales (2008), into females and males. As both genera, *Micromeryx* and *Hispanomeryx*, seem to be present in the fauna from Gratkorn and a sexual dimorphism cannot be excluded, the tibia is left in open nomenclature as Moschidae gen. et sp. indet.

Palaeoecological characterisation for Moschidae from Gratkorn

With an estimated body mass of about 4 to 5 kg (min.: 3.8 kg, max. 5.0 kg; *n*=6), ***M. flourensianus*** is by far smaller than all other ruminant taxa from Gratkorn (excluding *Hispanomeryx*) and indicates an adaptation to a more or less closed environment with sufficient understory, as can be observed for all modern ruminants of this size class (Köhler 1993; Rössner 2010). Köhler (1993) reconstructs a diet of soft plants and fruits, but also some degree of omnivory in terms of, e.g. larvae and carrion for the genus, and a solitary or living in small groups lifestyle. Isotopic data ($\delta^{13}C$ and $\delta^{18}O$; Tütken et al. 2006; Aiglstorfer et al. 2014a, this issue) and microwear analyses (Merceron et al. 2007; Merceron 2009) reconstruct a browsing diet with considerable intake of fruits or seeds and occasional grazing for the small moschid *Micromeryx flourensianus*. ***Hispanomeryx*** is also described by Köhler (1993) as an animal adapted to wood or bush with understory. Sánchez et al. (2010a) highlight the sympatric occurrence of either two species of *Micromeryx* or of *Micromeryx* and *Hispanomeryx* as common in the Miocene of Spain, and tentatively assign differences in body size and dentition as a result of the sympatry, meaning their occupation of different ecological niches. At the moment, due to the scarce remains of ?*Hispanomeryx*, a distinctive ecological niche recorded in different isotopic signals of the tooth enamel cannot be verified for Gratkorn.

Family Cervidae Goldfuss, 1820

Genus *Euprox* Stehlin, 1928

Type species: *Euprox furcatus* (Hensel, 1859)
Further species: *Euprox dicranocerus* (Kaup, 1839), *Euprox minimus* (Toula, 1884)

Euprox furcatus (Hensel, 1859)

Holotype: fragmented antler sin. (MB.Ma.42626) from Kieferstädel (today: Sośnicowice; Poland).

Dentition, maxillae and mandibulae

Material: GPIT/MA/2739 (fragments of maxillae with P2–M3 dex. and P3–M3 sin.; mandibula sin. with p2–m3), GPIT/MA/2737 (fragment of maxilla sin. with D2–M1; labial wall M2 (not erupted)), GPIT/MA/2738 (fragment of maxilla dex. with D3–M1), UMJGP 204695 (fragment of maxilla sin. with P2–M3), GPIT/MA/2386 (M1–3 sin.), UMJGP 204063 (M2–3 sin.; P3 sin.; labial wall of P2 sin.?), UMJGP 204716 (D2 sin.), GPIT/MA/2749 (fragment of P3 or P4 sin?), UMJGP 204066 (Mx sin.), UMJGP 204065 (M3? sin.), GPIT/MA/2374 (M1 or 2? dex.), UMJGP 210690 (M1 or 2? sin.), UMJGP 204717 (Mx dex.), UMJGP 203445 (M3? sin.), GPIT/MA/2415 (Mx dex. fragment), GPIT/MA/2394 (Mx dex fragment), UMJGP 203686 (mandibula dex. with d2–m1 and mandibula sin. with d2, d3–m2), UMJGP 203737 (sin. and dex. mandibula with p2–m3; i2 or 3? dex, UMJGP 210691 (mandibula sin. and dex. with p2–m3, i1 sin. and two fragmented ix), GPIT/MA/2390 (mandibula dex. with p2–m3), GPIT/MA/2393 (dex. mandibula fragment with m1–m3), UMJGP 204686 (mandibula dex. with p3–m3), GPIT/MA/2399 (mandibula sin. with p4–m3), UMJGP 204711 (mandibula sin. with m2–3; fragments of m1; p4), UMJGP 204674 (p2 dex., p3 sin.), UMJGP 210957 (i1dex.), GPIT/MA/2384 (i1 dex.), UMJGP 204669 (d4 sin.), UMJGP 204713 (m3 dex.); GPIT/MA/2755 (m3 dex.).

From the finding position, preservation, and degree of dental wear, GPIT/MA/2403 (D3 sin.), GPIT/MA/2378 (D4 sin.), GPIT/MA/2404 (M1? sin. fragment), GPIT/MA/2406 (M2? sin. fragment), GPIT/MA/2382 (D4 dex.), GPIT/MA/2402 (M1–2 dex.), GPIT/MA/2408 (M3? fragment, not erupted), GPIT/MA/2405 (Px? fragment, not erupted), GPIT/MA/2407 (fractured and fragmented longbone) and maybe GPIT/MA/2411 (fragment of phalanx proximalis), and GPIT/MA/2412

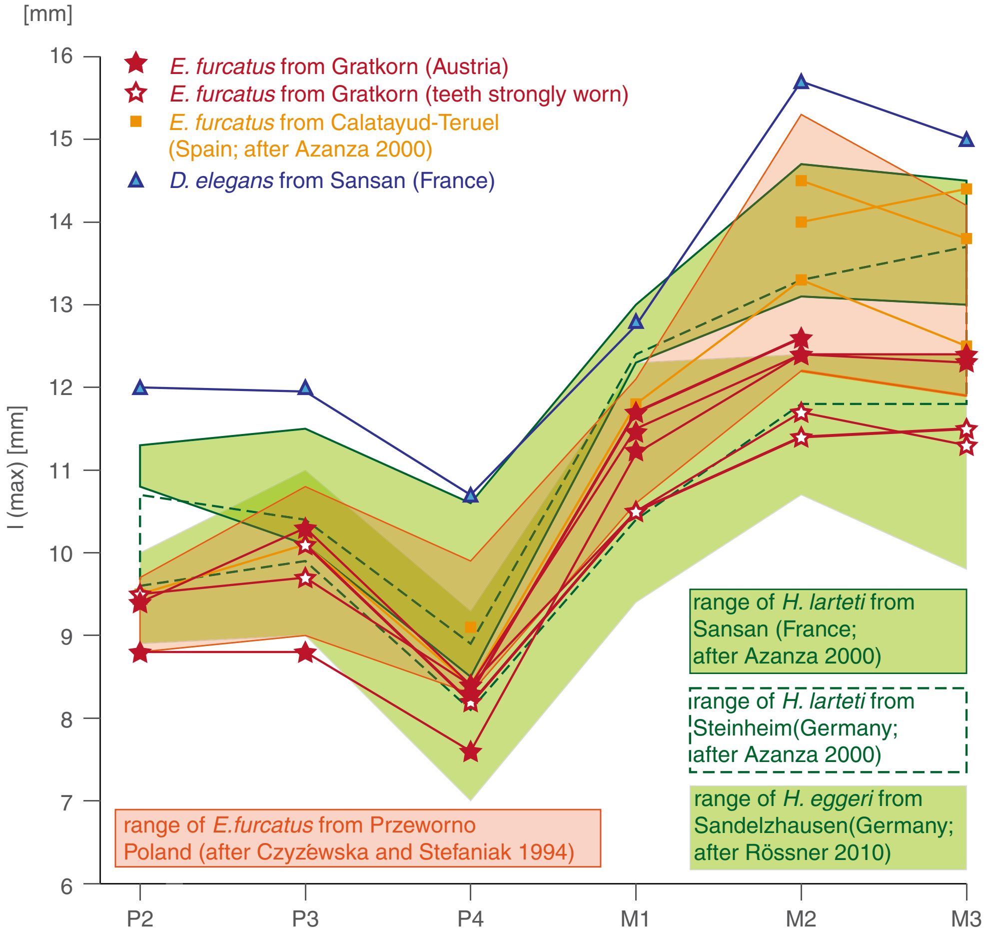


Fig. 10 Upper tooth rows (P2–M3) of *Euprox furcatus* from Gratkorn in comparison to other Miocene Cervidae (note: *E. furcatus* from Gratkorn with strongly worn teeth shows lower values): *E. furcatus* from Calatyud-Teruel (after Azanza 2000) and from Przeworno (after Czyzewska and Stefaniak 1994), *D. elegans* from Sansan (own measurements), range of *H. eggeri* (after Rössner 2010), range of *H. larteti* from Steinheim a. A. (after Azanza 2000), range of *H. larteti* from Sansan (after Azanza 2000)


a1
a 2
b1
b2
b3
c1
c2
c3
d
e1
e2
f1
f2
f3
g1
g2
h1
h2
i1
i2
j1
j2
k1
k2
l1
l2
l3
l4
l5
m
n1
n2

◀**Fig. 11** Dental and postcranial material of *Euprox furcatus*, *Tethytragus* sp., and Ruminantia gen. et sp. indet.: **a** *E. furcatus* C sin. (GPIT/MA/2736; *1* labial view, *2* posterior view), **b** *E. furcatus* mandibula dex. with d2–m1 (UMJGP 203686; *1* labial view, *2* lingual view, *3* occlusal view), **c** *E. furcatus* i1 dex. (GPIT/MA/2736; *1* lingual view, *2* labial view, *3* posterior view), **d** *Euprox furcatus* maxilla sin. with D2–M1 (GPIT/MA/2737), **e** *E. furcatus* maxilla sin. with P2–M3 (UMJGP 204695; *1* occlusal view *2* labial view), **f** *E. furcatus* mandibula sin. with p2–m3 (GPIT/MA/2733; *1* occlusal view, *2* labial view, *3* lingual view), **g** *E. furcatus* mandibula dex. with p3–m3 (UMJGP 204686; *1* occlusal view, *2* lingual view), **h** *E. furcatus* Mc dex. (UMJGP 204722; *1* proximal view, *2* dorsal view), **i** *E. furcatus* humerus sin. (GPIT/MA/2418; *1* lateral view, *2* caudal view), **j** *Tethytragus* sp. P2–4 dex. (GPIT/MA/2753; *1* occlusal view, *2* labial view), **k** *Tethytragus* sp. M2–3 sin. (GPIT/MA/2392; *1* occlusal view, *2* labial view), **l** *Tethytragus* sp. Mt sin. (GPIT/MA/4143; *1* proximal view, *2* lateral view of distal part, *3* distal view, *4* dorsal view, *5* plantar view), **m** Ruminantia gen. et sp. indet. humerus sin. in cranial view (UMJGP 204721), **n** Ruminantia gen. et sp. indet. femur dex. (UMJGP 210695 *1* lateral view; *2* distal view); *scale bar* 10 mm

(fragment of humerus dex.) most likely represent one individual. For the same reasons, GPIT/MA/2383 (d4–m1 sin.), GPIT/MA/2385 (d4–m1 dex.), GPIT/MA/2413 (Mx fragment) and GPIT/MA/2414 (Mx fragment) most likely represent one individual, as do GPIT/MA/2381 (p3 dex.), GPIT/MA/2748 (m1 dex.), GPIT/MA/2750 (m2 dex.), and GPIT/MA/2380 (m3 dex.).

From dental features, finding position, preservation, and degree of dental wear, GPIT/MA/2736 (C sin. and dex.; fragments of maxillae with P2–M3 dex. and P3–M3 sin.; fragmented ix; i1 dex.; fractured mandibula dex. with p2–m3), GPIT/MA/2733 (mandibula sin. with p2–m3) and UMJGP 210955 (antler sin. with part of frontal) belong to one young adult male.

Description

The dentition is brachyoselenodont, and medium sized (Figs. 10, 11; online resource 4).

Maxilla and dentition (Figs. 10, 11): Sabre-like canines are recorded (Figs. 11a, 12f). They are curved posteriad, have a triangular to drop-shaped, laterally compressed cross-section, and are covered by enamel anteriorly and labially. A slight undulation of the enamel is due to growth striation. In contrast to the tragulid canine from Gratkorn (Fig. 2a), the teeth do not possess a wear pattern at their tips and are slightly sinuous-shaped in anterior view. The **D2** (Fig. 11d) is two-rooted and has an elongate, lingually rounded, moderately triangular shape. The labial cone is dominant, anterior and posterior styles are present and the posterolabial crista is longer than the anterolabial crista. In labial view, a well-pronounced rib at the labial cone is well developed, decreasing in width towards occlusal. One dominant crest from the labial cone and smaller additional crests posterior of it cross the fossa. There is no distinct cingulum. With its more triangular shape, the **D3** (Fig. 11d) differs from the D2. Besides a very small anterior cone, a clearly present paracone and a strongly developed metacone form the labial wall. Meso- and metastyle are prominent, the rib at the paracone is not as developed as in D2, but a clear rib is present at the metacone. The incision between anterolingual crista and protocone is quite weak, while an additional crest connects para- and protocone. At the dominant lingual cone, the metaconule, external and internal premetaconulecrista originate. There is an anterolingual cingulum. The **D4** (Fig. 11d) is typically trapezoid-shaped with an enlarged parastyle (less strong than in tragulids). It possesses the selenodont crown pattern of the upper molars with higher labial than lingual cones, an internal postprotocrista, developed ento- and mesostyle, wing-like metastyle, and a lingual cingulum. Labial ribs at the labial cones are not strongly developed. The **P2** (Fig. 11e) is three-rooted and triangular in shape. Besides the total size, the rounding of the lingual wall is variable, ranging from more acute (GPIT/MA/2739) to strongly rounded (GPIT/MA/2736). The labial cone is dominant with a narrow anterior and wider posterior incision at the labial wall, producing a well-pronounced labial rib. Anterolingually, a weak depression sets off the anterolingual cingulum from the lingual cone. Anterior and posterior styles are present, of which the latter is wing-like and enlarged, elongating the posterolabial crista in ratio to the anterolabial one, which is short. Additional crests cross the fossa, including the central fold. The tooth has no clear cingulum. The **P3** (Fig. 11e) is similar in shape to the P2, but labiolingually wider and lingually more rounded, with a lingual cingulum of varying strength, and a narrower anterior incision on the labial wall. The **P4** (Fig. 11e) is horseshoe-shaped with a rounded lingual side. The labial cone is dominant, with a more developed labial rib than in P2 and P3. The posterior style is weaker than in P2 and P3, and only as strong as the anterior style with the anterolingual crista being only slightly shorter than posterolingual one. The lingual cingulum is pronounced. The **upper molars** (Fig. 11d, e) are selenodont with a rectangular to trapezoid shape, widening towards labial with higher labial cones. The mesostyle is distinct, while the metastyle is reduced and wing-like. The size of para- and entostyle varies, but usually increase from M1 to M3 (entostyle sometimes included in the cingulum in M1; Fig. 11e1). The labial rib at the paracone is distinct enclosing a narrow incision with the parastyle. In all specimens, the internal postprotocrista is well developed with occasionally small additional crests. Sometimes, the premetaconulecrista is split at its anterior end into two or three small anterior branches fusing with the postprotocrista. It is long, intruding inbetween paracone and metacone. The presence of a metaconule fold is variable and sometimes not more than a thickening of the postmetaconulecrista. The lingual cingulum reaches from anterior to posterior, usually disappearing at the lingual aspects of protocone and metaconule (more pronounced in M2). The M3 differs from the anterior molars by a smaller labiolingual width posteriorly. The size increase from M1 to M3 is less distinct than in Tragulidae.

The **mandibulae** (Figs. 11b, f, g, 12f) from Gratkorn show a slender corpus mandibulae (for detailed information and measurements see online resource 4) and nest well in the size variability of *Euprox* vel *Heteroprox* from Steinheim a. A. for the height of the corpus. Where observed, one foramen mentalis is positioned underneath the anterior alveola of p2. The premolar tooth row is shorter than the molar tooth row (online resource 4). The **i1** (Fig. 11c) is of spate-like shape and widens from base to tip, but less than in Tragulidae. It is lingually concave and curved posteriad. The lingual plane has a strong groove along the posterior rim. The i2/3 and the incisiviform c(?) are pen-like, lingually concave, bend posteriad, with a small anterior crest on the lingual plane and a deep groove close to the posterior rim as in the i1, but are not increasing in anteroposterior width occlusally as the latter. Only one **d2** (Fig. 11b) is preserved fragmentarily. It is elongate with one anterior conid, a dominant mesolabial conid, and a posterolabial conid. The posterolingual conid and the posterior stylid are present. The transverse cristid is directed posterolingually, but does not reach the posterolingual conid. The posterolabial cristid fuses with the posterolabial conid. The latter nearly closes the back valley (oriented perpendicularly to the longitudinal axis of the tooth) by connecting with the posterolingual conid and posterior stylid. The posterior valley is oriented obliquely to the length axis of the tooth, but wider than the back valley and open lingually with a labial wall less high than in the back valley. The **d3** (Fig. 11b) is longer than the d2, but otherwise similar in morphology. It clearly possesses an anterior conid and stylid, and a small tubercle at the lingual side in the anterior valley. It differs from the d2 by a stronger posteriorly rotated transverse cristid, and a more closed posterior valley. The back valley is closed lingually. The **d4** (Fig. 11b) is elongate with three lingual and three labial conids. The lingual conids are higher than the labial ones. The metastylid is stronger than mesostylid and entostylid. Internal and external postprotocristid are present and form a v-structure, often termed as *Palaeomeryx*-fold. The postmetacristid is short, while the well-pronounced internal postprotocristid turns lingually before reaching the prehypo- and preentocristid. The latter are only fused at the base, as are the posthypocristid and entostylid. Anterior ectostylid and ectostylid are large, and anterior and posterior cingulid are present. The **p2** (Fig. 11f) is similar in morphology to the d2, but wider. Size and morphology also vary among the different specimens. Except for GPIT/MA/2390 (fragmented p2 with open posterior valley), in all specimens the transverse cristid is directed more posteriad than in the deciduous tooth, more or less closing the oblique posterior valley. The anterior conid is pronounced and basally fused with the lingual cingulid. There is no anterior stylid. A posterior thickening is considered the homologue of the mesolingual conid. As in the d2, the back valley is oriented perpendicularly to the longitudinal axis of tooth, but not always closed. The incision on the labial wall anterior of the posterolabial conid is present in all specimens, but the strength varies. The **p3** (Fig. 11f, g) is similar in shape to the p2, but wider, and the meso- and posterolingual conid are more developed. The posterior valley is usually closed (not in GPIT/MA/2390 and UMJGP 204674). The back valley is very narrow and in some cases completely closed. The strength of the incision on the labial wall anterior of the posterolabial conid is variable. The shape of the **p4** (Fig. 11f, g) is similar to p3, but the mesolingual conid is as pronounced as the mesolabial conid and clearly better developed than in the preceding premolars. The transverse cristid is positioned more posterior and fused with the posterolingual cristid or with the anterolingual cristid, which is bent to the posterior. The posterior valley is nearly or fully closed and separated from the back valley by the fusion of posterolingual and posterolabial conid (only in UMJGP 204686 the posterolingual conid is isolated and the posterior and back vallies are fused). The back valley is narrow and obliquely to perpendicularly aligned. Only an anterolingual cingulid is present. In the selenodont **lower molars** (Fig. 11b, f, g), the axes of the lingual conids are oblique to the length axis of the tooth. The metastylid is strongly pronounced and the entostylid present. The postprotocristid is split into internal and external cristid forming a v-structure often termed the *Palaeomeryx*-fold (with increasing wear, this feature becomes less apparent). The preprotocristid is long and fused with the shorter premetacristid only basally. The prehypocristid is long and fuses with the posterior wall of the postprotocristid, as does the short preentocristid, which is fused with the postprotocristid in specimens with higher degrees of attrition. The postentocristid is short and fused with the posthypocristid only basally. The anterior cingulid is stronger than the posterior one. The ectostylid is pronounced, slightly decreasing in size from m1 to m3. Size increases significantly from m1 to m2. In m3, the hypoconulid is pronounced and is clearly set off from the talonid. The posthypocristid is usually split posteriorly (length of branches variable). By the fusion with the preentoconulidcristid (in GPIT/MA/2399 with the prehypoconulidcristid), it closes the back fossa anteriorly (only in GPIT/MA/2755 the back fossa opens anteriorly), while the fusion of posthypoconulidcristid and entoconulid closes the back fossa posteriorly. In general, the entoconulid is small, and thus the third lobe appears more or less monocuspidate. The hypoconulid is moved posterolingually giving the third lobe a lingually turned and elongated shape with a lingual depression at the entoconulid. The presence and size of the posterior ectostylid is variable.

Antlers

Material: GPIT/MA/02398 (antler sin.), UMJGP 204062 (antler dex.), UMJGP 210955 (antler sin. with part of frontal), UMJGP 204670 (pedicle sin. with antlerbase lost due to gnawing), UMJGP 203443 (fragment of pedicle sin.)

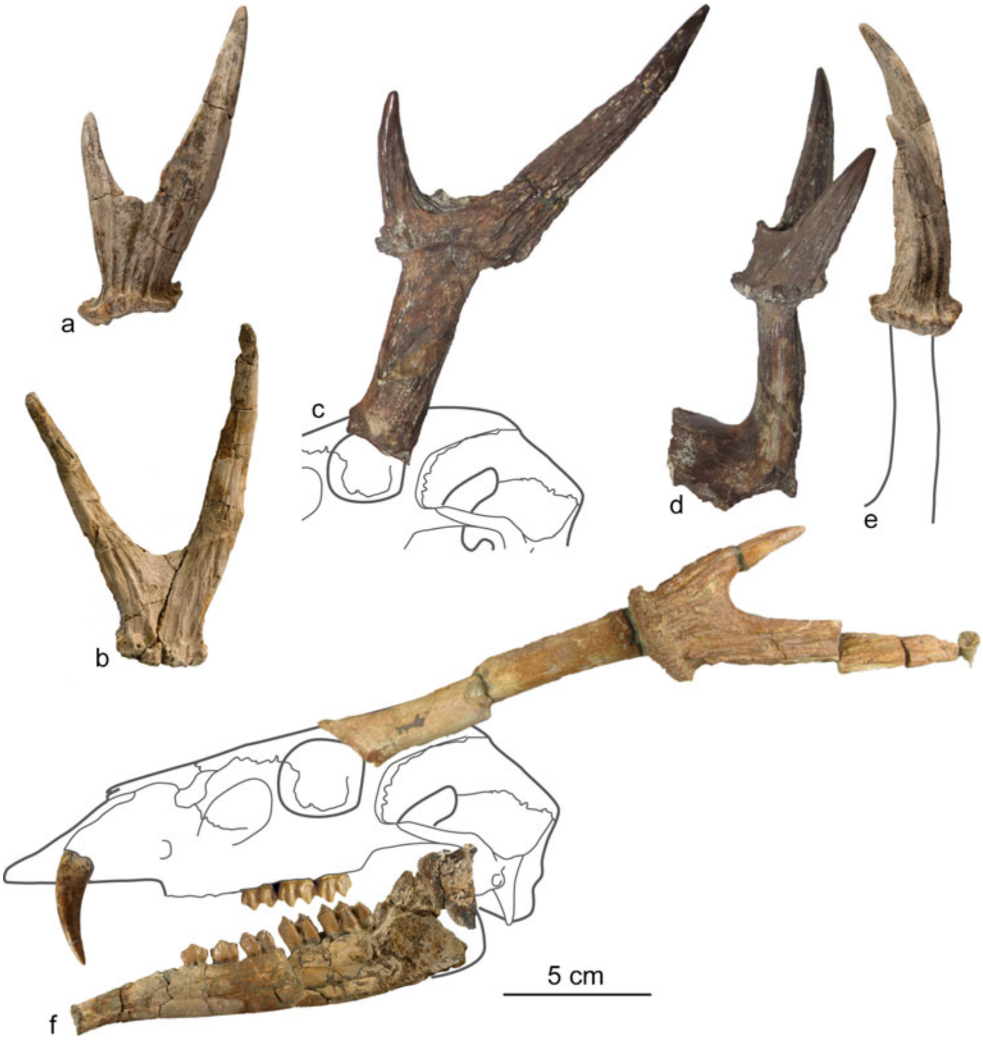


Fig. 12 Cranial appendages of *E. furcatus* from Gratkorn in comparison to female *D. elegans* from Sansan: **a** antler sin. from Gratkorn (lateral view; GPIT/MA/2398), **b** antler dex. from Gratkorn (medial view; UMJGP 204062), **c** antler sin. of *D. elegans* from Sansan with reconstructed orientation (MNHN Sa 3451; lateral view), **d** same as c (anterior view), **e** same as (**a**) with reconstructed orientation (anterior view), **f** reconstruction of *E. furcatus* from Gratkorn in lateral view with orientation of antler (UMJGP 210955) and GPIT/MA/2736 (mandibula and maxilla mirrored); skull drawing after Thenius (1989; *Muntiacus*)

Description

All three complete antlers (Fig. 12; for detailed information and measurements, see online resource 4) are bifurcated, comprising a short anterior and a long posterior branch. Two of the complete ones are shed antlers, while one specimen is still attached to the pedicle and a fragment of the frontal (UMJGP 210955). Two foramina supraorbitale are recorded on the frontal anteromedially of the pedicle. The latter is slightly convex laterally and clearly set off from the coronet. Its cross-section changes from triangular to subcircular from proximal to distal. The surface of the pedicle is smooth, and has a slightly elongated and narrow groove running anteroproximally to mediodistally ending about 20 mm proximally of the antler's base on specimen UMJGP 204670. The antler's base is a clear coronet with pearls, showing a anteroposterior suboval shape. The coronet is inclined to the anterior with different degrees and encloses with the length axis of the pedicle angles ranging from 45° to nearly 90°. A distinct lateral inclination is absent. There is a constriction above the coronet and the length of the antler shaft ranges from 32 to 38 mm. Both branches are curved distally pointing to median. The cross-section of the branches is variable from triangular to subrounded (in GPIT/MA/2398, the posterior branch is medially concave). Tapering of the branches can be gradual but also with a clear incision from where the branch incurves concavely. All preserved antlers show a well - ornamentation in terms of longitudinal ridges along the shaft and the branches.

Postcrania

Material: GPIT/MA/2418 (humerus sin.), UMJGP 210699 (distal part of humerus dex.), UMJGP 204722 (metacarpal dex.), GPIT/MA/2407 (fractured and fragmented longbone), GPIT/MA/2411 (fragment of phalanx proximalis too fragmentary to allow description), GPIT/MA/2412 (fragment of humerus dex. too fragmentary to allow description)

Description (Fig. 11; for detailed information and measurements, see online resource 4):

A **humerus** sin of *E. furcatus* (GPIT/MA/2418; Fig. 11i) is fairly well preserved, showing the distal articulation and a part of the caput humeri. In contrast to the distal part, most of the proximal part is compressed and fragmented. The preserved length from epicondylus lateralis to the caput humeri is about 155 mm. The distal part and some fragments of the shaft of a humerus dex. (UMJGP 210699) show the same morphology and dimensions. In both humeri, the cross-section of the distal shaft is rounded with a clear edge terminating in the epicondylus medialis. The fossa olecranii is deep but not open as in Suidae. The trochlea humeri is trapezoid in cranial view. The external crest is clearly set off from the trochlea laterally as is typical for Cervidae (Heintz 1970) and also observed in *Euprox* vel *Heteroprox* from Steinheim a. A. (e.g. SMNS 42698, GPIT/MA/3011 and 3007), in contrast to a less marked crest in Bovidae (Heintz 1970). Heintz noted a different ratio of proximodistal width of the medial depression versus transversal width of the trochlea for Cervidae (0.55–0.64) and Bovidae (0.45–0.55). With a height/width ratio of 0.61 (UMJGP 210699: 14.5/23.7) and 0.59 (GPIT/MA/2418: 14.4/24.9), the two humeri would clearly fall into the range of Cervidae, as do *Euprox* vel *Heteroprox* from Steinheim a. A. [five distal humeri dex. (GPIT/MA/3007); four distal humeri sin. (GPIT/MA/3011)] ranging from 0.57 to 0.60. Also, the two humeri correspond in size to *E. furcatus* from Przeworno (Czyzewska and Stefaniak 1994). Both humeri differ from Tragulidae by a less pronounced decrease in the proximodistal width of the trochlea from medial to lateral, the more pronounced external condyle on the trochlea and a strongly developed epicondylus medialis (Gailer 2007; Hillenbrand et al. 2009; Morales et al. 2012).

Metacarpal III and IV are fused to a cannonbone (UMJGP 204722; Fig. 11h). As this is not the case in Tragulidae, the metacarpal can be assigned to Pecora. It is quite slender with a delicate proximal articulation. The cross-section of the shaft is rounded dorsally and palmarily concave. A weak sulcus longitudinalis dorsalis on the dorsal surface runs from the midline distally to the junction of medial and lateral articulation facet. The proximal articulation facet is rounded triangular in cross-section with a larger medial facet for the articulation of os carpale secundum and tertium. The size and shape of the fossa between the facets is unknown due to fragmentation. With a dorsopalmar width of 14.8 mm and a mediolateral width of 20.5 mm, the metacarpal is within the morphological and size range of *Euprox* vel *Heteroprox* from Steinheim a. A. (e.g. SMNS 4801, GPIT/MA/3020), and fits well to *E. furcatus* from Przeworno (Czyzewska and Stefaniak 1994). The specimen differs from *Miotragocerus* vel *Tethytragus* (Atzelsdorf, Austria; Hillenbrand et al. 2009) by a smaller size and the more filigree habitus of the proximal articulation surface. Due to fragmentation, the existence of a longitudinal groove on the palmar side of the proximal articulation surface, as would be typical for Bovidae (Heintz 1970), cannot be rejected nor verified, but the well-pronounced incision on the dorsolateral aspect (a typcial character for cervids, following Heintz 1970) argues for an assignation to *E. furcatus.*

Comparison

The type series of *Euprox furcatus* comprises an isolated antler (holotype), a second antler and a canine from Kieferstädel (today: Sośnicowice, Poland). Size and morphology of the antlers from Gratkorn exhibit a great resemblance with the holotype and other specimens assigned to the species (online resource 4; Fig. 12; Hensel 1859; Stehlin 1928; Czyzewska and Stefaniak 1994; Azanza 2000). In detail, the characteristics are (1) the strong inclination of the pedicle to posterior, (2) the anteromedial location of the foramina supraorbitale, (3) the clearly developed suboval and only slightly anteroposterior elongated coronet, (4) the constriction of the shaft above the coronet, (5) the shaft length of 32–38 mm, and (6) the simple bifurcation of the antler into a shorter anterior and a longer posterior branch (Fig. 12). In addition, Hensel (1859) described an anterior inclination of the antler base relative to the antler pedicle and a strong surface ornamentation of the holotype comparable to the specimens from Gratkorn. The narrow groove running anteroproximally to mediodistally on specimen UMJGP 204670 is shared with one paratype of the species (Hensel 1859; p. 263). Presumably, it represents the course of a branch of the superficial temporal artery (observed to provide the blood support for the antler in modern Cervidae; Suttie and Fennessey 1990). All antlers from Gratkorn show a clearly shorter anterior branch than the holotype, but as the length of the branches is variable and increasing in size during the lifetime of the animal (Stehlin 1928), the length of anterior and posterior branches are not considered diagnostic here. Furthermore, the dimensions of the Gratkorn specimens are in the size range of *E. furcatus* from Przeworno (Poland), Arroyo del Val (Spain) and Steinheim a. A. (Germany; Czyzewska and Stefaniak 1994; Azanza 2000; personal observation).

The cervid from Gratkorn differs from Miocene cervids, such as *Procervulus ginsburgi* Azanza, 1993, *Lagomeryx* Roger, 1904, *Paradicrocerus* Gabunia, 1959, *Palaeoplatyceras* Hernández-Pacheco, 1913, and *Heteroprox moralesi* Azanza, 2000, by a clear and simple dichotomy in the antlers (Stehlin 1937; Azanza and Ginsburg 1997; Azanza 2000; Rössner 2010). It differs from other Miocene taxa possessing a bifurcated antler like *Procervulus dichotomus* (Gervais, 1859), *Heteroprox larteti* (Filhol, 1890), *Heteroprox eggeri* Rössner, 2010, and *Dicrocerus* Lartet, 1837 by a modern coronet (Stehlin 1928, 1939; Ginsburg and Crouzel 1976; Ginsburg and Azanza 1991; Rössner 1995; Azanza 2000). *Heteroprox* and *Procervulus* differ from the Gratkorn specimen furthermore by a less inclined pedicle and the lack of a clear distinction between pedicle and antler (Stehlin 1928; Haupt 1935; Azanza 2000; Rössner 2010). Additionally, *Heteroprox* shows an "antlerbase" mediolaterally less wide than in the Gratkorn specimens and *E. furcatus*, and a medial instead of an anteromedial position of the foramen supraorbitale (Stehlin 1928; Rössner 2010). The Gratkorn specimen differs from *Dicrocerus* by a longer and less steeply inclined pedicle, a smaller lateral expansion of the antler, and smaller dimensions in dentition and antlers (Haupt 1935; Stehlin 1939; Thenius 1948, 1950; Ginsburg and Azanza 1991; Azanza 1993; Rössner 2010; Fig. 12). Only female *Dicrocerus* individuals and more gracile males overlap with the specimens from Gratkorn, e.g. in dimensions of the antler plate, but clearly differ in the morphological features described. The specimen from Gratkorn is distinct from the stratigraphically younger *Euprox dicranocerus* (Kaup, 1839) and *Amphiprox anocerus* (Kaup, 1833) by a clearly shorter antler shaft (Haupt 1935; Azanza 2000). *Euprox minimus* (Toula, 1884) (Thenius 1950) is smaller than the cervid from Gratkorn. In Late Miocene Cervidae, such as, e.g. *Cervavitus, Pliocervus*, and *Procapreolus*, the antlers are monopodial with three or more tines (Azanza et al. 2013). From antler morphology, the cervids from Gratkorn can thus be clearly assigned to *Euprox furcatus.*

The dental material from Gratkorn is also in accordance with the morphological and dimensional variability of the medium-sized brachyoselenodont Miocene cervids *Euprox furcatus* and *Heteroprox larteti* (Figs. 10, 11; online resource 4; also note here interindividual variation due to different degrees of wear: GPIT/MA/2739 is from a rather old individual with stronger worn teeth). Like *E. furcatus, Heteroprox larteti* (Filhol, 1890) is defined on an isolated antler (antler dex. from Sansan (MNHN 3371)). A species differentiation based on dental material between *E. furcatus* and *H. larteti* is hindered due to the close resemblance of the two species (Stehlin 1928), the co-occurrence in the locality Steinheim a. A., yielding so far the richest material of both species (unfortunately, lower dentition and postcranial material of *E. furcatus* associated with the diagnostic antlers of the male have never been described from Steinheim a. A.; in both taxa, females do not possess cranial appendages), and a large intraspecific variability. Differences in the dentition among specimens of *Euprox* vel *Heteroprox* from Steinheim a. A. are small and not really distinct. In the Gratkorn specimens, the external postprotocristid in the lower molars is not strongly developed in general. Czyzewska and Stefaniak (1994) describe a reduced external postprotocristid in *E. furcatus* from the late Middle Miocene locality Przeworno, thus fitting well to the specimens from Gratkorn. Azanza (2000), in contrast, describes a more pronounced external postprotocristid in *E. furcatus* from the Middle Miocene of Spain in comparison to *H. larteti.* Furthermore, she notes a more parallel alignment of the lingual lobes in the lower molars of *E. furcatus* (in contrast to *Heteroprox,* where they should be more oblique), as well as a weak metastylid for *E. furcatus*. The specimens from Gratkorn show an oblique alignment of the lingual conids and a clearly developed metastylid, as also does, e.g. *Euprox* sp. described from the Late Miocene locality Atzelsdorf (Hillenbrand et al. 2009). Azanza (2000) observes a more inner position of the entoconulid and a distinct concavity for the inner wall of the third lobe of the lower m3. This observation could be well in accordance with the lingual turn of the third lobe and a lingual depression at the entoconulid observed in the m3 of the Gratkorn specimens. These features are also present with moderations in a few mandibulae of *Euprox* vel *Heteroprox* from Steinheim a. A. A mandibula associated with *H. larteti* from Sansan described by Ginsburg and Crouzel (1976; MNHN Sa 3399), is unfortunately strongly worn and does not allow a clear observation concerning these characters. However, as far as can be reconstructed on MNHN Sa 3399, it had a less elongated third lobe and a more pronounced entoconulid than the specimens from Gratkorn. In the description of *E. furcatus* from Przeworno (Czyzewska and Stefaniak 1994), neither a lingual turn of the third lobe nor a lingual depression at the entoconulid in the m3 is mentioned or figured, but the sentence "there is a labial cusp and this lobe has well-developed anterior and posterior wings" (Czyzewska and Stefaniak 1994, p. 61.) indicates a monocuspidate third lobe in accordance with *E. furcatus* from Gratkorn. Thus, the morphology of the third lobe may prove a useful tool for species differentiation in the future.

Azanza (2000) also included dental material from Steinheim a. A. in her description and observed less significant stages for her characters in *E. furcatus* from Steinheim a. A. in comparison with the Spanish material. She thus concluded that it could also be an indication that the Spanish material represents a different species, which could explain the differences observed in the Spanish material to *E. furcatus* from Gratkorn and Przeworno.

Concerning postcranial material, a large size variability can be observed for *Euprox* vel *Heteroprox* from Steinheim a. A. (specimens at SMNS and GPIT; Stehlin 1928). The Gratkorn postcranial material assigned to *E. furcatus* mostly nests in the smaller size ranges of the variability from Steinheim a. A. This could be due to the smaller postcranial dimensions of *E. furcatus* compared to *H. larteti.* However, to verify this assumption, an intensive study of the material from Steinheim a. A. would be necessary.

In summary, the cervid remains from Gratkorn are assigned to *Euprox furcatus* as they show most dimensional and morphological overlap with this species. No indications have so far been found for a second cervid taxon at Gratkorn. In contrast to the still richer assemblage from Steinheim a. A., at Gratkorn antler and complete upper and lower dentition (GPIT/MA/2736, GPIT/2733, UMJGP 210955) can for the first time be assigned to one individual (young adult male) of

Euprox furcatus and might thus be helpful for the evaluation of species characteristics.

Stratigraphic range

The genus *Euprox* is present in the Central Paratethys realm from the middle Middle Miocene with the first representative *E. minimus* from Göriach (Austria; 14.5 ± 0.3 Ma; Thenius 1950), to the Late Miocene with *E. dicranocerus* from Wien III (Austria; 10.5 Ma; Thenius 1948). As Late Miocene two-tined muntiacines and three-tined cervids can easily be misclassified, and as the taxonomic status of *Cervavitus*/*Euprox sarmaticus* Korotkevich, 1970 and *Cervavitus*/*Euprox bessarabiensis* Lungu, 1967 seems still to be in discussion (Azanza et al. 2013), they are not taken into consideration here. The record from Kohfidisch (Austria; Late Miocene; Turolian; *Euprox* sp.; Vislobokova 2007) is not included for the same reason, and because it so far comprises only scarce material and no antlers (Vislobokova 2007; Azanza et al. 2013). The species *E. furcatus* first appears at about 14.2 Ma (Klein-Hadersdorf, Austria; Böhme et al. 2012) and is currently recorded only in the Middle Miocene, with abundant findings from, e.g. Steinheim a. A., Przeworno, and Arroyo del Val (Czyzewska and Stefaniak 1994; Azanza 2000). The rich assemblage from Gratkorn is the first record of the species in the Styrian Basin.

Palaeoecological characterisation

The body mass of *Euprox furcatus* from Gratkorn is estimated to have been 24–30 kg (min: 23.8 kg, max: 29.9 kg; n=6; specimens with a higher degree of wear were not included in the equations). With a shoulder height of about 60–70 cm (articulated female *Euprox* vel *Heteroprox* from Steinheim a. A.; on exhibition at the SMNS), *E. furcatus* is therefore comparable in habitus to the modern red muntjac (*Muntiacus muntjak;* Mattioli 2011). In contrast to *D. elegans*, in which frontal appendages are recorded for both genders (Ginsburg and Azanza 1991), it is assumed for *E. furcatus* that only males were bearing antlers (Heizmann and Reiff 2002), as also indicated by an antler-less articulated *Euprox* vel *Heteroprox* skeleton from Steinheim a. A.

Thenius (1950) described *E. furcatus* as adapted to dry environments in contrast to the more humid adapted *H. larteti*, while Czyzewska and Stefaniak (1994) interpreted *E. furcatus* as a mobile species between more open and arid biotopes and more wooded areas due to dental and postcranial morphology. Isotopic measurements on well-defined material of *E. furcatus* are so far rare. Stable isotope analyses (δ^{13}C and δ^{18}O) on the material from Gratkorn described here do not support feeding in open and dry environments, but rather point to subcanopy browsing (Aiglstorfer et al. 2014a, this issue).

Isotopic measurements (^{87}Sr/^{86}Sr) indicate that *E. furcatus* from Gratkorn was not a permanent resident of the locality but temporarily inhabited different areas (maybe in the Styrian Basin; Aiglstorfer et al. 2014a, this issue).

Infraorder Pecora Linnaeus, 1758
Family Palaeomerycidae Lydekker, 1883
Type species: *Palaeomeryx kaupi* von Meyer, 1834

Palaeomerycidae gen. et sp. indet.

Material: UMJGP 203441 (Mc sin.)

Description and comparison

So far, the largest ruminant from Gratkorn is recorded only by a fragmented metacarpal sin. It is assigned to the family *Palaeomerycidae* (Fig. 13). Dimensions (L=305 mm, DAPp preserved=36.7, DTp preserved=58 mm; DAPd (estimated) about 30 mm; DTd (estimated) about 60 mm) overlap with "*Palaeomeryx eminens*" Meyer, 1851 from Steinheim a. A. It is slightly larger than cf. *Ampelomeryx magnus* (Lartet, 1851) (Astibia 2012). As typical in Palaeomerycidae, the cross-section of the diaphysis is rounded dorsally and palmarily less concave than in Cervidae, but distally more dorsopalmarily flattened than in the latter (Astibia 2012). As in cervids, a weak sulcus longitudinalis dorsalis can be observed on the dorsal surface running from the junction of medial and lateral articulation facet proximally to the midline distally (ending about 50–60 mm proximal of the distal end in a deeper fossa). Proximal articulation facets are not preserved. Morphology of the specimen from Gratkorn is well in accordance with "*Palaeomeryx eminens*" from Steinheim a. A. (Fraas 1870, tab. 7, fig. 7). As in "*Palaeomeryx eminens*" from Steinheim a. A. the sagittal crests on the distal condyles are not strongly set off from the central part of the condyles in dorsal view, comparable to Cervidae, but different from Bovidae (see, e.g. Leinders 1979). It differs from *Germanomeryx* Rössner, 2010 by the closure of the sulcus longitudinalis dorsalis (Köhler 1993). The metacarpal from Gratkorn differs from Giraffidae of similar dimensions by the less concave palmar depression (see, e.g. Bohlin 1926; Solounias 2007). From dimensions and morphology, and taking into consideration the record of "*Palaeomeryx* cf. *eminens*" from the early Late Miocene locality of Atzelsdorf (Hillenbrand et al. 2009), the Gratkorn specimen most likely represents "*Palaeomeryx eminens*". However, as only one metacarpal has so far been excavated from Gratkorn, and the taxonomy inside the family is still in discussion (see, e.g. Astibia 2012), a determination as Palaeomerycidae gen. et sp. indet. is the most reasonable for the moment.

Fig. 13 Mc sin. of Palaeomerycidae gen. et sp. indet.: **a** proximal view, **b** dorsal view, **c** distal view; *scale bar* 2 cm

Stratigraphic range

Palaeomerycidae are typical representatives of European Middle Miocene faunal assemblages. The family is recorded from the Early Miocene (Gentry et al. 1999; Astibia 2012) until the Late Miocene (Astibia 1987; Hillenbrand et al. 2009). Late Miocene findings are so far restricted to the early Late Miocene with the localities of Atzelsdorf (Austria; 11.1 Ma; Hillenbrand et al. 2009) and Carrilanga 1 (Spain; Astibia 1987), which is older than the first record of *Hipparion* from Nombrevilla (López-Guerrero et al. 2011). The record of "*P. eminens*" from the Eppelsheim Fm (Tobien 1961) is not taken into consideration here as a Late Miocene representative, as the Eppelsheim Fm comprises a stratigraphically mixed fauna from Middle and Late Miocene and the specimens thus also could, and most likely do, comprise Middle Miocene elements (Böhme et al. 2012). A continuous size increase in Palaeomerycidae has been hypothesised, with the largest representative being "*Palaeomeryx eminens*", e.g. from the middle Middle Miocene of Steinheim a. A. (Gentry et al. 1999; Ginsburg 1999). However, findings of the large-sized *Germanomeryx* (Rössner 2010) in the early Middle Miocene indicate a more differentiated size evolution among palaeomerycids. Anyhow, the size of the Palaeomerycidae gen. et sp. indet. from Gratkorn described here is well in accordance with "*Palaeomeryx eminens*" from Steinheim a. A. (Fraas 1870) and thus fits well into a late Middle Miocene assemblage. The youngest record of "*Palaeomeryx* cf. *eminens*" described so far is from the early Late Miocene locality Atzelsdorf (Hillenbrand et al. 2009).

Palaeoecological characterisation

Köhler (1993) classifies "*Palaeomeryx eminens*" as a browser of soft, juicy leaves, or aquatic plants, solitary or living in small groups, with slow-gear adapted locomotion (she also included in this description *Germanomeryx* from Sandelzhausen). As there is only one metacarpal of a palaeomerycid so far recorded from Gratkorn, no further information on ecological adaptations can be gained. Rössner (2010) states that, at least for *Germanomeryx* from Sandelzhausen, feeding on aquatic plants can be excluded, and Tütken and Vennemann (2009) reconstructed *Germanomeryx* as a canopy folivore.

In any case, with an estimated bodymass of 270 kg, large territories would be necessary to supply enough plant material for this palaeomerycid from Gratkorn.

Family Bovidae Gray, 1821
Genus *Tethytragus* Azanza and Morales, 1994

Type species: *Tethytragus langai* Azanza and Morales, 1994
Holotype: skull roof with horn cores (MNCN BAR-73).
Type locality: Arroyo de Val-Barranca (Zaragoza, Spain).
Further species: *Tethytragus koehlerae* Azanza and Morales. 1994, *Tethytragus stehlini* (Thenius, 1951).

Tethytragus sp.

Dentition

Material: GPIT/MA/2753 (P2–4, M3 dex., labial wall of M2 dex.), GPIT/MA/2392 (M2–3 sin.)

Description (for measurements, see online resource 5)

Some upper teeth of the ruminant material from Gratkorn can be assigned to the family Bovidae. Due to field position, preservation and wear, the teeth are assigned to one individual. **Dentition** (Fig. 11j, k): The **P2** is of elongated trapezoid to rectangular shape. The anterolabial cone is dominant, while the posterolabial cone is not really distinct and in addition strongly worn. Although not distinct, an anterolingual cone is set off from the more dominant posterolingual cone by an incision on the lingual wall. A deep incision (not reaching the base of the tooth crown) on the anterolabial wall separates a pronounced anterior style from the anterolabial cone, while a posterior style is not developed. Due to a depression posterior to the anterolabial cone, a distinct rib can be observed on the labial wall of the cone. Several crests cross the fossa. The **P3** is similar in wear and morphology to the P2, but of more triangular shape. The labial incision is narrower than in the P2, the incision on the lingual wall is stronger, and the tooth crown is higher. The **P4**, which is also worn, is of triangular, lingually rounded shape with one labial and one lingual cone. The anterior incision on the labial wall is shallower than in the anterior premolars, but the rib at the labial cone is well pronounced. Besides, a distinct anterior style, a clearly developed posterior style is present. In the fossa, a small central fold can be observed. The **M2** shows a typical ruminant selenodont dentition with higher labial than lingual cusps. The labial wall at the paracone is missing. The tooth is brachyo- to mesodont and the lingual tooth crown elements are separated from the labial elements. The parastyle is clearly developed and encloses an incision with the distinct labial rib at the paracone. The mesostyle is the strongest style and possesses a distinct rib, while the metastyle is weak and wing-like. On the lingual side, a small entostyle is developed attached to the posterolingual wall of the protocone. The labial wall of the metacone is planar and nearly vertically inclined. The lingual wall encloses an angle of about 55° with the basal plane of the tooth crown in anterior view and of 50° in posterior view. The tooth possesses no internal postprotocrista and only a slight indication for a metaconule fold, but a short anterior cingulum. The **M3** is similar in shape to the M2. The incision enclosed by parastyle and the rib at the paracone is shallower and the mesostyle more column-like than in the M2, while the labial wall of the metacone is more vertical and planar and the metastyle is more reduced. Both M3 show a splitting into internal and external postprotocrista, weakly developed or only indicated anterior cingulum, and no entostyle.

Postcrania

Material: GPIT/MA/4143 (Mt and cuneiforme sin.)

Description

Metatarsals III and IV are fused to a slender **cannonbone** (GPIT/MA/4143; Fig. 11l; online resource 5). The cross-section of the shaft is rounded dorsally and concave palmarily (flattening distally). A strong sulcus longitudinalis dorsalis runs on the dorsal surface from the junction of the proximal medial and lateral articulation facets distally ending between the two distal condyles. It is not closed distally. The proximal plane is subrounded in cross-section with an elongate dorsolateral to medioplantar facet for the articulation with the cuneiforme on the mediodorsal side. There are three facets for articulation with the cubonavicular (large on the lateral side, slender mediolaterally elongated on the plantar side, and a small oval in the medioplantar corner). In dorsal view, the transversal width gradually increases distally. The area for the extensor tendon on the dorsal surface is distinct, but not long, though it is more strongly developed than in the modern *Capreolus capreolus*. Distally, two condyles exhibit clearly defined and dorsally and plantarily set off sagittal crests. In dorsal view, they are set off especially externally. The external part of the condyles has a more triangular shape in dorsal view, while the internal is more rectangular. The intertrochlar incision forms a "v". Directly proximal of the lateral condyle, the metatarsal shows a biting mark on the dorsal surface. The **cuneiforme** sin. (GPIT/MA/4143) articulates well with the metatarsal. It possesses a concave proximal facet for articulation with the cubonavicular and distally a dorsally convex and plantarily concave facet for articulation with the metatarsal. In proximal view, a planar lateral wall for articulation with the cubonavicular and a rounded medial wall are visible.

Comparison

With the steep lingual wall, the more developed crown height and the simple crown morphology, the teeth clearly differ from the similar-sized cervid teeth from Gratkorn, and justify assigning to the family Bovidae. Taxonomy in Bovidae is based to a great extent on horn cores (see, e.g. Köhler 1987; Gentry 1994). As horn cores have not been recorded from Gratkorn so far, only a tentative species assignation can be given here. According to size and morphology, the teeth belong to a small-sized, rather brachyo- to mesodont species. Most bovid genera so far recorded from the late Middle Miocene of Central Europe [*Protragocerus* Depéret, 1887, *Austroportax* (Sickenberg, 1929), *Miotragocerus* Stromer, 1928 and *Tethytragus* Azanza and Morales, 1994 (Gentry et al. 1999; van der Made 2012)] are larger than the bovid from Gratkorn (Fig. 14a). Only *Tethytragus koehlerae* Azanza and Morales 1994 from Çandir (Turkey) overlaps in dimensions (Köhler 1987). Besides dimensions, the Gratkorn specimen shares with *Tethytragus koehlerae* the tooth crown height, the clearly developed styles, a pronounced paracone rib at the upper molars, the reduced entostyle, and a planar labial wall at the metacone. However, with a smooth enamel surface, the Gratkorn specimen differs from this species which possesses wrinkled enamel (Köhler 1987; van der Made 2012). *Tethytragus langai* possesses a smooth enamel surface, but differs from the Gratkorn specimen by a larger size (Azanza and Morales 1994; Fig. 14b). Azanza and Morales (1994) assigned three species to the genus: *T. langai, T. koehlerae*, and *Tethytragus stehlini*. Until today, no dental material is unambiguously referred to *T. stehlini* (Thenius 1951), which was described on the basis of isolated horn cores from the Middle Miocene localities of Mikulov (=Nikolsburg, Czech Republic) and Klein-Hadersdorf (Austria). Its taxonomic status is still in discussion. Some authors consider it to be synonymous with *T. langai* due to features in dentition from Klein-Hadersdorf (Austria), in which case it would have priority over *T. langai* (van der Made 2012; van der Made, personal communication). Others regard both species as valid due to differences in the size and shape of the horn cores (Azanza and Morales 1994). In any case, other teeth so far assigned to the genus than *T. koehlerae* are larger in dimensions than the Gratkorn specimen. Size and morphology of the metatarsal from Gratkorn are in accordance with *Tethytragus koehlerae* from Çandir, figured by Köhler (1993), being only slightly shorter (however, the specimen from Çandir looks fragmented and completed with an at least 10-mm cast). The metatarsal differs from cervids by the clearly open metatarsal sulcus, typical for Bovidae (Leinders 1979). *Turcocerus gracilis* Köhler,1987 differs from the Gratkorn specimens by a larger size, higher crowned molars and stronger styles (Köhler 1987; van der Made 2012). Besides size, the Gratkorn specimen differs in morphology from *Miotragocerus* sp. vel *Tethytragus* from Atzelsdorf (see, e.g. 2008z0051/0014) by a more developed rib at the paracone, a more planar labial wall at the metacone in M3 and a less pronounced metastyle in upper molars (see, e.g. 2008z0051/0002, 14, 15). An isolated P4 (BSPG/1926/V/34) assigned to *Miotragocerus*? *monacensis* by Stromer (1928) from the late Middle Miocene locality Aumeister (Munich, Germany) is slightly larger than the specimen from Gratkorn and differs in a more strongly developed central folding. A more planar labial wall at the metacone and a less pronounced metastyle than in *Miotragocerus* has been described for M3 in *Eotragus* and *Protragocerus* by Romaggi (1987). With the simple molar morphology, the separated lingual walls and its small size, the bovid from Gratkorn is in the range of the Early and Middle Miocene taxa *Eotragus* and *Pseudoeotragus* (Figs. 11, 14). However, the Gratkorn bovid differs from *Eotragus* (van der Made 1989 and 2012) in a P4 being less wide, in upper molars being higher crowned with a more planar labial wall at the metacone, and in a more slender and column-like mesostyle. In *Eotragus* (van der Made 1989, 2012), the incision between anterior style and anterolabial cone in P2–4 is not as developed as in the specimen from Gratkorn. *Pseudoeotragus* (van der Made 1989, 2012) possesses a wider P4 and is higher crowned, shows a parastyle more parallel to the paracone rib, and possesses a more planar labial wall in the upper molars than the specimen from Gratkorn.

Conclusively, the entity of morphological and metrical dentition characters of the Gratkorn bovid corresponds best to those of *Tethytragus koehlerae*. However, due to the smooth enamel surface in the Gratkorn specimens, the lack of any associated horn core remains so far, and as there is no dental material unambiguously assigned to *T. stehlini* for comparison, the Gratkorn specimen is left in open nomenclature as *Tethytragus* sp.

Stratigraphic range

The genus *Tethytragus* is a typical Bovidae for the Middle Miocene of Europe (including Turkey; Azanza and Morales 1994; Bibi and Güleç 2008; van der Made et al. 2013). First records are noted from the Middle Miocene localities Inönü I and Paşalar (*Tethytragus* sp.; van der Made 2012). Late Miocene findings are rare and have so far only been recorded from Turkey, described as *T. koehlerae* and *Tethytragus* cf. *T. koehlerae* (Gentry 2003; Bibi and Güleç 2008). The authors of both publications remarked on the unlikelihood that it actually represents the same species as the Middle Miocene *T. koehlerae*, and van der Made et al. (2013) alluded to morphological differences of systematic value between the Middle and the Late Miocene occurrences. In Western Europe, *T. koehlerae* is so far recorded from the late Middle Miocene locality La Grive, which is similar in age to the Gratkorn locality, and, with reservations, from Castelnau Barbarens, Gers, and Arrajegats (both Middle Miocene), as well as from the middle Middle Miocene Crêt-du-Locle (van der Made 2012). *Tethytragus* sp. is recorded from the Spanish

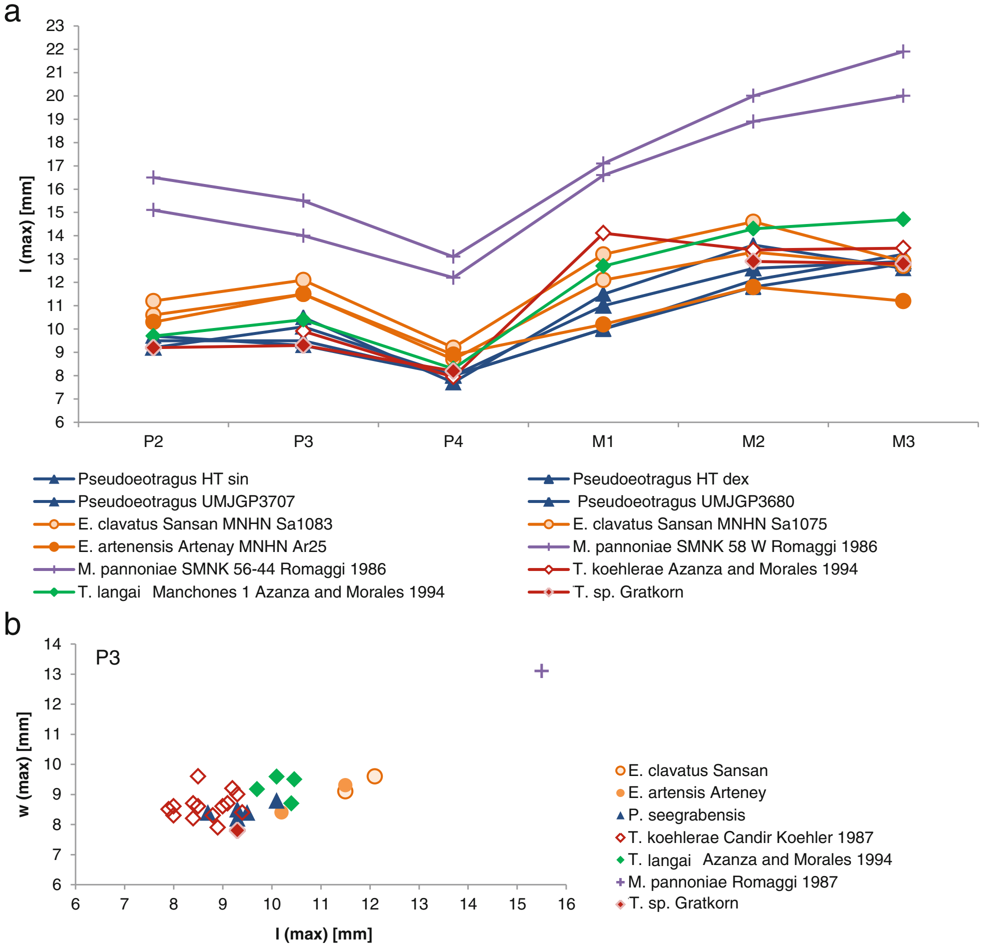


Fig. 14 Upper tooth row of *Tethytragus* sp. from Gratkorn in comparison to other Miocene Bovidae: **a** length of teeth in upper tooth row (data own measurement or after reference given), **b** bivariate plot of P3 (own measurement or after citation given)

locality Abocador de Can Mata (DeMiguel et al. 2012), which is contemporaneous with the Gratkorn locality and could represent the same species. The record of *Tethytragus* sp. is therefore well in accordance with the stratigraphic range of the species.

Palaeoecological characterisation

With a body mass of about 27–29 kg (min: 27.4 kg, max: 29.1 kg; *n*=2), *Tethytragus* sp. from Gratkorn is one of the medium-sized ruminants from the locality. *Tethytragus koehlerae* from the locality Çandir is classified as adapted to humid shrubland, feeding on a wide variability of soft plants, and maybe even sometimes showing an omnivore diet (Köhler 1987, 1993). Following Köhler (1993), most postcranial characters point to an open habitat, but she also notes indications for a wooded or even mountainous habitat, thus defining a more generalistic species. However, the metatarsal of *Tethytragus koehlerae* from Çandir is classified by her as typical for wooded or more open environment. The strongly developed sulcus dorsalis and the gradual and not abruptly distal width increase in the specimen from Gratkorn would fit well with this reconstruction. Some features observed on the metatarsal of *Tethytragus* sp. from Gratkorn, such as the “v” shaped intertrochlear incision, the dorsally and plantarily set off condyles and the moderately developed area for the extensor tendon, would be in contrast more characteristic for more mountainous habitats (Köhler 1993). As we so far lack further postcranial material of the species, a more precise locomotional adaptation cannot be given, and we thus assume a certain degree of variability in the locomotion of *Tethytragus* sp. from Gratkorn, comparable to the specimens from Çandir, and tentatively assume that it possessed some adaptations to mountainous environments. Stable isotope analysis ($\delta^{13}C$ and $\delta^{18}O$; Aiglstorfer et al. 2014a, this issue) reconstruct canopy feeding (feeding in the upper part of the forest, where evaporation is higher) for *Tethytragus* sp. This could be accomplished for a medium-sized ruminant species with the capability of climbing and jumping, as known also for caprine bovids in mountainous regions (Leinders 1979), enabling it to reach vegetation in higher levels of a wooded environment. With the close vicinity of the Alpine mountain chain, the adaptation of one ruminant species to a more mountainous habitat is not unlikely. With a $^{87}Sr/^{86}Sr$ value very close to the local ratio, *Tethytragus* aff. *koehlerae* can be considered as a permanent resident of the locality, and thus was most likely able to cope with seasonal variations in its diet (for further discussion, see Aiglstorfer et al. 2014a, this issue).

Ruminantia gen. et sp. indet.

Material : UMJGP 204721 (fragment of a humerus sin.), UMJGP 210695 (distal half of a femur dex.)

Description and comparison

Most of the unidentified postcranial elements from Gratkorn do not allow a proper description and assignment due to fragmentary preservation (furthermore, some specimens are not so far sufficiently prepared to allow an affiliation) and are therefore not described here. Two specimens, either assignable to *E. furcatus* or *Tethytragus* sp., are displayed, and with further comparison material they might be assigned to one of these species.

A fragment of a **humerus** sin. (UMJGP 204721; Fig. 11m; Dtdf = 27.5; Dtd ~31) is similar to the humeri of *E. furcatus* described above, but mediolaterally wider mainly due to the widening and shallowing of the medial, larger condyle. Furthermore, the fossa at the mediodistal rim of the medial condyle is more pronounced and deeper than in *E. furcatus*. Following Heintz (1970), the ratio of 0.55 [proximodistal width (15 mm) of the medial trochlear depression versus transversal width of the trochlea (27.5 mm)] can be observed both in Cervidae and Bovidae (for details, see discussion above). Morphological features allowing a distinction from Cervidae and assignment to Bovidae for post-Miocene species (medial depression in distal view not more caudally than the epicondylus lateralis and the external crest of the trochlea not as distinct as in Cervidae; Heintz 1970) are not as distinct in the Miocene species. Both characters can be observed in one of the humeri of *E. furcatus* from Gratkorn. As the humerus (UMJGP 204721) described here is different in morphology from the humeri assigned to *E. furcatus*, but cannot be assigned to Bovidae without reservations, it is left at the moment in open nomenclature as Ruminantia gen. et sp. indet.

The distal half of a **femur** dex. with strong biting marks on the medial and lateral sides of the trochlea patellaris (UMJGP 210695; Fig. 11n) is weathered and fractured. Both condyles are well developed, the fossa intercondylica is moderately deep and less pronounced than in modern Cervidae (see, e.g. Gailer 2007, fig. 20). The specimen shares with Cervidae [e.g. *Euprox* vel *Heteroprox* from Steinheim a. A. (GPIT/MA/3005 and 3006)] a depression on the proximal edge of the condylus lateralis and a cavity on the proximolateral edge of the condylus medialis. With DTd between 35 and 36 mm and a DAPd larger than 38 mm, the specimen is in the lower range of variability of *Euprox* vel *Heteroprox* from Steinheim a. A. (GPIT/MA/3005 and 3006) and larger than *D. crassum* from Sansan (Morales et al. 2012) and Steinheim a. A. (SMNS 4950), but smaller than *E. furcatus* from Przeworno (Czyzewska and Stefaniak 1994). As no femur of *Tethytragus* sp. was available for comparison, and as we cannot estimate the degree of sexual dimorphism in the dimensions of limb bones for *Euprox furcatus*, UMJGP 210695 is left in open nomenclature as Ruminantia gen et sp. indet.

Summary

With a minimum number of 34 individuals (Havlik et al. 2014, this issue), ruminants comprise the most abundant large mammal group from the Late Middle Miocene Gratkorn locality. As, up to now, only isolated and rare remains have been recorded in Central Europe from the late Middle Miocene, the locality fills a gap between the records from the earlier Middle Miocene and the Late Miocene. *Euprox furcatus* is the most abundant large mammal found at the locality, while *Dorcatherium naui* is the second most frequent species. Moschids are represented by some remains of *Micromeryx flourensianus*, and the first hints are given for a Central European occurrence of *Hispanomeryx*. In addition, sparse remains confirm the presence of Palaeomerycidae gen. et sp. indet. and the bovid *Tethytragus* sp. Besides the record of *D. naui*, the ruminants from Gratkorn fit well into a typical late Middle Miocene assemblage. The specimens from Gratkorn comprise the first evidence for *E. furcatus* and *M. flourensianus* from the Styrian Basin. *E. furcatus* is well in accordance with the Middle Miocene records from Steinheim a. A. (Germany) and Przeworno (Poland), and no unambiguous features could be found in the dentition to distinguish it from the early to middle Middle Miocene species *Heteroprox larteti*. *M. flourensianus* from Gratkorn is most similar in morphology to conspecific material from Atzelsdorf (~11.1 Ma), and distinct from the type material from Sansan (~14.5–14.0 Ma) by a less-pronounced external postprotocristid and a slightly higher tooth crown height. Although the assignment of younger *Micromeryx* findings from Central Europe to the species *M. flourensianus* cannot be challenged with the scarce material from Gratkorn and the so far missing scientific descriptions of the type material from Sansan and from the rich locality Steinheim a. A., the morphological change from early to late records inside the species can be mentioned.

The record of *D. naui* from Gratkorn is one of the stratigraphic oldest described so far, but well in accordance in morphology and dimensions with Late Miocene representatives of the species. The record of *D. naui* from Gratkorn thus does not support the idea of

D. naui evolving out of *D. crassum*. In comparison with other tragulid records from the Miocene of Europe, it rather enforces the assumption that *D. naui* has to be considered part of a phylogenetic lineage, together with *D. guntianum*, characterised by (1) a bicuspid p2/d2, (2) a tricuspid p3 with a less dominant mesolabial conid than in *D. crassum*, (3) a p4 with a more complex posterior valley, (4) more selenodont, more slender and higher crowned lower molars, (5) a labially turned third lobe in the lower m3, as well as (6) upper molars with less bulky styles than in *D. crassum*, and (7) a non-fusion of tibia and malleolus lateralis. This lineage is distinct from the lineage including *D. crassum*, *D. peneckei*, and *D. vindebonense* (see also Rössner and Heissig 2013 and others), which show, e.g. more bunoselenodont and lower crowned dentition, a tricuspid p3 with a dominant mesolabial conid, and a fusion of tibia and malleolus lateralis.

Since ruminants are the most abundant large mammals in Gratkorn, they are important for ecological considerations of the respective ecosystem. While the mostly subcanopy browsing *E. furcatus* was not a permanent resident of the locality and temporarily inhabitated areas in the South (perhaps the Styrian Basin), isotopic measurements indicate that the probably browsing and facultative frugivore *D. naui* and the canopy browser *Tethytragus* sp. (Aiglstorfer et al. 2014a, this issue) were more or less permanent residents at the locality and thus most likely were able to cope with seasonal variation of the diet. A caprine-like postcranial adaptation could have enabled *Tethytragus* sp. to canopy browsing and furthermore to greater flexibility concerning food supply in comparison to the cervid *E. furcatus*. The small moschid *M. flourensianus* assumably was a browser with a considerable intake of fruits or seeds and occasional grazing. Due to the scarce remains of ?*Hispanomeryx*, a distinctive ecological niche cannot be reconstructed. Most likely, it exhibited a similar ecology as *M. flourensianus*, but, as indicated by the different body sizes (Sánchez et al. 2010a), the two sympatric moschids probably occupied different niches. Due to limited material, no ecological niche can be reconstructed for the Palaeomerycidae gen. et sp. indet. from Gratkorn, but taking into consideration data for other members of the family (e.g. Köhler 1993; Tütken and Vennemann 2009; Rössner 2010), it might represent a canopy browser, which, due to its large size and the possible limitation of available biomass at the locality, was not a permanent resident at Gratkorn but must have displayed a wider habitat range.

Acknowledgements The authors are indebted to P. Havlik for fruitful discussions and correction of the manuscript. M.A. wants to thank S. Kötter, A. Tröscher and A. Beckmann for their help in the search for comparison material. J van der Made, J. Morales, I. Sánchez (Museo Nacional de Ciencias Naturales, Madrid), E. Heizmann (SMNS), B. Azanza (Universidad de Zaragoza), N. Spassov (NMNHS), N. Heckeberg (SNSB-BSPG and LMU München, Department of Zoology Cambridge), F. Fack, G. Metais, B. Mennecart, M. Pickford (MNHN) and T. Wiedl (University of Graz) are thanked for help and fruitful discussions. D. Vasilyan, J. Prieto (both University Tübingen) and F. Witzmann (Museum für Naturkunde Berlin) are thanked for taking pictures of specimens for comparison. M. Gross (UMJGP), U. Göhlich (NHMW), D. Nagel (IPUW), L. Costeur (NMB), C. Argot (MNHN), G. Scharfe (IGM), D. Alba (ICP), R. Ziegler (SMNS), M. Rummel (NMA), H. Lutz (NHMM), T. Engel (NHMM), H. Stapf (SSN), J. Rösinger and E. Weber (both University Tübingen, Zoological Collection), N. Spassov and L. Hristova (NMNHS), E. Bernard (BMNH), and P. Havlik (GPIT) are thanked for access to comparison material. W. Gerber (University Tübingen) is thanked for taking pictures, P. Havlik, M. Gross, H. Luginsland (GPIT), R. Ellenbracht (GPIT), H. Stöhr (GPIT) N. Winkler (UMJGP), J. Fuß (GPIT) are furthermore thanked for preparation or great support in preparation of the material. This research received support from the SYNTHESYS Project (FR-TAF-1892) which is financed by the European Community Research Infrastructure Action under the FP7 "Capacities" Program. B. Azanza and L. Costeur greatly helped to improve the manuscript with careful reviews and helpful advice. And last but not least the authors want to thank students and volunteers from Graz, Munich and Tübingen for their help in excavations from 2005 to 2013.

Appendix: Historical context for the description of the species *Dorcatherium naui* and considerations on species validity of different *Dorcatherium* species

The genus *Dorcatherium* was erected by Kaup in 1833 in a letter to Prof. Bronn (published in *Neues Jahrbuch für Mineralogie, Geognosie und Petrefaktenkunde*, 1833, p. 419), on a ruminant mandibula with p3–m3 (and alveolae for p1–2) from Eppelsheim (Rheinland-Pfalz, Germany), based on the presence of four premolars, and the rostral extension of the premolar to the level of the symphysis. Due to the resemblance of tooth morphology to that of a deer, he chose the name *Dorcatherium* (ἡ δορκάς greek for gazella, deer). In the same letter, he erected the type species, which he named *naui* after his friend, Geheimrat von Nau. The catalogue of gypsum casts of the Palaeontological Collection in Darmstadt (Kaup and Scholl 1834) refers to the mandibula, described in 1833, and a fragment of a maxilla with P4–M3. Casts of both were sent to Berlin, Bonn, Frankfurt, London, Lyon, Paris, Strasburg, Stuttgart, and Zürich (Kaup and Scholl 1834).

The other medium-sized *Dorcatherium* species besides *D. naui*, *Dorcatherium crassum*, is more common in the Miocene of Europe. It was erected by Lartet (1851) as ?*Dicrocerus crassus* and he had already noticed the similarity of the upper canines with those in chevrotains (at that time seen as close relatives of *Moschus* and *Moschus* as a cervid genus; Milne Edwards erected the family Tragulidae in 1864). The first description is often cited as *D. crassum* (Lartet, 1839), but no indication can be found in any of the works of Lartet published in 1839 for the species name "*Dorcatherium* *crassum*" nor in the first mentioning of remains of the species by Blainville (1837): "Des dents canines supérieures d'un petit ruminant sans bois ou à bois pédonculé des sous-genres moschus ou cervulus;" (Blainville 1837, p. 425) (for detailed discussion of the scientific history concerning the species, see Morales et al. 2012). With *D. crassum*, Milne Edwards (1864) included a fossil species in his newly erected family Tragulidae, together with the modern genera *Hyemoschus*, and *Tragulus* (including *T. meminna* which is considered today to represent a third tragulid genus, *Moschiola*), but affiliated it to the genus *Hyemoschus*. Although he observed the similarity between his *Hyemoschus crassus* and *Dorcatherium naui*, he did not include the latter in the Tragulidae due to the presence of a p1, which is completely reduced in the modern representatives of the family. Finally, Schlosser (1916) found sufficient morphological accordance of both species to affiliate *Hyemoschus crassus* to the genus *Dorcatherium*.

Today, five *Dorcatherium* species are generally accepted from the Miocene of Europe, differing in dimensions, dental and postcranial morphology and stratigraphic range (Fig. 1): the small-sized *D. guntianum* von Meyer, 1846 (late Early to Middle Miocene; MN 4–7/8; Seehuber 2008; Sach and Heizmann 2001; Rössner and Heissig 2013), the medium-sized *D. naui* (late Middle to Late Miocene; MN 7/8–11; Czyzewska and Stefaniak 1994; Rössner 2007, 2010; Alba et al. 2011; this publication) and *D. crassum* (Lartet,1851) (late Early to Middle Miocene; MN 4–7/8; Eronen and Rössner 2007; Alba et al. 2011; Rössner and Heissig 2013), the larger-sized *D. vindebonense* von Meyer, 1846 (late Early to Middle Miocene; MN4–6; Thenius 1952; Sach and Heizmann 2001; Rössner 2007, 2010; Rössner and Heissig 2013), and the large-sized *D. peneckei* (Hofmann 1893) (early Middle Miocene; MN5–6; Rössner 2007, 2010; Rössner and Heissig 2013).

D. puyhauberti, Arambourg and Piveteau, 1929 (Late Miocene; MN9–13; Gentry et al. 1999; Rössner and Heissig 2013) and *D. jourdani* (Déperet, 1887) (Late Miocene; MN 9–11; Gentry et al. 1999; Rössner and Heissig 2013) have been documented only rarely, with only a few specimens, which possess no unambiguous features distinguishing them from other European species and could be synonymous to *D. guntianum* and *D. naui*, respectively (for further information, see discussion in the section on *Dorcatherium naui* of this publication).

D. rogeri, erected by Hofmann in 1909 due to a misunderstanding in von Meyer (1846), must be considered synonymous with *D. vindebonense* (Thenius 1952). The quite small *D. bulgaricum* Bakalov and Nikolov, 1962 from the West-Mariza-Basin (?Pliocene, Bulgaria; Rössner 2007) was erected on two mandibulae with m1–3. Although both specimens show clearly developed internal postmeta- and postprotocristids, the assignation to the genus *Dorcatherium* is ambiguous. As far as it could be observed on the figures in Bakalov and Nikolov (1962; originals supposed to be lost), the specimens possess a strongly split posthypocristid, especially in the m3. This has so far been described only in the m3 of *Dorcatherium* cf. *pigotti* from Arrisdrift (basal Middle Miocene; Morales et al. 2003). In any case, the splitting of the posthypocristid is much stronger in *D. bulgaricum* than the minor splitting observed in *D. crassum* (Alba et al. 2013) and in *D. naui* from Gratkorn. Furthermore, *D. bulgaricum* possesses a rudimentary paraconid. "A small accessory cusplet" is described by Pickford (2002, p. 97) only in the Early Miocene *D. iririensis* from Africa. However, with a small hypoconulid in m2 and a rounded lingual wall in P4, the latter also differs significantly from other *Dorcatherium* species. A clearly developed paraconid can be observed, for example, in the lophiomerycid *Zhailimeryx* (Guo et al. 2000). Morales et al. (2012) also observed more similarities in *D. bulgaricum* to the Oligocene genera *Lophiomeryx* Pomel, 1853 and *Cryptomeryx* Schlosser 1886 (synonymised with *Iberomeryx*; Métais et al. 2001; Mennecart et al. 2011) than to other *Dorcatherium* species. The stratigraphic age of *D. bulgaricum* is furthermore ambiguous and could also be Paleogene (M. Böhme, personal opinion). We thus did not consider the species *Dorcatherium bulgaricum* in our discussions.

The Miocene tragulid genus *Dorcabune* Pilgrim, 1910 is so far only known, but with several species, from Asia (Rössner 2007). As *Dorcatherium* and *Dorcabune* overlap in morphological key features, a revision of the two genera would probably result in at least two morphotypes of Miocene tragulids with a differentiation into more bunodont (including *D. crassum, vindebonense* and *peneckei*) and more selenodont forms (including *D. naui* and *guntianum*; Rössner 2007 referring also to Mottl 1961; Fahlbusch 1985; Qui and Gu 1991). Other Miocene tragulid genera described from Asia are *Siamotragulus* Thomas et al., 1990 and *Yunnanotherium* Han, 1986.

Five *Dorcatherium* species have been recorded from the Miocene of Africa : *D. songhorensis* Whitworth, 1958, *D. pigotti* Whitworth, 1958, *D. iririensis* Pickford 2002 and *D. chappuisi* Arambourg, 1933, as well as a second tragulid genus, *Afrotragulus,* with the species *A. parvus* (Witworth, 1958) and *A. moruorotensis* (Witworth, 1958) (Sánchez et al. 2010b).

To get a better idea about the relationships of and faunal exchanges between Asian, African and European Miocene tragulids, a revision of the different taxa and lineages as also proposed in the section on *Dorcatherium naui* in this publication and by Sánchez et al. 2010b is surely needed.

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