

New records of *Dorcatherium guntianum* (Tragulidae), stratigraphical framework, and diphyletic origin of Miocene European tragulids

Gertrud E. Rössner · Kurt Heissig

Received: 30 November 2012 / Accepted: 20 May 2013 / Published online: 16 November 2013
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Abstract Seven hitherto unpublished *Dorcatherium guntianum* teeth from the Early Miocene of Germany are described. Morphology and size of the teeth are documented in detail and taxonomic affiliation is assessed based on comparisons to type materials of European tragulids. The fossils represent one of the earliest European *Dorcatherium* records and the oldest unequivocal evidence of *D. guntianum* from Germany. A review of the European *Dorcatherium* occurrence pattern suggests that a bunoselenodont and a selenodont lineage immigrated into Europe simultaneously from the East or Southeast, and corroborates the interpretation of the genus as being diphyletic. Moreover, our data add support to immigration scenarios that have been linked with the emerging freshwater wetlands, which formed as a result of the regression in the Western Paratethys.

Keywords Northern Alpine Foreland Basin · Early Miocene · Günzburg-Umgehungsstrasse · Upper Freshwater Molasse · Systematics · Palaeobiogeography

Abbreviations

BSPG	Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany
aw	Anterior width
d	Lower deciduous premolar
D	Upper deciduous premolar
dex	Dextral
l	Length
m	Lower molar
M	Upper molar
pw	Posterior width
sin	Sinistral
w	Width
GER	Gertrud E. Rössner

Editorial handling: D. Becker & D. Marty.

Electronic supplementary material The online version of this article (doi:10.1007/s00015-013-0132-x) contains supplementary material, which is available to authorized users.

G. E. Rössner (✉) · K. Heissig
SNSB—Bayerische Staatssammlung für Paläontologie und Geologie, 80333 Munich, Germany
e-mail: g.roessner@lrz.uni-muenchen.de

G. E. Rössner · K. Heissig
Department für Geo- und Umweltwissenschaften,
Ludwig-Maximilians-Universität München (LMU),
80333 Munich, Germany

G. E. Rössner
GeoBio-Center, Ludwig-Maximilians-Universität München
(LMU), 80333 Munich, Germany

1 Introduction

Tragulidae are a clade of ruminant artiodactyls that is considered to have branched off the ruminant stem lineage during the Late Eocene (Métais et al. 2001; Hernández-Fernández and Vrba 2005) or Late Oligocene to Early Miocene (Hassanin et al. 2012) based on morphological and/or molecular evidence. Among the living Ruminantia, tragulids are graded the most ancestral group (e.g. Webb and Taylor 1980; Janis and Scott 1987; Hernández-Fernández and Vrba 2005; Hassanin et al. 2012). In contrast to their Recent disjunct and restricted distribution in tropical Africa and Asia (Meijaard 2011), the Miocene fossil record

reflects a wide distribution of these animals throughout the Old World, including Europe (Pickford 2001; Rössner 2007). The genus *Dorcatherium* constitutes a major part of the Miocene tragulid record (Janis 1984; Thenius 2000: 182; Pickford 2001; Rössner 2007) and the entity of tragulids from the Miocene of Europe (which is in urgent need of revision, however, this is beyond the scope of this paper) (Mottl 1961; Fahlbusch 1985; Gentry et al. 1999; Rössner 2007).

Dorcatherium guntianum is one of the tragulid species known from the Lower and Middle Miocene of central and Western Europe. Its frequent appearance, although with only a few specimens per fauna, made it a constantly listed species in the context of systematic exploration of the terrestrial Miocene. However, illustrations of *D. guntianum* specimens in the literature are rare (see synonymy list below) and usually only show a limited number of the skeletodental components. The most extensive configuration to date has been provided by Sach (1999 pl. 14 fig. 1-8). Interestingly, Roger (1902:5) refers to *D. guntianum* as the more abundant species compared to the congeneric *D. crassum*. However, other investigations conducted subsequently during the last century have not supported Roger's (1902) conclusion. For example, among the most extensive *D. crassum* material described to date (Viehhausen, Germany, Rinnert 1956; Sandelzhausen, Germany, Rössner 2010; Sansan, France, Morales et al. 2012), no remains of *D. guntianum* occur, even though this material derives from strata, which fall within the range of

D. guntianum. Indeed, there is a lot of collected, but hitherto unpublished *D. guntianum* material in various museum collections (personal observation GER, included in online resource 2), which might enhance the current knowledge in the near future. The most extensive collection of fossils of *D. guntianum* thus far comes from Hambach 6C (Lower Rhine Embayment, Germany, late European Land Mammal Zone MN5, Mörs et al. 2000; systematic description of the specimens not yet completed; Rössner and Mörs in prep.). The biochronological range of *D. guntianum* has been indicated in Fahlbusch (1985), Gentry et al. (1999), and Rössner (2007) as MN4 to MN6 (latest Early to middle Middle Miocene) based on literature search and collection data (Eronen and Rössner 2007). Recently, Seehuber (2009) presented evidence suggesting that this taxon even extends into MN8 (late Middle Miocene).

The species *Dorcatherium guntianum* was established by von Meyer (1846: 472), who recognized that it is morphologically equal but smaller than the type species *Dorcatherium nauii* Kaup, 1833 (figured and described in Kaup 1832–1839 part V and plates 21–25). However, the species has not been systematically analysed to date, although it has been reported a typical faunal element of the European Miocene (Fortelius 2012).

In this paper we examine *D. guntianum* teeth found at the fossil site Günzburg-Umgehungsstrasse (Reichenbacher et al. 1998: 137) (Figs. 1, 2), which has a well-known stratigraphical context (Reichenbacher et al. 1998), and is located geographically and stratigraphically close to the

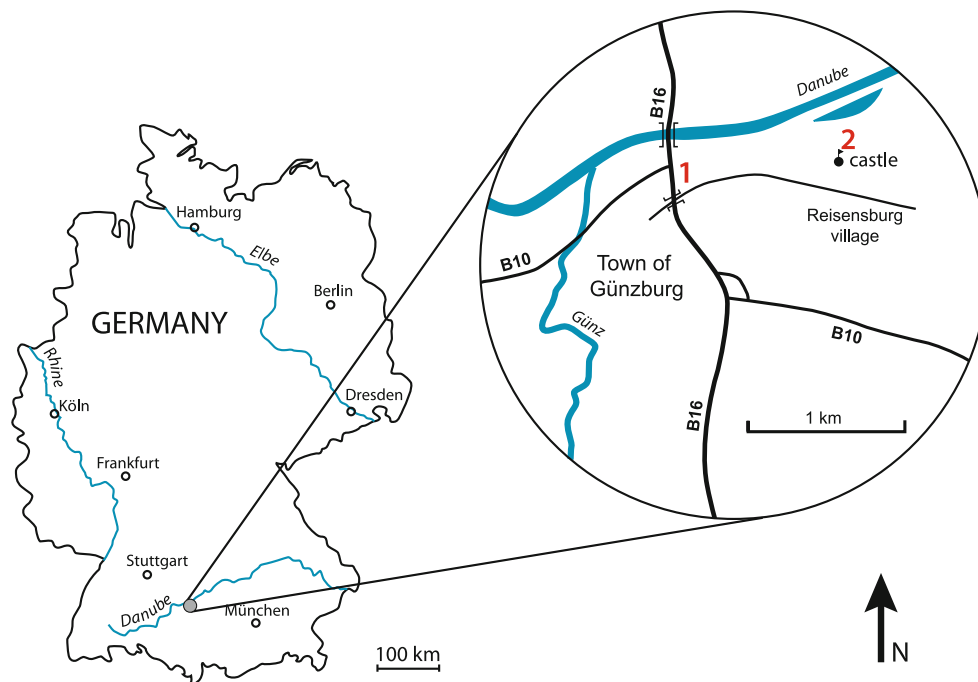
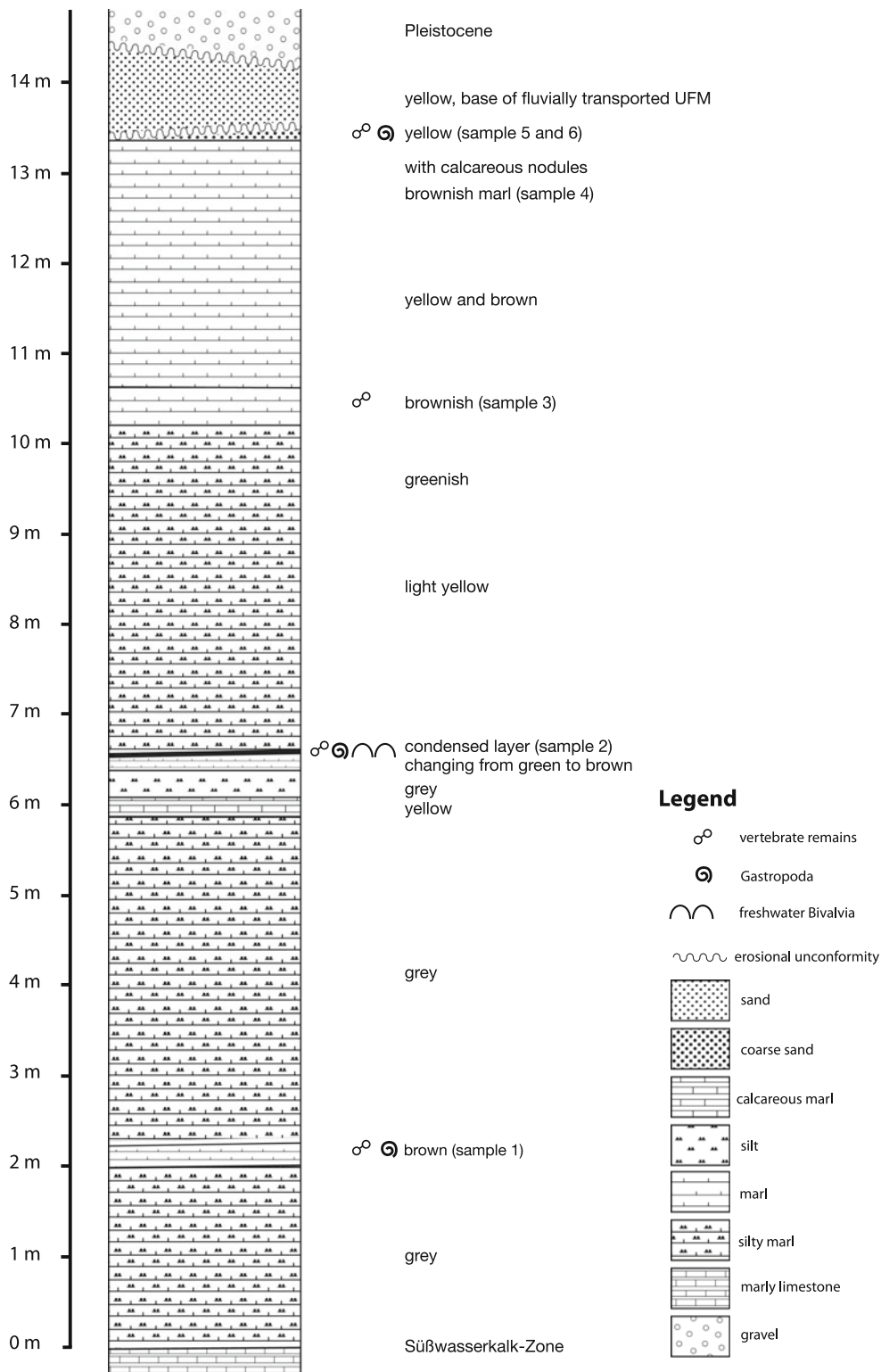


Fig. 1 Locations of the sites Günzburg-Umgehungsstrasse (1) (described in this paper) and the nearby Reisenburg (2) type locality of *D. guntianum*

Fig. 2 Composite section of the roadcut at Günzburg-Umgehungsstrasse. UFM Upper Freshwater Molasse



type locality of the species (Reisensburg, see below and Fig. 1). Within this well-known framework, these teeth constitute another unequivocal record of *D. guntianum* from the Miocene of Europe, and are important evidence of the Early Miocene tragulid dispersal and

palaeobiogeography. The teeth thus provide a valuable addition to our knowledge of the evolutionary history of the species as well as of the European tragulids in general and allow that new hypotheses can be made with regard to phylogeny and immigration scenarios of these animals.

With this study we commemorate the late Jean-Pierre Berger, whom we remember as an excellent scientist and marvellous colleague, and who has devoted a substantial part of his scientific life to the understanding of the developmental history of Central European Basins with regard to geology and biology aspects. His spirit and passion strongly influenced research in this field over the past 25 years.

2 Materials and methods

In the years 1995 and 1996, road constructions for a new portion of the highway B16 around the town of Günzburg (Bavaria, Germany) gave access to a section of the basal deposits of the Upper Freshwater Molasse (Reichenbacher et al. 1998) (Fig. 2). This section, called Günzburg-Umgehungsstrasse, has been logged, and is described and figured in detail in this study for the first time (Fig. 2). Several dozens of kilograms of samples have been taken by the authors from different places in the section (Günzburg-Umgehungsstrasse samples 2, 4, 5, 6; see Fig. 2) and screen-washed. The residues have been picked and yielded mainly gastropod and microvertebrate remains, but also eight isolated teeth of Ruminantia, which have been compared to type materials covering the morphological/taxonomical range in question. Seven teeth are attributed to *D. guntianum* (from samples 4, 5, and 6) and are described in detail and figured in Fig. 3. One tooth (Fig. 4) belongs to a procervuline cervid (Pecora, Ruminantia, Artiodactyla) of unknown affinity (Procervulinae indet., BSPG 1995 XII 7; listed as *Procervulus dichotomus* in the appendix of Eronen and Rössner 2007), and is not further discussed here. To assess the significance of the new *D. guntianum* with regard to the dispersal of Miocene tragulids in Europe, spatiotemporal occurrences have been compiled from observations made in several collections (see ESM captions), NOW database (dataset downloaded November 1st 2012, Fortelius 2012), and literature (Alba et al. 2011; Stromer 1928; Giersch 2004).

Measurement procedures follow Rössner (1995) (distances given in mm), and the terminology for the tooth crown elements follows Bärmann and Rössner (2011). All teeth are deposited at the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (BSPG) under acquisition collection number BSPG 1995 XII.

3 Section and geological context

The lithostratigraphical position of the fossil site Günzburg-Umgehungsstrasse at the base of the Miocene Upper Freshwater Molasse (UFM) in the southern German Northern Alpine Foreland Basin (NAFB), as well as the general sedimentological and biostratigraphical frame, and

a faunal list (excluding the procervuline cervid tooth, BSPG 1995 XII 7, Fig. 4) were published in Reichenbacher et al. (1998). The UFM is the youngest lithostratigraphic group of the Molasse sediments in the NAFB. It documents heterochronically from East to West the ultimate drying up of the Western Paratethys Sea in central Europe during the Early Miocene (Doppler 1989; Reichenbacher et al. 1998). It is widely distributed in the NAFB extension from Geneva to Vienna and composed of limnofluvial sediments.

The UFM is highly significant since it reports one of the most important sources of terrestrial fossils from the European Miocene (e.g. Rössner and Heissig 1999; Eronen and Rössner 2007; Abdul Aziz et al. 2008, 2010). The UFM documents the dawn of a vast freshwater wetland biome emerging subsequently after the Western Paratethys Sea regression (Doppler 1989 tab. 1; Reichenbacher et al. 1998). Deposits of the UFM are known to be rich in *Dorcatherium* remains, and represent one of the major provenances of this genus (Fahlbusch 1985; Rössner 2004, 2010; Eronen and Rössner 2007; Fortelius 2012).

The fossil site Günzburg-Umgehungsstrasse is situated 800 m Northeast of the town of Günzburg between the Danube and the road bridge from Günzburg to Reisingen over the newly built B 16 (48°27'40.0"N, 10°17'6.5"E). The road cut of the B 16 across the escarpment of a Pleistocene Danube terrace exposed the underlying sediments of the basal Upper Freshwater Molasse on both sides of the B 16 (Fig. 1). The lowermost three meters of the section (Fig. 2) were exposed on the western side of the road in a draining ditch, while the rest of the section was exhibited on the eastern side of the road cut. The section covers the sequence above the topmost stratum of the lowermost, partly calcareous strata of the UFM (Süßwasserkalk-Zone, Doppler 1989, tab. 1) to the basal, fluvial sands of the UFM (Fig. 2). It corresponds to the so called Limnic Series of the Upper Freshwater Molasse (Doppler 1989, tab. 1), which, close to the northern margin of the NAFB, is less thick than in its more southern parts. The Limnic Series rests on the transitional strata of the underlying local brackish deposits (Kirchberger Schichten). The small micromammal fauna (see below) allows to correlate the Günzburg-Umgehungsstrasse site with the uppermost part of the European Land Mammal Zone MN4b (Central Paratethys Age Karpatian) (Heissig 1997, wherein the site is named Günzburg; Reichenbacher et al. 1998).

4 Depositional environment

Below the section (Fig. 2) a calcareous basis represents the final stage of the limnic transitional "Süßwasserkalk-Zone" composed of marly and calcareous strata of an early

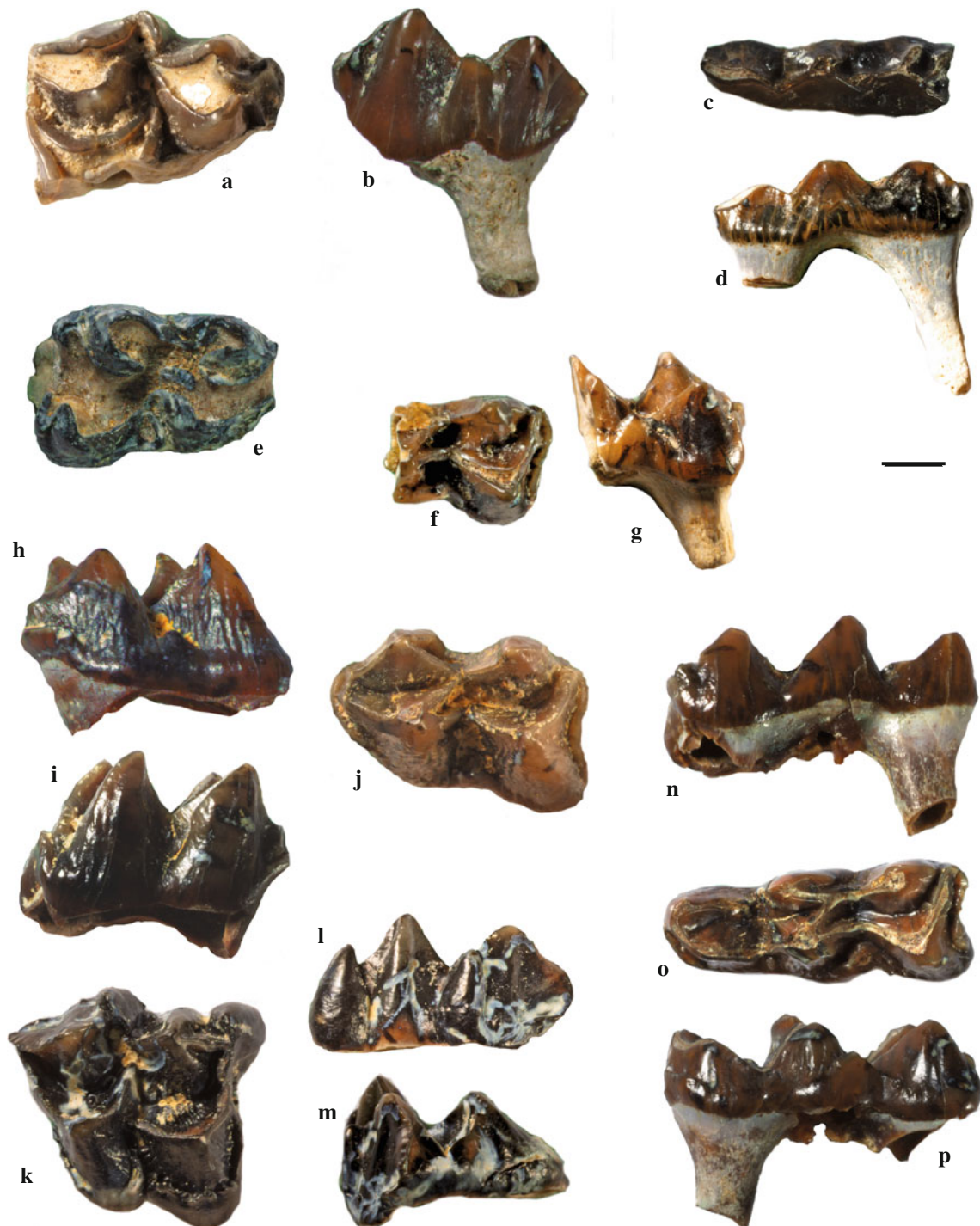


Fig. 3 The seven *D. guntianum* teeth included in this study. BSPG 1995 XII 2 incomplete dex M1/2/3, **a** occlusal view, **b** labial view. BSPG 1995 XII 3 sin d3, **c** occlusal view, **d** labial view. **e** BSPG 1995 XII 4 dex m1/2, occlusal view. BSPG 1995 XII 5 sin incomplete d4, posterior portion, **f** occlusal view, **g** labial view. BSPG 1995 XII 9 sin

m1/2, **h** labial view, **i** lingual view, **j** occlusal view. BSPG 1995 XII 6 dex D4, **k** occlusal view, **l** labial view, **m** posterior view. BSPG 1995 XII 8 sin d4, **n** lingual view, **o** occlusal view, **p** labial view. Scale bar 2 mm

Karpatian delta into the brackish sea of the Upper Brackwater Molasse, which persisted longer in the West of the NAFB than in the East (Reichenbacher et al. 1998; Berger et al. 2005). The section represents the distalmost part of

mostly overbank silt and clay deposits of an axial mica-sand-bearing stream coming from the East in a flat, swampy valley (Doppler and Schwerd 1996). The lack of paleosols in the basalmost grey-coloured deposits (Fig. 2,

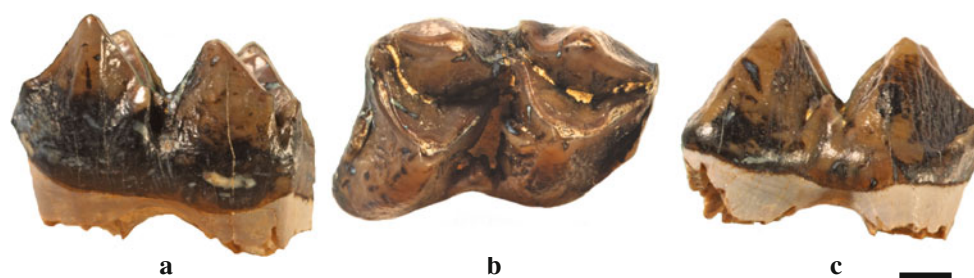


Fig. 4 Single tooth of Procervulinae indet., BSPG 1995 XII 7 dex m1/2, **a** lingual view, **b** occlusal view, **c**: labial view. $l = 11.7$, $aw = 6.7$, $pw = 8.3$. Scale bar 2 mm

0–5.7 m) indicates a more or less regular flooding of these lowlands (Schmid 2002). A brown horizon (Fig. 2, 2.0–2.2 m) is indicative of a rare period of drought, which allowed weathering, incipient soil formation, and the accumulation of organic remains (Schmid 2002). The sedimentology of the upper part of the section (Fig. 2) points to a more differentiated floodplain environment. Grey colours of fresh, unweathered material are replaced by light colours (Fig. 2, from 6.4 m onwards) with decreasing contents of silt. The variegated colour of green and brown parts in the upper part of these beds (Fig. 2, 9.9–2.9 m) are interpreted to be indicative of soil formation with oxidation from a dry surface along desiccation cracks (Schmid 2002). Occurrence of calcareous nodules (Fig. 2, 12.4–2.9 m), which postsedimentarily formed in a soil horizon, may have been the result of weathering processes or of re-sedimentation of coarse particles. Finally, the sandy sediments on top of the section reflect an increasing energy of the fluvial regime. They include the highest fossil concentration of the section within a lens of coarse sand (Fig. 2, 13.3–13.5 m), suggesting that fossils have been washed out from floodplain sediments by the meandering river. While the clay fraction was removed at the undercut slope, coarser particles (including fossils and concretions) have probably been deposited immediately on the slip-off slope or in depressions at the bottom of the river bed. The yellowish sands resting above an erosional surface (Fig. 2, 13.4 m and above) indicate the onset of the typical fluvial realm of the Older Series of the UFM (Dehm 1951). In a landscape of widely-meandering rivers, large floodplains and ephemeral lakes, nearly all sediments except fluvial sands were successively removed soon after their deposition and possibly soil formation, and thus only the sandy deposits remained. The ephemeral floodplains did not leave any sediment, except the reworked calcareous concretions and reworked fossils (Dehm 1952) in coarse sandy layers.

The UFM series of this section generally points to a regressive phase, in which the fluvial system was very distal and developed gradually to a somewhat less distal system. Since the silts and marls were deposited at the distal end of a fluvial system, these were probably sedimentated rather

rapidly. This is corroborated by the occurrence of the same fauna throughout the lower and upper horizons.

5 Fossil content and biostratigraphy

A large number of indeterminable mollusc fragments constitute the major part of the fossil content. Vertebrate remains are mainly disarticulated bones of small reptiles and amphibians. Mammal remains are comparatively scarce, but biostratigraphically significant. A more detailed faunal list, including the *D. guntianum* teeth (Fig. 3) but excluding the procervuline cervid tooth (Fig. 4), has been published in Reichenbacher et al. (1998).

Some of the mammal taxa recorded from Günzburg-Umgehungsstrasse are important biostratigraphic markers. For example *Ligerimys*, a genus of rather large eomyids, disappeared from Central Europe towards the end of MN4b (Ziegler and Fahlbusch 1986). Several other taxa are replaced in the earliest faunas of MN5 by more advanced relatives. One of these, *Megacricetodon collongensis* is exclusively known from MN4b in Central Europe (Heissig 1989: fig. 7). This species is the most frequent rodent at Günzburg-Umgehungsstrasse. In MN5, it is replaced by *Megacricetodon bavaricus* in later deposits of the UFM. Likewise, *Galerix symeonidisi* is replaced by *G. exilis*, *Microdyromys praemurinus* by *M. miocaenicus*, and *Democricetodon* aff. *francoicus* by *D. mutilus* (Fahlbusch 1964). Most of these taxa are also known from the site Rauscheröd (Ziegler and Fahlbusch 1986), which has a similar stratigraphic position in the eastern part of the NAFB, where marly sediments concordantly rest on the deltaic series of sands and gravels of the Upper Brackwater Molasse.

6 Systematic palaeontology

Mammalia Linnaeus, 1758
 Eutheria Huxley, 1880
 Laurasiatheria Waddell et al., 1999
 Artiodactyla Owen, 1848

Ruminantia Scopoli, 1777

Tragulina Flower, 1883

Tragulidae Milne-Edwards, 1864

Genus *Dorcatherium* Kaup, 1833

Type species *Dorcatherium naui* Kaup, 1833

D. guntianum von Meyer, 1846

Synonymy (not comprehensive; terminology according to Matthews 1973).

v*.1846 *Dorcatherium Guntianum*; von Meyer, p. 472.

.1884 *Hyaemoschus crassus* Lart. Spec., Toula, p. 397f, pl. III, fig. 20 a-d.

1886 *Hyaemoschus guntianus* H. v. Meyer; Schlosser pl. II fig. 12, 24, 26, 27; pl. VI fig. 22-23.

1896 *Hy. Guntianus*, v. Meyer; Roger, p. 226.

1898 *Dorcatherium guntianum*, H. v. M.; Roger, p. 32.

1900 *Dorcatherium guntianum*, H. v. M.; Roger, p. 67f, pl. III fig. 11.

v 1900 *Paläomeryx Meyeri*, Hofm.; Roger, p. 63, pl. III fig. 10.

v 1902 *Dorcatherium guntianum*, H. v. M.; Roger, p. 4ff, pl. I fig. 3.

1904 *Dorc. guntianum*; Roger, p. 19.

v 1905 *Hyaemoschus Guntianus* H. v. Meyer; Hofmann and Zdarsky, p. 588f pl. XV fig 15-17.

v 1934 *Dorcatherium guntinum* v. Meyer; Roman and Viret, p. 46, pl. VI fig. 17-19

?1955 *Dorcatherium guntianum* Meyer; Crusafont et al., p. 186, pl. VIII fig. 4.

1961 *Dorcatherium guntianum* H. v. Meyer; Mottl, p. 22ff pl. II fig. 1a-b.

?1979 *D. guntianum*; Moyà-Solà, p. 56.

v 1985 *Dorcatherium guntianum* H. v. Meyer; Fahlbusch, pl. 2 fig. 10-11.

?1987 *Dorcatherium guntianum* von Meyer, 1847; Ginsburg and Bulot, p. 70, fig. 15-16.

1999 *Dorcatherium guntianum* H. von Meyer; Sach, p. 80ff, pl. 14 fig 1-8.

?2001 cf. *Dorcatherium guntianum* H. v. Meyer; Sach and Heizmann, p. 39, pl. 5 fig. 7.

v 2009 *Dorcatherium guntianum* von Meyer, 1846; Seehuber, p. 180ff; pl. 22 fig. 1, 3, 4, 6; pl. 23 fig. 3.

Material considered (measurements see Table 1).

Günzburg-Umgehungsstrasse, sample 4 (Fig. 3): BSPG 1995 XII 2 incomplete dex M1/2/3, Fig. 3a-b; BSPG 1995 XII 3 sin d3, Fig. 3c-d; BSPG 1995 XII 4 dex m1/2, Fig. 3e.

Günzburg-Umgehungsstrasse, sample 5 (Fig. 3): BSPG 1995 XII 5 sin incomplete d4, Fig. 3f, g; BSPG 1995 XII 6 dex D4, Fig. 3k-m.

Günzburg-Umgehungsstrasse, sample 6 (Fig. 3): BSPG 1995 XII 8 sin d4, Fig. 3n-p; BSPG 1995 XII 9 sin m1/2, Fig. 3h-j.

Provenance and age. Günzburg-Umgehungsstrasse, Upper Freshwater Molasse, Older Series (according to Dehm 1951), OSM unit A (according to Heissig 1997), Sedimentary cycle OSM 0 (according to Heissig 1997), latest European Land Mammal Zone MN4b (according to Reichenbacher et al. 1998), Central Paratethys Age Karpatian (Reichenbacher et al. 1998), Mediterranean Age Late Burdigalian.

Description. All teeth are brachyodont with a selenodont ruminant morphology. Deciduous teeth are slightly lower crowned than the permanent ones. The d4s and m1/2s are characterised by an interior and exterior postmetacristid, as well as interior and exterior postprotocristid (*Dorcatherium*-fold, *Tragulus*-fold, M-structure, Σ -structure). A metastylid is absent in the latter. Labial columns of metaconid and entoconid are bent slightly towards anterior. Ectostylids are low, but pronounced. Internal postmetacristid, internal postprotocristid, and preentocristid fuse centrally. Internal postprotocristid and prehypocristid are unfused. Premetacristid and preprotocristid fuse anteriorly, constituting a rounded shape. Postentocristid and posthypocristid are unfused.

Table 1 Measurements (in mm, taken by GER) of *Dorcatherium guntianum* teeth studied herein

Collection number	Tooth	aw or w	pw	l	h
BSPG 1995 XII 2	dex M1/2/3	–	–	8.7	–
BSPG 1995 XII 3	sin d3	2.9	–	9.0	2.9
BSPG 1995 XII 4	dex m1/2	5.1	5.6	8.4	–
BSPG 1995 XII 5	sin d4	4.3	–	–	–
BSPG 1995 XII 6	dex D4	7.2	7.0	9.0	5.0
BSPG 1995 XII 8	sin d4	4.5	–	10.8	3.8
BSPG 1995 XII 9	sin m1/2	5.0	4.9	9.2	4.9

aw = anterior width, d = lower deciduous tooth, D = upper deciduous tooth, dex = dextral, h = height, l = length, m = lower molar, M = upper molar, pw = posterior width, sin = sinistral, w = total width

There is a small anterior and posterior cingulid and an additional labial cingulid in d4s. BSPG 1995 XII 8 (Fig. 3n–p) lacks a mesostylid, and the transition from mesofossa to anterior fossa is not narrowed. The anterior fossa is lined by two small labial conids, and two small lingual conids are connected to each other via cristids.

The d3 is slender and long, constituted by anterior conid, mesolabial conid, and posterolabial conid, all interconnected by crests. The anterior stylid is weak. The transverse cristid, posterolingual cristid and posterolingual stylid are short, parallel, and directed towards the posterolingual corner. The mesolingual conid is very small. The posterolabial conid is in an isolated and somewhat exposed posterior position.

The labial M-fragment shows a labially strong parastyle, mesostyle, and paraconus column. The labial end of premetaconulecrista does not contact with any of the labial cristae. There is no posterior fusion of postmetacrista and postmetaconulecrista, as well as no contact between postparacrista and premetacrista. The labial paraconus column is slightly bent towards posterior.

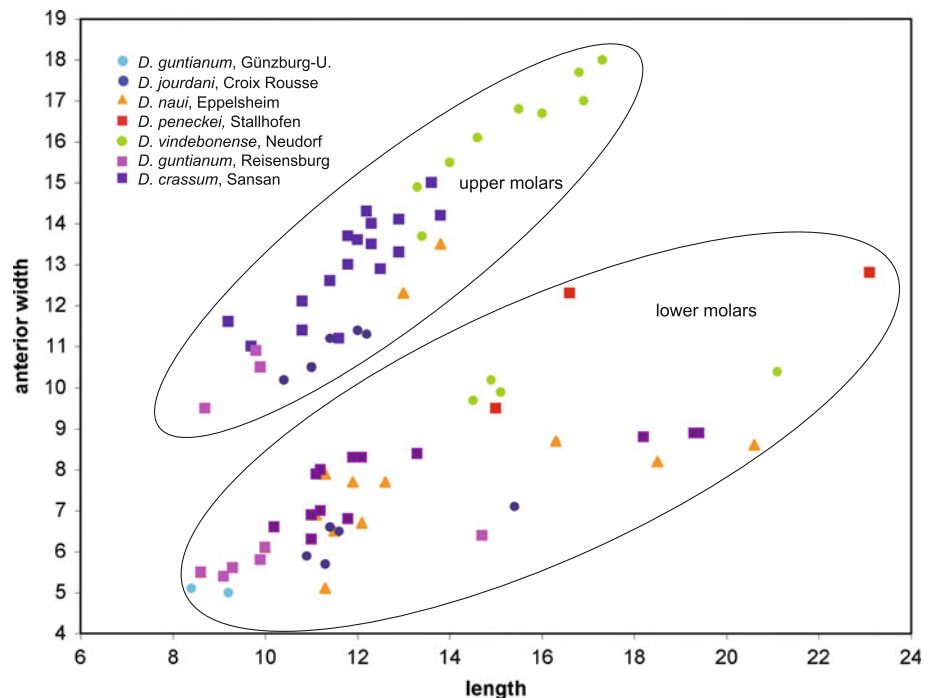
The D4 has a pronounced parastyle and trapezoid shape in contrast to upper ruminant molars in general. It exhibits a strong mesostyle and labial paraconus column. The anterior lobus is longer than the posterior lobus and the posterior lobus is wider than the anterior lobus. The postprotocrista is not fused with the premetaconulecrista. Postparacrista is in contact with the mesostyle. A strong

cingulum surrounds the protoconus basis. The cingulum around the metaconule is weakly developed.

6.1 Taxonomical affinities

The brachyodonty, together with several features of the lower molars and d4s (exterior postmetacristid, mesostylid absent), upper molar (prominent parastyle, mesostyle and paraconus column), D4 (pronounced parastyle, trapezoid shape, strong anterolingual cingulum), as well as d3 (shortness of transversal crests, absence of explicit lingual elements) are indicative of tragulids (e.g. Mottl 1961; Fahlbusch 1985; Janis and Scott 1987; Gentry et al. 1999; Rössner 2007). Among European *Dorcatherium* species the selenodont morphology of the tragulid teeth from Günzburg-Umgehungsstrasse lets exclude the affiliation to *D. crassum*, *D. vindebonense* or *D. peneckeii*, since those are all bunoseledont, but rather suggests affinities to *D. nauii*, *D. guntianum*, *D. puyhauberti* or *D. jourdani*. The molars are comparably small and show largest similarity with the size of the type material of *D. guntianum* from Reisenburg (MN4b, Schlosser 1886) including the only but incomplete upper molar (BSPG 1995 XII 2) from Günzburg-Umgehungsstrasse with $l = 8.7$ (Figs. 5, 6, online resource 1), and thus are assigned to *D. guntianum*. Deciduous teeth of *D. guntianum* from Günzburg-Umgehungsstrasse show largest similarity in size with *D. guntianum* from Reisenburg and *D. jourdani* from Croix Rouse (?MN9, Déperet 1887). Thus, the proportional difference in size of permanent and deciduous

Fig. 5 Bivariate plot of length and anterior width of upper and lower molars of *D. guntianum* from Günzburg-Umgehungsstrasse in comparison with European *Dorcatherium* type material. The only incomplete M from Günzburg-Umgehungsstrasse (BSPG 1995 XII 2, Fig. 3a, b, $l = 8.7$) corresponds to *D. guntianum* from Reisenburg type locality. All measurements taken by GER



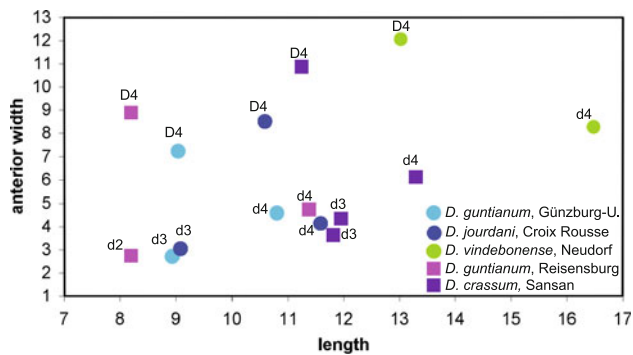


Fig. 6 Bivariate plot of length and anterior width of upper and lower deciduous premolars of *D. guntianum* from Günzburg-Umgehungsstrasse in comparison with European *Dorcatherium* type materials. All measurements taken by GER

cheek teeth in *D. jourdani* compared to *D. guntianum*, can be treated as a distinctive feature between both species.

7 Discussion

Selenodont tragulid morphology and correspondence in size with teeth of the *D. guntianum* type series (sin P3, P4, M2 and M3 from Reisenburg of the Wetzler collection, Schlosser 1886; Dehm 1984, BSPG 1881 IX) (Figs. 5, 6; Table 1, online resource 1) indicate conspecific origin of the *Dorcatherium* teeth from Günzburg-Umgehungsstrasse with *D. guntianum*.

Based on the currently known temporal range of *D. guntianum* (MN4 to MN8, see above) the MN4b fossils of *D. guntianum* from Günzburg-Umgehungsstrasse described here represent one of the oldest known record of the species. Moreover, Günzburg-Umgehungsstrasse is geographically close to the *D. guntianum* type locality Reisenburg. The stratigraphical and chronological positioning of the type locality remained controversial (Zöbelein 1983) prior to Reichenbacher (1993), Heissig (1997:538, tab. 1), and Reichenbacher et al. (1998: 136ff), who provided new data based on detailed biochronological analyses of the Reisenburg type section and the adjacent section of Günzburg-Umgehungsstrasse. According to these authors, the deposits of at Günzburg-Umgehungsstrasse are the oldest strata of the UFM yielding terrestrial vertebrates. They are correlated with the oldest part of the Reisenburg type section (Reichenbacher 1993). The underlying strata of the Reisenburg type section and Günzburg-Umgehungsstrasse consist of freshwater limestones of the Karpatian (Süßwasserkalk-Zone according to Doppler 1989 fig. 2), and below the brackish Ottnangian Kirchberger Schichten, which represent part of the local transition from fully marine to fully continental conditions. As a result, the stratigraphic framework indicates that the

D. guntianum fossils from Reisenburg und Günzburg-Umgehungsstrasse represent the oldest known tragulid remains from the UFM, and that tragulids occurred in the NAFB together with the establishment of fully continental conditions.

Within a range of 10–30 km to the West of Reisenburg type section and the fossil site Günzburg-Umgehungsstrasse several localities with even older *Dorcatherium* remains have been described. For example, the important vertebrate fossil site Langenau 1 (Sach and Heizmann 2001) is located in fluvial deposits, which are considered to represent the northern extension of the Kirchberger Schichten based on intercalations with marine clupeids (Osteichthyes) (Martini 1983; Böttcher 1987). Eggingen-Mittelhart 3 is positioned in the brackish Grimmelfinger Schichten, a channel fill incised in the Upper Marine Molasse underlying lithostrata of the Kirchberger Schichten (e.g. Reichenbacher et al. 1998; Doppler et al. 2005). Both localities are known for their vertebrate assemblages, including *Dorcatherium* (Sach and Heizmann 2001). While Langenau 1, containing *D. cf. crassum*, is correlated with MN4b, Eggingen-Mittelhart 3 contains *D. crassum* and cf. *D. guntianum*, has been biochronologically dated as MN4, but in between typical MN4a and MN4b faunas (Sach and Heizmann 2001 pl. 5 fig. 6, 7). These remains represent the hitherto earliest records of tragulids from the NAFB, but persuasive evidence of *D. guntianum* has not been provided from either of these sites to date.

No occurrence of *Dorcatherium* has been reported from Europe prior to MN4 (Rössner 1997). *Dorcatherium* fossils from MN4 (apart from those from Germany discussed above) have been described from Austria (Rössner 1998), France (e. g. Stehlin 1907; Roman and Viret 1934; Ginsburg and Bulot 1987; Ginsburg 1989), and Spain (Moyà-Solà 1979). Fossils from MN1 and MN3 come from Africa and Asia (Barry et al. 2005; Pickford 2001; Geraads 2010). Figure 7 provides an overview of the *Dorcatherium* occurrences in Europe. Consistent with the oldest records from the NAFB (see above), this overview identifies *D. guntianum*, together with *D. crassum* as the ancestral species of the Miocene tragulid dispersal in Europe, being sympatrical in the Middle Miocene with *D. vindebonense* and *D. peneckeii*. *Dorcatherium nauti*, *D. jourdani*, and *D. puyhauberti* are exclusive Late Miocene species, with the exception of recently discovered late Middle Miocene *D. nauti* from Spain (Alba et al. 2011), Poland (see Alba et al. 2011), and Austria (Gross et al. 2011). Although *Dorcatherium* has been reported from many sites in Asia and Africa, no European *Dorcatherium* species has been recorded from outside Europe. This suggests that the place of speciation for both founder species of the Miocene tragulids in Europe (*D. guntianum* and *D. crassum*), each with a specific dietary adaptation (Kaiser and Rössner

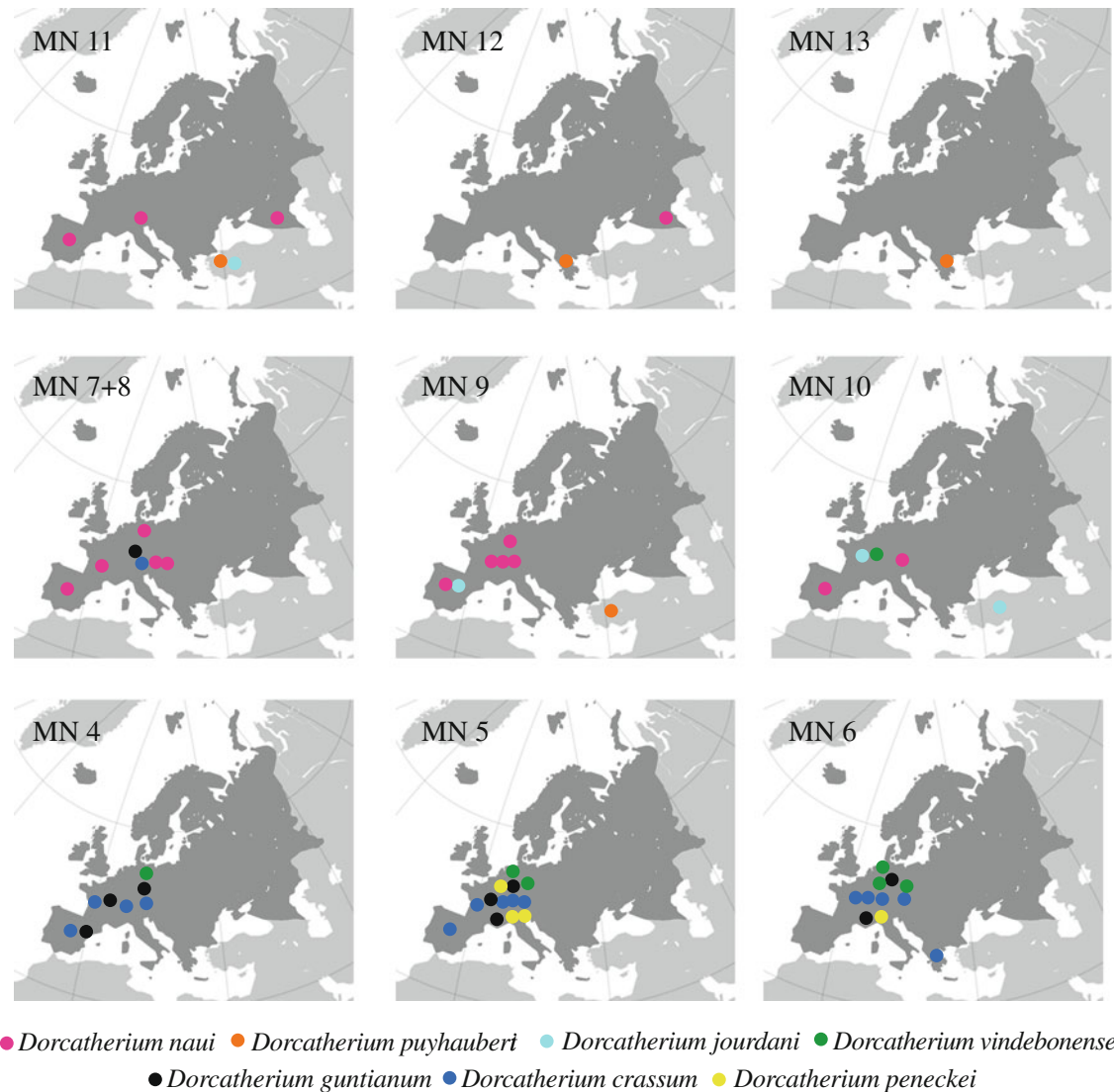


Fig. 7 Spatiotemporal occurrence pattern of European *Dorcatherium* based on literature data, NOW database (Fortelius 2012), and visited collections (see ESM 2 caption). Position of dots are symbolic and do

not reflect the precise place of occurrence. Corresponding list of *Dorcatherium* occurrences is shown in ESM 2

2007), has to be assumed within Europe. However, with respect to the two hypothetical phylogenetic lineages within the genus, (i. e. a selenodont one (molars with sickle-shaped cones/conoids; *D. guntianum*, *D. nauai*, *D. puyhauberti*, *D. jourdani*), and a bunoselenodont one (molars with cones/conoids intermediate in shape between fully rounded and fully sickle-shaped, *D. crassum*, *D. vindebonense*, *D. peneckeii*) (Mottl 1961; Fahlbusch 1985; Qiu and Gu 1991; Sánchez et al. 2010), the question arises as to whether two species independently immigrated from Africa or Asia or one tragulid species split into two lineages soon after its arrival in Europe. Since the difference in further skeletodental features, such as the fused/unfused connection of malleolar and tibia and the premolar/deciduous premolar overall morphology (personal observation

GR), is sufficiently anatomically profound, there is strong support for a diphyletic origin of European tragulids.

However, it should also be mentioned that the literature and databases record of European *Dorcatherium* (see Fig. 7, and listed in ESM 2) is problematical in part, especially if details are considered. Although apomorphies in bone and tooth morphology allow for a clear discrimination of *Dorcatherium* from other ruminants, species affiliation always is to be viewed with care. Published studies often suffer from missing comparisons with type specimens, and many inventories mentioning *Dorcatherium* specimens without illustration of the fossil remains render it impossible to scrutinise identification. Heavy wear in teeth blurs differences of bunoselenodont and selenodont morphology. For instance, this caused a long standing

confusion of similar-sized *D. crassum* and *D. nauti* (see Roger 1896; Hofmann and Zdarsky 1905; Hünermann 1983; Alba et al. 2011), which unfortunately also gained foothold in databases (Fortelius 2012) and reference works (Gentry et al. 1999). Insufficient knowledge of premolar/deciduous dentition, as well as an increase in upper molar size from M1 to M3 with interspecific size overlaps has resulted in another quality of confusion. Upper molars of selenodont *Dorcatherium* species may even be mistaken for early cervids since styles and cingula are reduced in size. Although many questions remain unresolved and large numbers of specimens remain insufficiently studied, the type materials provide good reference points in the overall palaeobiogeographic distribution of bunoselenodont and selenodont morphotypes.

European tragulid occurrences are tightly and almost exclusively associated with limnofluvial deposits, indicating an adaptation of these animals to wet habitats. Tragulids are thus virtually unknown from the many karstic fissure filling sites of Europe (Thenius 1959; Rössner 2004), where superficial open water did not form a regular environmental component. This is in accordance with the habitat preferences of extant tragulids, i.e. gallery forests along rivers or wetlands in equatorial Africa and Asia, which comprise surface water supply as a necessity since these animals have a peculiar escape behaviour by hiding under water (Dubost 1978; Meijaard et al. 2010). During the Miocene the circum-Mediterranean and Paratethys realm passed through the emergence of vast freshwater wetlands as a result of regression events linked to plate tectonics (Rögl 1998). These processes must have produced a wealth of ideal biomes for tragulids to colonise and diversify as shown for the NAFB by Rössner (2004). The deposits and rich fossil record reflect highly differentiated ecotonal mosaic environments with patches of forests, standing as well as flowing water bodies, and manifold kinds of transitions (e.g. Eronen and Rössner 2007; Merceron et al. 2012).

8 Conclusions

The *Dorcatherium guntianum* remains from the fossil site Günzburg-Umgehungsstrasse constitute a persuasive record of this Miocene Central and Western European species. Moreover, the stratigraphic frame of this provenance is well-studied, and thus we feel safe to conclude that the remains from Günzburg-Umgehungsstrasse represent one of the oldest known records of the species and the oldest known reliable record from Germany. Although the diversification and evolutionary history of the Miocene European *Dorcatherium* is far from being completely understood, a diphyletic origin can be hypothesized based on the general occurrence pattern depicting the simultaneous appearance

of *D. guntianum* and *D. crassum* in Europe. Immigration from the East and/or Southeast seems to have been facilitated by the formation of exhaustive wet habitats containing countless bodies of open freshwater.

Acknowledgments We thank Damien Becker (Porrentruy) and Kirsten Grimm (Mainz) for the invitation to contribute to this volume in memory of the late Jean-Pierre Berger. GER acknowledges the support from G. Daxner-Höck (Vienna), F. Duranthon (Toulouse), B. Engesser (Basel), V. Fahlbusch (Munich), H. Furrer (Zurich), A.W. Gentry (London), L. Ginsburg (Paris), U.B. Göhlich (Vienna), E.P.J. Heizmann (Stuttgart), M. Hugueney (Villeurbanne), D. Kälin (Zurich), M. Köhler (Sabadell), H. Luginland (Tübingen), P. Mein (Villeurbanne), S. Moyà-Solà (Sabadell), A. Prieur (Villeurbanne), B. Reichenbacher (Munich), M. Rummel (Augsburg), B. Sanchez (Madrid), O. Sandrock (Darmstadt), F. Schrenk (Darmstadt), D. Soria (Madrid), P. Tassy (Paris) during various visits to collections under their care. M. Focke, M. Schellenberger, and L. Geissler (all Munich) prepared figures. M. Krings (Munich) helped with language correction. E. Heizmann (Stuttgart) and B. Reichenbacher (Munich) gave essential comments on the manuscript and helped to improve it. Several collection visits were supported by funds from the Deutsche Forschungsgemeinschaft (DFG) (Ro 1197/3-1).

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