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New palaeontological and geological age constraints for the arrival and dispersal of Miocene tragulids (Tragulidae, Artiodactyla) in Europe

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Abstract

Miocene tragulids of Europe are known to “suddenly” appear in the fossil record during the biochronological Mammal Unit MN4 (late Early Miocene, late Burdigalian) and are commonly associated with the younger subunit MN4b. However, this is a blanket assessment what lacks more detailed investigation. In this study new *Dorcatherium guntianum* and *Dorcatherium crassum* remains from the German part of the North Alpine Foreland Basin are described and figured. The yielding site, Forsthart, is located in eastern Bavaria in the Central Paratethys facies, and well assessed in regional stratigraphy and supraregional biochronology (MN4b). Hence, it provides a further point of reference of the evolutionary history of Miocene tragulids at minimum 16.5 mya. Moreover, recent revisions of stratigraphy and European tragulid (*Dorcatherium*) occurrence data correlate the oldest German record of *Dorcatherium guntianum* with minimum 16.5 mya (subchron 5Cn.2r) and the oldest German record of *Dorcatherium crassum* / *Dorcatherium* with minimum 17.8 mya (uppermost subchron 5Dr.2r) and MN4a (what so far corresponds to the minimum appearance datum for *Dorcatherium* in Europe). Comparison with further first appearance data of *Dorcatherium* in Europe indicates a heterochronous dispersal from the East / Southeast to the West / Southwest.

Key words: Late Early Miocene, North Alpine Foreland Basin, *Dorcatherium guntianum*, *Dorcatherium crassum*, Forsthart, MN4, Germany, Western Paratethys, Central Paratethys.

Zusammenfassung

Das älteste Vorkommen miozäner Traguliden in Europa findet sich in der biochronologischen Säugetiereinheit MN4 (spätes Früh-Miozän, spätes Burdigalium) und wird als “plötzliches” Auftreten in der Regel der jüngeren Untereinheit MN4b zugeordnet. Eine solch pauschale Einstufung entbehrt jedoch einer soliden Datengrundlage. In dieser Arbeit werden neue Belege von *Dorcatherium guntianum* und *Dorcatherium crassum* aus dem deutschen Teil des Nordalpinen Vorlandbeckens beschrieben und abgebildet. Die Fundstelle, Forsthart, liegt in Ost-Bayern in der Fazies der Zentralen Paratethys, und ist gut in der regionalen Stratigraphie und der überregionalen Biochronologie (MN4b) verankert. Daher kann mit ihr ein neuer Referenzpunkt zur Verbreitungsgeschichte der miozänen Traguliden mit mindestens 16,5 Millionen Jahren vor heute festgelegt werden. Unter Berücksichtigung jüngster Revisionen der regionalen Stratigraphie und der Traguliden-(*Dorcatherium*-)Vorkommen in Europa kann außerdem das im deutschen Raum älteste Vorkommen von *Dorcatherium guntianum* mit mindestens 16,5 Millionen Jahren (Subchron 5Cn.2r) und das von *Dorcatherium crassum* bzw. *Dorcatherium* mit mindestens 17,8 Millionen Jahren (oberster Teil Subchron 5Dr.2r) und MN4a (was dem Mindestalter für das Auftreten von *Dorcatherium* in Europa entspricht) korreliert werden. Ein Vergleich dieser Daten mit den Erstauftreten miozäner Traguliden in anderen Teilen Europas weist auf eine heterochrone Ausbreitung in Europa von Osten / Südosten nach Westen / Südwesten hin.

Schlüsselwörter: Spätes Unter-Miozän, Nordalpines Vorlandbecken, *Dorcatherium guntianum*, *Dorcatherium crassum*, Forsthart, MN4, Deutschland, Westliche Paratethys, Zentrale Paratethys.

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1. Introduction

In Europe, tragulids (Tragulidae, Artiodactyla, Mammalia) were common terrestrial faunal elements in the Miocene as their widespread fossil remains (all associated with the genus *Dorcatherium*) reflect. The latter are not described to occur in fossil assemblages before the late Early Miocene (late Burdigalian) in the younger part of the Neogene European Mammal Unit MN4 (de Bruijn et al. 1992, Mein 1999a). Thus, they are interpreted to have immigrated within MN4 according to their “sudden” appearance at that time in the fossil record (see Fahlbusch 1985, Ginsburg 1989, Rössner 1997, Pickford 2001, Rössner & Heissig 2013, Clauss & Rössner 2014, Aiglstorfer et al. 2014 and references therein). This immigration event had importance for European biochronology (de Bruijn 1992; Ginsburg 1989; Rössner 1997, 1998; Made 1999; Mein 1999b; Gentry et al. 1999; Sach & Heizmann 2001), by contributing to differentiation between the older part of MN4 (often named MN4a) without *Dorcatherium* and the younger part of MN4 (often named MN4b, e.g. Heissig 1997) with *Dorcatherium*, and may be linked to the final sea retreat in the Western as well as in the western Central Paratethys realm (Pippèrr & Reichenbacher 2017) and related emergence of vast freshwater wetlands because of specific ecological adaptations (Rössner 2004, Rössner & Heissig 2013). *Dorcatherium crassum* and *Dorcatherium guntianum* are reported to be the first representatives of the two founder lineages of the European Miocene tragulid population (Fahlbusch 1985). However, when going into detail, there is uncertainty about the exact timing of the immigration event and further particulars on phylobiogeography (Rössner & Heissg 2013). In search of earliest *Dorcatherium* occurrences in Europe, well studied and thick continental lithological sequences with a highly elaborated stratigraphic/geochronologic framework can help to peg this part of the evolutionary history of these animals. The clearly diagnosable morphological characters in bones and teeth of tragulids in general and even tragulid species (e.g. see Aiglstorfer et al. 2014 and references therein) allow for the identification of scarce and fragmentary earliest Miocene tragulid occurrences.

Recently, Rössner & Heissig (2013) described the supposedly oldest known reliable *D. guntianum* record (that is younger than the oldest known *D. crassum* / *Dorcatherium* remains from Germany, see also Aiglstorfer et al. 2014: Fig. 1) and the oldest known *D. guntianum* and *D. crassum* co-occurrence from the North Alpine Foreland Basin (NAFB). The NAFB is one of the most continuous Miocene sedimentary archives in Europe composed of several lithostratigraphic "Molasse" groups (for details see Pippèrr & Reichenbacher 2017 and references therein) and a major source of knowledge on Miocene mammals (Rössner & Heissig 1999). Descriptions of tragulid fossils from the NAFB have a long history (e.g., Meyer 1846; Roger 1900, 1902; Schlosser 1886; Stehlin 1914; Hünermann 1981a, 1981b; Hünermann 1983; Fahlbusch 1985; Rössner 1998, 2002, 2010; Gentry et al. 1999; Sach 1999; Sach & Heizmann 2001; Eronen & Rössner 2007; Hillenbrand et al. 2009; Seehuber 2009, 2015). The fossils reported on in Rössner & Heissig (2013) come from upper Lower Miocene sediments at the Günzburg-Umgehungsstrasse site in western Bavaria (see Fig. 1). The sediments directly overlie brackish strata from the ultimate Paratethys regression in the NAFB and belong to the Western Paratethys facies (in contrast to the Central Paratethys facies East of Munich). They are limnofluvial deposits and the basal strata of the Upper Freshwater Molasse Group (Obere Süsswassermolasse, OSM), the youngest among the Molasse groups (for details on the stratigraphy consult Pippèrr & Reichenbacher 2017).

In the present study, I describe further fossils of *D. guntianum* and *D. crassum* coming from similarly

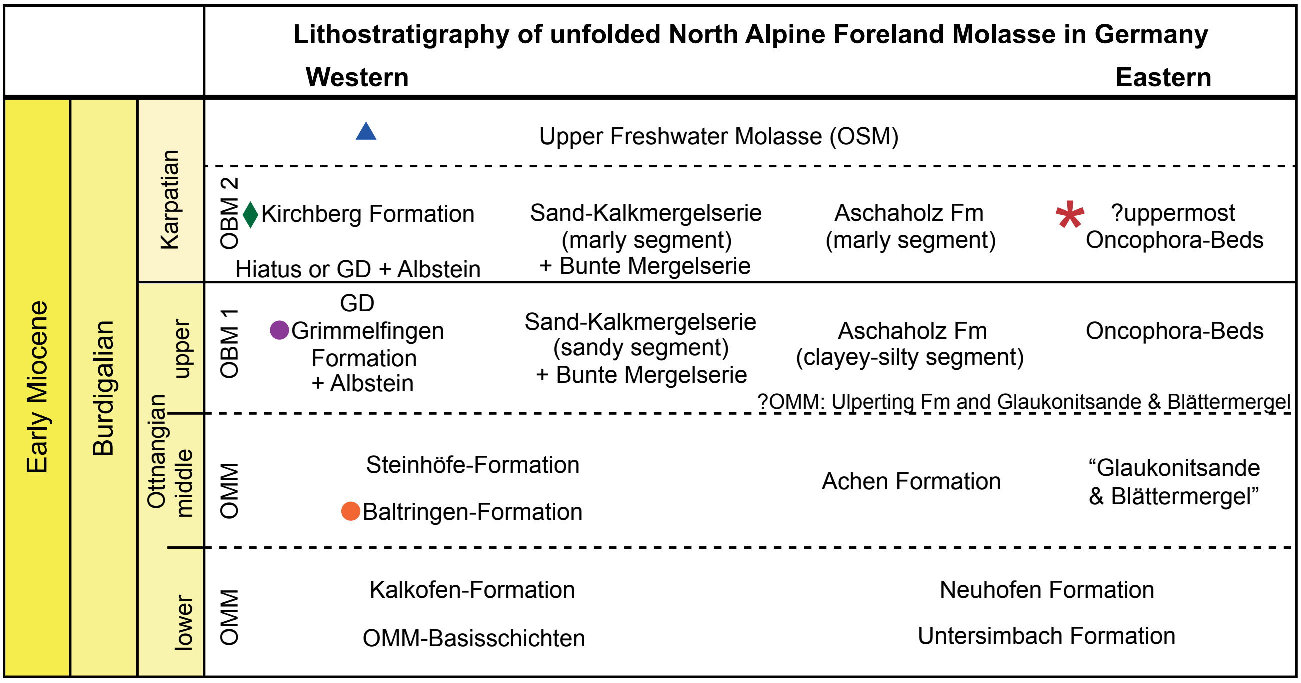

Figure 1: Lithostratigraphic position of the discussed fossil sites in the German part of the North Alpine Foreland Basin modified from Fig. 6 in Pippèrr & Reichenbacher (2017). ▲ = Günzburg-Umgehungsstrasse, ◆ = Gerlenhofen, ● = Eggingen-Mittelhart 3, ● = Sulmingen, * = Forsthart. The basis of the Baltringen Formation correlates with the basis of the middle Ottnangian at 17.8 Ma (Pippèrr et al. 2007). OBM = Upper Brackish Molasse group, OMM = Upper Marine Molasse Group.

aged limnic strata in the eastern Bavarian Central Paratethys facies (Limnische Süßwasserschichten in Ost-Niederbayern, Doppler 1989: Tab. 1; Limnische Süßwasserschichten in Östliche Vorlandmolasse, Doppler et al. 2005: Tab. 2; Lakustrische Schichten, Pippèrr & Reichenbacher 2017). The site, Forsthart, is a pivotal mammalian fossil site for stratigraphic correlation across the NAFB (see Heissig 1997, Böhme et al. 2002, Reichenbacher et al. 2013 and references therein) and received lots of attention during extensive biostratigraphic research in the Bavarian part of the NAFB and concerted efforts in Europe-wide Neogene mammal chronology in the 1980s (Ziegler & Fahlbusch 1986, Bruijn et al. 1992). The five specimens specified here are not only the first macromammals described from Forsthart, but also the first tragulid remains reported on from the uppermost Lower Miocene in SE Germany (SE German part of NAFB). The new data are discussed in the context of recent revisions of the regional stratigraphy (Reichenbacher et al. 2013, Pippèrr & Reichenbacher 2017, Sant et al. 2017) and resulting consequences for the interpretation of events around the arrival and dispersal of Miocene tragulids in Europe.

2. Material and Methods

Recently, four teeth and one astragalus of tragulids were discovered at the Staatliche Naturwissenschaftliche Sammlungen Bayerns – Bayerische Staatssammlung für Paläontologie und Geologie (SNSB-BSPG) in a cabinet containing undescribed material of the late Volker Fahlbusch (Rössner et al. 2009). They were labeled coming from the Forsthart site.

Metrical and morphological comparison was performed using the type material from Reisensburg / Günzburg (SNSB-BSPG 1881 IX, Wetzler collection; von Meyer 1846: 472, Schlosser 1886: pl. VI fig. 22, 23; Dehm 1984), and material from Günzburg-Umgehungsstrasse (Rössner & Heissig 2013), Sansan (Morales et al. 2012), Sandelzhausen (Rössner 2010), Hambach 6 (Mörs et al. 2000), Griesbeckerzell and Walda (Rössner 2002).

Measurements follow Rössner (1995) and the dental terminology recommended by Bärmann & Rössner (2011) is employed.

3. Systematic Palaeontology

Mammalia Linnaeus, 1758
Eutheria Huxley, 1880
Laurasiatheria Waddell et al., 1999
Artiodactyla Owen, 1848
Ruminantia Scopoli, 1777
Tragulina Flower, 1883

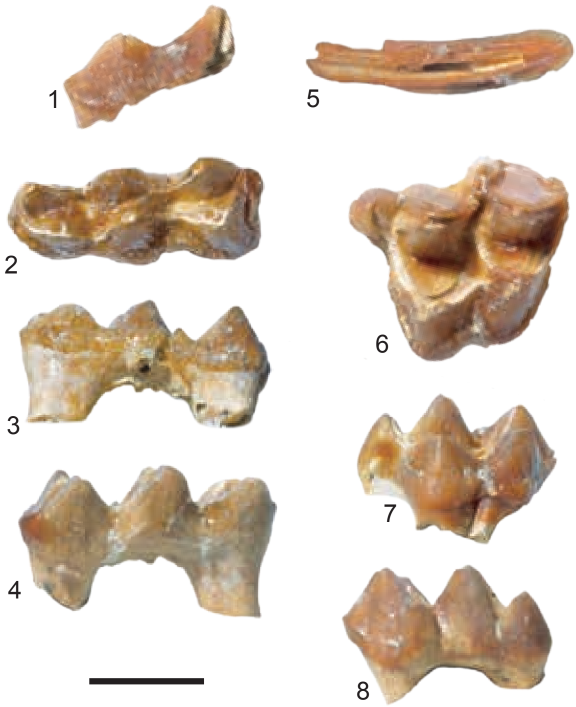

Figure 2: Tragulid teeth from Forsthart. 1) SNSB-BSPG 1959 XXVII 1116 *Dorcatherium* cf. *crassum*, right posterior d2 fragment (labial view); 2-4) SNSB-BSPG 1959 XXVII 1114 *Dorcatherium guntianum*, left d4 (2 occlusal view, 3 labial view, 4 lingual view; 5) SNSB-BSPG 1959 XXVII 1117 Tragulidae indet., left i2 or i3 (lingual view; to the left: root, to the right: crown tip); 6-8) SNSB-BSPG 1959 XXVII 1115 *Dorcatherium guntianum*, left D4 (6 occlusal view, 7 lingual view, 8 labial view). Scale bar equals 5mm.

Tragulidae Milne Edwards, 1864
Dorcatherium Kaup, 1833

Type species: *Dorcatherium naui* Kaup, 1833

Dorcatherium guntianum (von Meyer, 1846)
Specimens referred to: SNSB-BSPG 1959 XXVII 1114 left d4 (length 11.0 mm, width 4.0 mm) (Fig. 2: 2-4), SNSB-BSPG 1959 XXVII 1115 left D4 (length 8.8 mm, anterior width 7.2 mm, posterior width 7.3 mm) (Fig. 2: 6-8).

Both teeth have a brachyo-selenodont ruminant crown morphology. The d4 is slightly worn. It has an external postmetacristid and an external postprotocristid. The external postprotocristid fuses with the prehypocristid and the internal postprotocristid fuses with the preentocristid and the internal postmetacristid. There is no metastylid, mesostylid or entostylid, but an anterior, labial, and posterior cingulid. Metaconid and entoconid are bent slightly towards anterior in lingual view. There is no anterior ectostylid, but a posterior one. The tooth size falls within the range of *D. guntianum* from Reisensburg and Günzburg-Umgehungsstrasse (Fig. 3).

The D4 is trapezoidal in shape and has a very prominent parastyle, a pronounced mesostyle, and a weak metastyle. The labial column of the paracone

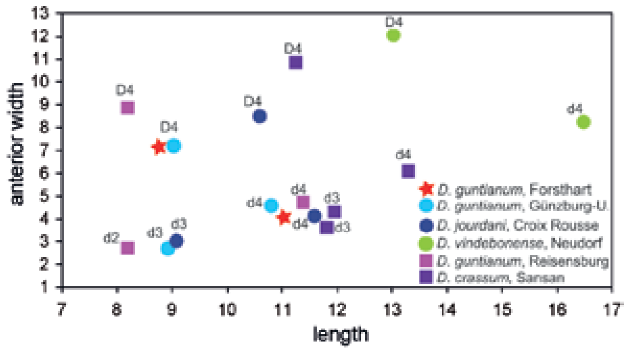

Figure 3: Bivariate plot of milk teeth metrics of European *Dorcatherium* type materials including *D. guntianum* from Günzburg-Umgehungsstrasse and Forsthart (modified from Rössner & Heissig 2013).

is pronounced as well. The anterior lobe is clearly larger than the posterior lobe. A weak cingulum runs from anterior to lingual to posterior. This morphology coincides with a D4 of the type material (SNSB-BSPG 1881 IX 647, Schlosser 1886: pl. VI fig. 22, 23). The size of specimen 1959 XXVII 1115 falls closest to the D4 from Günzburg-Umgehungsstrasse (Fig. 3).

Dorcatherium crassum (Lartet, 1851)

Specimen referred to: SNSB-BSPG 1959 XXVII 1116 right posterior d2 fragment (length 7.6 mm, width 2.7 mm) (Fig. 2: 1), SNSB-BSPG 1959 XXVII 1118 right astragalus (largest width 15.6, lateral height 28.0 mm, medial height 25.0 mm, largest depth 14.6 mm) (Fig. 4).

Although fragmentary, the preserved morphology of specimen 1959 XXVII 1116 is clearly brachyoselenodont, showing a very low-crowned milk cheek tooth with solely one anteroposterior row of cuspids and no lingual elements. This is typical for a tragulid d2. The tooth fragment comprises part of the posterolabial conid, indicated by the short posterolabial cingulid (see Morales et al. 2012, fig. 29) and part of a second conid. It differs from d2 of *D. guntianum* or *D. naui* which do not have a cingulid (*D. guntianum* type material, for *D. naui* see Kaup 1939: 97, pl. 23a fig. 4; Aiglstorfer et al. 2014: Fig. 2e), but corresponds in this with *D. crassum* (Rössner 2010: fig. 1A; Morales et al. 2012: fig. 29+31). The overall length of this fragment corresponds more or less to the full length of a *D. guntianum* d2 (type material, Heissig & Rössner 2013 online resource 1), but also to the size of the respective part of a *D. crassum* d2.

The astragalus is characteristically artiodactyl with a proximal and a distal pulley. The mediolateral axes of both converge towards medial, but in a lesser extent than in suoids. This is typical for tragulids. The size falls within the range of variation in *D. crassum* (e.g. Morales et al. 2012) and is smaller than *D. naui* (Kaup 1939: pl. 23c, figs 6, 6a; Hillenbrand et al. 2009: pl. 1, fig. 12; Aiglstorfer et al. 2014: fig. 2S) and larger than *D. guntianum* (Fig. 4).

Figure 4: 1-2) SNSB-BSPG 1959 XXVII 1118 *Dorcatherium crassum*, Forsthart, right astragalus (1 dorsal view, 2 plantar view). 3-4) SNSB-BSPG 1881 IX 47, *Dorcatherium guntianum*, Reisensburg / Günzburg, Wetzler Collection, right astragalus (3 dorsal view, 4 plantar view). Scale bar equals 5mm.

Tragulidae indet.

Specimen referred to: SNSB-BSPG 1959 XXVII 1117 left i2 or i3 (length at crown base 2.4 mm, width at crown base 2.5 mm, height 8.0 mm) (Fig. 2: 5).

This is a slender spatulate tooth crown, slightly bent to posterior, lingually concave, labially convex, and with a central rip from tip to base on the lingual side. The morphology is typical for a tragulid artiodactyl second or third lower incisor (Milne Edwards 1864, Thenius 1989, Aiglstorfer et al. 2014). Since tragulid incisors are neglected so far in the literature and the available material for comparison lacks any reliably species-associated incisors no further taxonomic assessment is possible.

4. Discussion

The well-embedded status of the Forsthart site in local and regional stratigraphy provides a stable framework to accurately assess the age of the tragulid remains described herein. The freshwater sediments of the Forsthart site belong to the Limnic Freshwater Beds (Limnische Süsswasserschichten), classically associated with the basal Upper Freshwater Molasse (Obere Süsswassermolasse, OSM) in the eastern Bavarian NAFB (Doppler et al. 2005), but most recently reconsidered to possibly represent the ultimate strata of the underlying regressive part of the Upper Brackish Molasse (Oncophora Beds) (Pippèrr & Reichenbacher 2017) (Fig. 1).

The Forsthart site was sampled in 1959, 1974 as well as 1984 and yielded a rich micromammal fauna; so far, no macromammal remains were neither reported nor described. Based on the faunal composition, Ziegler & Fahlbusch (1986) were able to classify Forsthart with the Neogene European Mammal Unit MN4b (17.25 to 16.3 mya, according to Reichenbacher et al. 2013 and Sant et al. 2017) and, thus, to accurately correlate MN4b with the record of the final sea retreat before the ultimate changeover to a continental environment in the German Central Paratethys record. Heissig (1997) and Böhme et al. (2002) assessed Forsthart to the oldest regional Upper Freshwater Molasse Mammal Unit OSM A and oldest Upper Freshwater Molasse sedimentary cycle OSM 0 alike the Günzburg-Umgehungsstrasse site (there named Günzburg) some 200 km farther west and provenience of the recently published supposedly oldest known *D. guntianum* record (Rössner & Heissig 2013).

However, Pippèrr & Reichenbacher (2017) pointed to potential contemporaneity of the Limnic Freshwater Beds (Limnische Süßwasserschichten, Doppler et al. 2005: Tab. 2; Lakustrische Schichten, Pippèrr & Reichenbacher 2017), as present in Forsthart, with the topmost part of the Upper Brackish Molasse (Upper Kirchberg Formation) below the Günzburg-Umgehungsstrasse containing Upper Freshwater Molasse section (Fig. 1). Reichenbacher et al. (2013) were able to suggest an even more detailed chronological assessment and found Forsthart to be around 0.1 Ma older than Günzburg-Umgehungsstrasse (there named Günzburg 2). Moreover, they correlate Forsthart with the uppermost part of chron 5Cr, absolute age around 16.8 Ma, for what Sant et al. (2017) proposed a possible alternative correlation with the top of subchron 5Cn.2r at ~16.5 Ma (Hilgen et al. 2012) (Fig. 5).

According to the above, the tragulid remains from Forsthart, identified in the present work, represent findings from a key site for regional stratigraphic correlation with a relatively well integration into the global geochronology. Hence, *D. guntianum* and *D. crassum* from Forsthart allow for detecting co-occurrence of both species and immigration of *D. guntianum* into the western part of the Central Paratethys domain to a minimum age of 16.5 Ma, synchronous with the very onset of continental conditions in this area (Fig. 5).

As mentioned in Rössner & Heissig (2013), Sach & Heizmann (2001) described *D. crassum* and ?*D. guntianum* fossils from the Eggingen-Mittelhart 3 site. This is located in fluviatile deposits of the lowermost part of the Upper Brackish Molasse (Grimmelfingen Formation) 30 km West of Günzburg-Umgehungsstrasse (Fig. 1). Hence, it is older than Günzburg-Umgehungsstrasse and Forsthart and traces the tragulid record from Germany further back in time. Based on faunal similarities / dissimilarities Sach & Heizmann (2001) assessed Eggingen-Mittelhart 3 into European Mammal Units between the reference fauna of MN4 (La Romieu, France; Roman & Viret 1934, Ginsburg & Bulot 1987, Bruijn et al. 1992, Heissig 1997) (MN4b) and the older fauna from Artenay (France; Ginsburg & Heintz 1968, Ginsburg 1989, Bruijn et al. 1992) (MN4a). Yet, magnetostratigraphic

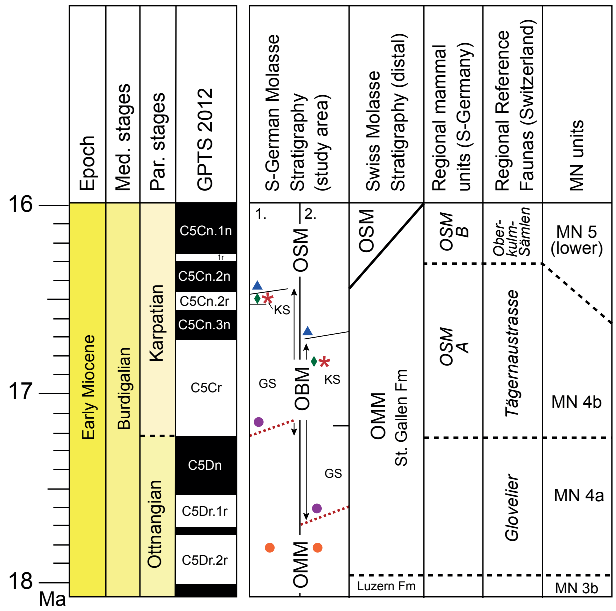

Figure 5: Ages of the discussed fossil sites. The Chart is modified from Fig. 7 in Sant et al. (2017). ▲ = Günzburg-Umgehungsstrasse, ◆ = Gerlenhofen, ● = Eggingen-Mittelhart 3, ● = Sulmingen, * = Forsthart. GS = Grimmelfingen Formation, KS = Kirchberg Formation.

data are ambiguous, and either indicate support for the former via correlation with chron 5Cr (~ 17.2 mya) (Sant et al. 2017: model 1), or correlation with subchron 5Dr.1r (Reichenbacher et al. 2013, Sant et al. 2017: model 2), and, thus, to be synchronous with Swiss MN4a faunas (Kälin & Kempf 2009: Fig. 10) from maximum 17.7 mya (Fig. 5).

Aiglstorfer et al. (2014: Fig. 1) give a chart with an extensive (but no complete) overview of the European Miocene tragulid / *Dorcatherium* record. They specify even older tragulids from sites south of Günzburg-Umgehungsstrasse: *D. guntianum* from Gerlenhofen (Sach & Heizmann 2001) and *D. crassum* from Sulmingen. The freshwater sands from Gerlenhofen lie within the Upper Kirchberg Formation (Gerlenhofer Sande in Kiderlen 1931: 312-313, for further lithostratigraphic assessment see Reichenbacher 1993) and hence can be considered at least as old as Forsthart (Fig. 1). The teeth from Sulmingen (SNSB-BSPG 1956 I 156) belong to a sample of terrestrial mammal fossils coming from the Baltringen Formation (Dehm 1951). The Baltringen Formation is part of the Upper Marine Molasse Group (Heckeberg et al. 2010, Pippèrr & Reichenbacher 2017), indicating that fossils coming from there are clearly older than those from the Upper Brackish Molasse Group (Doppler et al. 2005) (Fig. 1). The Baltringer Formation represents an especially extraordinary facies for terrestrial remains being interpreted as deposited in a shallow marine environment with tidal influences (Heimann et al. 2009).

Considering the above, *Dorcatherium guntianum* from Forsthart and Gerlenhofen are by now the oldest unambiguous records of the species with a minimum age of 16.5 Ma and a maximum age of 16.8 Ma. Eggingen-Mittelhart 3 yielded a potentially older *D. guntianum* with a minimum age of 17.2 Ma and a maximum age of 17.7 Ma. *Dorcatherium crassum* remains from Sulmingen represent the so far oldest *Dorcatherium* record in Germany with a maximum age of 17.8 Ma (basis Baltringen Formation = basis middle Ottnangian, subchron 5Dr.2r, Pippèrr et al. 2007, Pippèrr & Reichenbacher 2017) (Fig. 5).

In the European context, the latter occurrence exceeds the earliest reported tragulid remains from Austria (Oberdorf 4, MN4, chron 5Dn; Rössner 1998, Daxner-Höck 2001, Aiglstorfer et al. 2014: fig. 1), Switzerland (Hüllistein, MN5, chron 5Br; Kälin & Kempf 2009; Aiglstorfer et al. 2014: fig. 1), France (Aérotrain, MN4; Ginsburg 1989, Bruijn et al. 1992), Spain (Els Casots, regional biozone C of the Calatayud-Daroca Basin, subchron 5Cn.2n, uppermost MN4; Alba et al. 2014, Kälin & Kempf 2009: fig. 9, Hilgen et al. 2012), and Portugal (Quinta das Pedreiras, Quinta do Pombeiro, Quinta da Conceiçao; correlated with Spanish regional biozone C and D / minimum subchron 5Cn.2n, uppermost MN4; Antunes et al. 1994) in age and sets 17.8 mya as the minimum constraint for the timing of the Miocene tragulid immigration into Europe. In Early Miocene biochronology presence of *Dorcatherium* was generally considered as indicative for younger MN4 / MN4b (Fahlbusch 1985; Made 1999; Sach & Heizmann 2001) (though the correlation of MN4 with the Global Time Scale differs when used for Iberian Peninsula faunas or faunas coming from the rest of Europe, see e.g., Kälin & Kempf 2009). However, this is no more maintainable according to the current knowledge based on integrated stratigraphic efforts (see above). Rather than a synchronous appearance of *Dorcatherium* in Europe the overall pattern of the Miocene tragulid record known so far allows for the interpretation of a successive, heterochronous dispersal of *Dorcatherium* from the East / Southeast to the West / Southwest of Europe.

In this regard, a remaining issue with Miocene European tragulids is the documented early record of *D. crassum* and *D. guntianum* as representatives of two phylogenetic lineages in Germany, Switzerland, and France (Rössner & Heissig 2013: online resource 2). A record of both species outside Europe is not reported so far, what challenges the hypothesis of immigration into Europe. Hence, remains tracking back *D. crassum* and *D. guntianum*'s sympatric existence beyond hitherto known evidence and to the point of Miocene tragulid appearance in Europe are of importance to the reconstruction of the evolutionary history of the group.

Invasion of *Dorcatherium* into Europe has been related with the "*Gomphotherium*-landbridge" (Fahlbusch 1985, Made 1999, Harzhauser et al. 2007), a terrestrial corridor what emerged in the context of tectonical collision between Africa and Arabia and persisted from 19 to 16 mya (Rögl 1998, 1999). This was postulated based on faunal turnovers in Africa and the Indian Subcontinent (e.g., Madden & van Couvering 1976, Made 1999). However, older records of *Dorcatherium* as compared to Europe are not only known from Africa (Pickford 2001, Geraads 2010 and references therein), but also from the Indian subcontinent (Barry et al. 2005, Barry 2014 and references therein) and the palaeogeographic constellation with land connections via the Zagros area and Anatolia was not less convenient for migration than the "*Gomphotherium*-landbridge" (Goncharova et al. 2004, Hoek Ostende et al. 2015). Moreover, the appearance of tragulids in Africa prior to the "*Gomphotherium*-landbridge" is more of an enigma due to lacking Oligocene / earliest Miocene ancestors. Hence, it is reasonable to also consider that Miocene tragulid migration was complex with paths from Asia to Africa, and from Asia and Africa to Europe. Yet, Early Miocene mammal faunas are unknown in eastern and generally rare in southeastern Europe (Hoek Ostende et al. 2015). Surprisingly, the recent investigation of late MN3 / early MN4 artiodactyls from Aliveri (Greece) has not revealed a tragulid record (Hoek Ostende et al. 2015); however, this may be related to sampling bias (personal communication S. Mayda), the scarcity of macromammal fossils, or environmental specifics that did not suit the strict wetland adaptation of tragulids. Yet, detailed examination of the MN3 ruminant assemblage of Sabuncubeli (Turkey; Bruijn et al. 2006) will shed new light on that question (Rössner & Mayda in preparation).

5. Conclusions

Upper Lower Miocene continental sedimentary sequences of the German part of the NAFB provide key data for the arrival of Miocene tragulids in Europe. The highly elaborated stratigraphic / geochronologic framework allows to assume a minimum appearance datum for *Dorcatherium crassum* at 17.8 mya (what corresponds to the minimum appearance datum for *Dorcatherium* in Europe) and a minimum appearance datum for *Dorcatherium guntianum* at 16.5 mya. These findings predate the so far known earliest occurrences of *Dorcatherium* in other regions of Europe and indicate a heterochronous dispersal from the East / Southeast to the West / Southwest in Europe. Association of these early European Miocene tragulids with lowland sediments allow us to assume that the animals followed emerging freshwater wetlands in the Central and Western Paratethys realm in the context of the global sea-level fluctuations within the third-order cycles Bur 3 and Bur 4 (Pippèrr & Reichenbacher 2017), due to their presumably specific wetland adaptation (Rössner 2004, 2007; Rössner & Heissig 2013). Yet, this hypothesis has still to be substantiated with more data.

So far, missing records of *D. crassum* and *D. guntianum* ancestors outside of Europe indicate a pre-MN4 (> 18 mya) evolutionary history of *Dorcatherium* in southeastern Europe.

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