The aberrant hamster *Melissiodon* (Cricetidae, Rodentia) from the early Miocene of Echzell and other German and French localities

Sílvia Jovells-Vaqué & Thomas Mörs

Published online: 24 Apr 2022.

Submit your article to this journal ⬚

View related articles ⬚

View Crossmark data ⬚

Taylor & Francis
Taylor & Francis Group

The aberrant hamster *Melissiodon* (Cricetidae, Rodentia) from the early Miocene of Echzell and other German and French localities

Sílvia Jovells-Vaqué [a,b] and Thomas Mörs [c,d]

aDepartment of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University, Bratislava, Slovak Republic; bInstitut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain; cDepartment of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden; dBolin Centre for Climate Research, Stockholm University, Stockholm, Sweden

ABSTRACT

Melissiodon is a rare cricetid with a long stratigraphic range, present from the Oligocene until the Miocene, only found in western and central Europe except some specimens recovered in Anatolia. What makes *Melissiodon* special is its unique dental and mandible morphology that has led to many questions regarding its relationship to other cricetid genera and its type of diet. In this work, we have studied new material attributed to *Melissiodon* from the German localities Echzell (MN4) and Petersbuch (MN3 and MN4), and from the French locality Beaulieu (MN3). Moreover, we compared these specimens with the already published material from other localities across western and central Europe during the early Miocene (MN3 and MN4). In conclusion, the studied specimens and the comparison with other material from different European localities allow us to ascribe this new material as *Melissiodon dominans*, a widely dispersed species across Europe during the early Miocene

Introduction

Melissiodon is a rare cricetid only known from western and central Europe, with exception of a few specimens that have been recovered from Kargi-2, Anatolia (De Bruijn et al. 2013) and has a long time range, from early Oligocene (MP 23, Dawson 2003) to the early Miocene (MN4, Mödden 1999). However, *Melissiodon dominans* has recently been reported from the locality of Sant Mamet in the Vallès-Penedès Basin (Catalonia, Spain), correlated with MN5 (Jovells-Vaqué and Casanovas-Vilar 2018; Jovells-Vaqué 2020). As in most fossil rodent species, *M. dominans* is known only for its cranial remains, mainly from its isolated cheek teeth. Some mandible, maxillary, and other cranial materials are known from the fissure fill Petersbuch 28 in southern Germany (Mödden 1999), but the postcranial skeleton is still unknown. The peculiar morphology and the incompleteness of material caused discrepancies regarding the phylogenetic position of *Melissiodon*, and the validity of a family Melissiodontinae/dae. This genus had been considered as a monotypic subfamily (Schaub 1925; Mein and Freudenthal 1971) or family (Freudenthal et al. 1992; Mödden 1999). Ünay-Bayraktar (1989) also placed the genus *Erdinella* from the middle Oligocene of Turkish Thrace to the subfamily Melissiodontinae. In its turn, Wessels et al. (2018) described Melissiodontinae from the late Eocene and early Oligocene of Serbia. Recent phylogenetic studies by Maridet and Ni (2013) indicate that *Melissiodon* is related to Oligocene-early Miocene Asian and Anatolian cricetids, and therefore it should be included as a member of the Cricetopinae subfamily. It would be a senior synonym of Melissiodontinae.

Melissiodon owes its name due to its peculiar cheek tooth morphology of deep valleys and pits that resembles a honeycomb but little is known about its physiology. The unique morphology of the cheek teeth together with the particular slender and weak mandible of *Melissiodon* was already noted by Schaub in 1920 when describing the genus. Mein and Freudenthal (1971) suggested that its cheek

teeth might reflect a frugivorous diet. More recently, Hordijk et al. (2015) proposed that the long diastema with weak lower incisors that end below the m2, together with the complex high-crested cheek teeth, indicates an insectivorous diet. They compared the mandible and cheek teeth of *Melissiodon* with extant murine Sulawesi and Philippines shrew rats that possess similar mandibles and feed on soft-bodied invertebrates. Hordijk et al. (2015) pointed out that this very specific food source might have been the reason why *Melissiodon* survived the early Miocene European 'cricetid-vacuum' (Daams and Freudenthal 1989; Fahlbusch 1989) that coincides with palaeogeographic and climatic reorganisations caused by the beginning of the Mid-Miocene climate optimum (MCO) (Steinthorsdottir et al. 2021).

The goal of our paper is to describe dental material of *M. dominans* from the early Miocene MN4 locality of Echzell, and additional specimens from the early Miocene of Beaulieu 2 (MN3) in France and the fissure fills Petersbuch 36 (MN3) and Petersbuch 7 and 38 (MN4) in Germany, to get a better understanding of size variation in this species.

Geology, stratigraphy and faunal composition of the localities

Echzell is located in the southwestern part of the basaltic Vogelsberg volcanic complex, approximately 30 km NNE of Frankfurt am Main (Figure 1). The volcano was active during the entire Miocene and some maar lake sediments and reworked volcanoclastics have produced Miocene vertebrate remains (Mörs 2010), especially the disintegrated volcanic tuffs of the Echzell locality, preserved at the eastern edge of the Horloff Graben (Tobien 1954; Pineker and Mörs 2011; Mörs and Flink 2018; Vasilyan et al. in press). The faunal association is dominated by small mammals: a herpetotheriid marsupial, erinaceid, talpid,

Published online 24 Apr 2022

dimylid, soricid and heterosoricid insectivores, a megadermatid bat, sciurid, glirid, eomyid, cricetid, platacanthomyid and anomalomyid rodents and an ochotonid lagomorph (Vasilyan et al. in press). Among the hamsters, *Democricetodon franconicus* is very abundant, *Melissiodon dominans* is less abundant (although more abundant than in most other localities yielding this taxon) and *Eumyarion weinfurteri* is rare, documented by few teeth only. Large mammals are represented by a gomphothere elephant, a listriodontine suid and small ruminants, a rhinocerotid and a large amphicyonid carnivore (Tobien 1954). Among other tetrapods, amphibians are represented by an albanerpetontid allocaudate, salamanders, pelobatid, alytid, ranid and palaeobatrachid frogs; reptiles by a testudinid tortoise, an alligator, a gecko, chamaeleons, lacertid, scincid and anguid lizards and boid, colubrid and elapid snakes; and birds by passeriform songbirds (Vasilyan et al. in press). The biostratigraphic setting of Echzell is framed by taxa that have in central Europe their last appearance datum (LAD) in MN4, *Pseudotheridomys parvulus, Ligerimys florancei, M. dominans*; and by taxa that have their first appearance datum (FAD) in MN4, *D. franconicus, E. weinfurteri, Neocometes similis, Anomalomys minor* and *Gomphotherium angustidens* (Vasilyan et al. in press). The evolutionary stage of *N. similis* from Echzell is comparable to the MN4 locality Erkertshofen 2 (Fejfar and Kalthoff 1999; Pineker and Mörs 2011), and the derived evolutionary stage of the Echzell apeomyine rodents is very similar to the MN4 localities Dolnice 1 and Petersbuch 2 (Mörs and Flink 2018). Thus, Echzell represents a middle Orleanian, early Miocene fauna, correlated with the Mammalian Neogene unit MN4.

Beaulieu is located approximately 10 km NNW of Aix en Provence (Figure 1). The vertebrate remains of Beaulieu 2 derive from green lacustrine marls with reworked volcanic scoriae that overly an altered basaltic crater fill (Aguilar et al. 2003). The initial phreatomagmatic tuffs overlie Burdigalian marine sands (plankton biozone N6 + N7 based on foraminifera); the basalt shows normal polarity and is correlated with palaeomagnetic chron C5Dn, and an associated, unaltered dolerite has produced an Ar-Ar age of 17.5 ± 0.3 Ma (Aguilar et al. 1996, 2003). The mammalian fauna contains a herpetotheriid marsupial, erinaceid and talpid insectivores, the cricetid *M. dominans*, eomyids, glirids, and a sciurid among rodents, an ochotonid lagomorph, a rhinoceros, anthracotheriid, andegamerycid, palaeomerycid and cervid artiodactyls and ursid and viverrid carnivores (Aguilar et al. 2003). Additionally, turtle shells, crocodile teeth and squamate remains including an anguid lizard have been found (Aguilar et al. 1996; TM pers. observation). According to Aguilar et al. (2003), the biostratigraphic setting of Beaulieu is coined by the 'cricetid-vacuum', i.e., absence of hamsters with the exception of *M. dominans*, and the evolutionary development of *Ligerimys antiquus* places Beaulieu contemporaneous to the German MN3 locality Schnaitheim, and slightly younger than the German MN3 locality Wintershof-West. The combination of radiometric age, chronostratigraphic setting, plankton and mammal biozonation make Beaulieu an important early/middle Orleanian locality for the continental European early Miocene.

Petersbuch is located approximately 30 km NW Ingolstadt (Figure 1). The fossiliferous karstfissure fillings are situated within the White Jura-δ limestones. Petersbuch 36 can be correlated to MN3 by the presence of *M. dominans* and *L. florancei* and the absence of other cricetids (TM pers. observation). Additional faunal elements are a salamander, a bat and an artiodactyle (TM pers. observation).

The faunal association of Petersbuch 7 is correlated with MN4 and dominated by small mammals: a herpetotheriid marsupial, erinaceid, talpid, dimylid, soricid and heterosoricid insectivores,

bats, sciurid, glirid, eomyid, cricetid and platacanthomyid rodents and an ochotonid lagomorph (Bolliger and Rummel 1994; TM pers. observation). Among the hamsters, *D. franconicus* is much more abundant than *M. dominans* (TM pers. observation). Large mammals are represented by a gomphothere elephant, a palaeochoerid, cainotheriid and palaeomerycid artiodactyls, a rhinocerotid and mustelid and felid carnivores (Bolliger and Rummel 1994). Non-mammalian tetrapods comprise a crocodile-newt, an anguid lizard and birds (Bolliger and Rummel 1994; TM pers. observation).

The fauna from the lower part of the Petersbuch 38 fissure is correlated to MN4 according Rummel (2000). The fauna is dominated by small mammals and comprises Erinaceidae, Talpidae, Sorcidae, Chiroptera, Sciuridae, Gliridae, the eomyids *Pseudotheridomys parvulus* and *L. antiquus*, the cricetids *D. franconicus* and *M. dominans*, the platacantomyid *N. similis*, an ochotonid lagomorph; large mammals are represented by Artiodactyla and Carnivora and non-mammalian tetrapods by Anguidae, Emydidae and Aves (TM pers. observation).

Material and methods

The described material is housed at Hessisches Landesmuseum in Darmstadt (HLMD), Germany and Naturhistoriska riksmuseet in Stockholm (NRM), Sweden. Collection numbers are given in the main text as well as for figured specimens. All specimens have been obtained by screen washing. The Echzell material was excavated by the Geological Department of the HLMD in September 1953; two fossiliferous layers yielded vertebrate remains, one at 2.20 m depth both large and small mammals, and one at 11.0 m depth that produced the majority of small mammals and other microvertebrates (Tobien 1954). The Beaulieu 2 material was collected by one of the two authors (TM) during the BiochroM'97 congress excursion in April 1997. The Petersbuch material was collected by TM during student field courses, held at the Steinmann Institute, Rheinische Friedrich Wilhelms-Universität Bonn in the summer terms 1995 and 2000.

Dental terminology is modified after Freudenthal et al. (1994), Maridet and Ni (2013), and Jovells-Vaqué and Casanovas-Vilar (2018). Measurements are in millimetres taken with a Leica MZ6 microscope. Classification of *Melissiodon* follows Maridet and Ni (2013). Summary statistics and scatterplots were performed using the R and Rstudio software (R Core Team 2017). MN ellipses in the scatterplots (Figure 2 in the discussion part) contain data from several localities: MN3 ellipse contains L/W data from Maigen, Austria (Mein 1989); Merkur-North, Czech Republic ((Fejfar 1990; Fejfar et al. 2003); the German localities Schnaitheim (Dehm 1939; Hrubesch 1957); Wintershof-West, type locality (Dehm 1937, 1950; Hrubesch 1957); Wintershof-Ost (Dehm 1939; Hrubesch 1957); Wütherich (Hrubesch 1957; Schalk 1957); the French localities Beaulieu 2 (Aguilar et al. 2003); Bouzigues 2 (Aguilar et al. 1997); Estrepouy (Hugueney and Bulot 2011); Jauquet (Bulot et al. 2009); Saint-Vincent de Lamonjoie (Bulot et al. 2009); Hummelberg, Switzerland (Bolliger 1992); Lisboa AU, Portugal (Antunes and Mein 1992); the Spanish localities Bañon 2; Bañon 11A; Ramblar 1; Ramblar 3B; Ramblar 7 (Sesé 1987); Molí calopa; Sant Andreu de la Barca; Turó de les Forques (Jovells-Vaqué and Casanovas-Vilar 2018). MN4 ellipse contains L/W data from the Czech Republic localities Dolnice (Fejfar 1990); Mokrá – 1/2001 Turtle Joint site (Bonilla-Salomón et al. 2021); Orechov (Fejfar 1990); German localities Erkertshofen 2; Forsthart; Petersbuch 2; Rembach (Ziegler and Fahlbusch 1986); Béon 2 France (Bulot et al. 2009)); the Spanish localities Barranc de Campisano; Mas d'Antolino (Crespo Roures 2017); Montalvos 2 (Jovells-Vaqué and Casanovas-Vilar 2018). The ellipses are built using the ggplot2 library from the R program, following the 'stat_ellipse' formula. The Beaulieu 2 and Petersbuch

Figure 1. Map of the German and French localities mentioned in the text. 1: Echzell, 2: Petersbuch sites, 3: Beaulieu 2.

2 ellipses are independent from MN3 and MN4 ellipses to compare them with the studied material from the same localities. As we can see in Figure 2, the Beaulieu 2 (MN3) ellipse does not exactly follow the MN3 ellipse and the same happens with Petersbuch 2 (MN4). This is because the ellipses are constructed assuming a T-distribution (T-Student distribution). The T-Student is designed to work with normal distributed data with small data sets, as is the case of some sites such as Petersbuch 2 and Beaulieu 2. Having a small dataset, such as in Beaulieu 2, results in an ellipse that does not exactly follow the MN3 ellipse which contains more material (including Beaulieu 2 specimens). The same happens with Petersbuch 2 material related to the MN4 ellipse (includes Petersbuch 2 specimens).

Abbreviations

Institutional Abbreviations: HLMD – Hessisches Landesmuseum Darmstadt; NRM – Naturhistoriska riksmuseet/Swedish Museum of Natural History, Stockholm.

Anatomical Abbreviations: L – anteroposterior length; W – labiolingual width

Others: MN – European Mammal Neogene unit.

Systematic palaeontology

In this section, we describe specimens from different localities in Germany and France. The locality that has more material of *Melissiodon dominans* is Echzell. The other German sites are
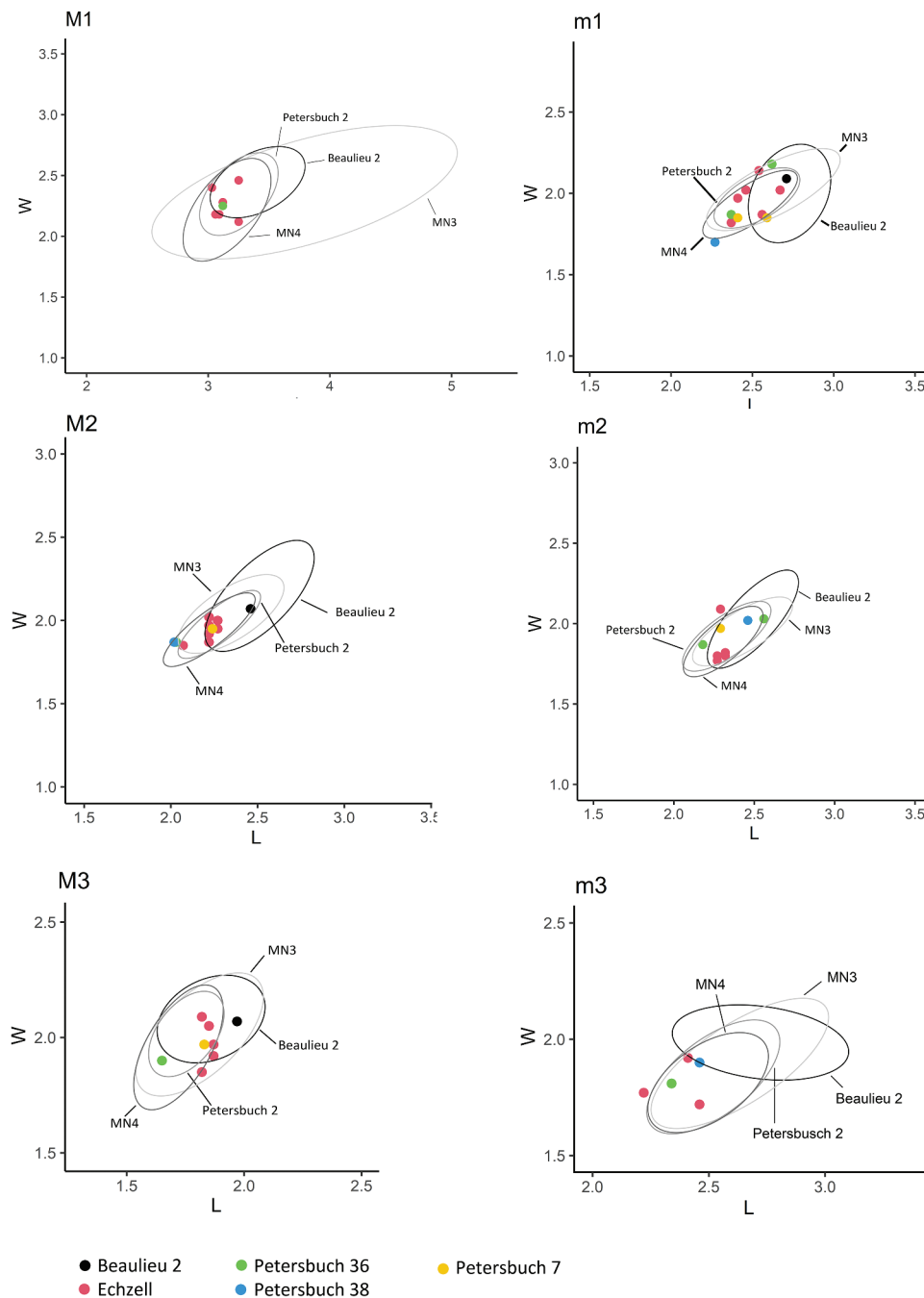
Figure 2. Length/Width scatter plot of *Melissiodon dominans* upper and lower molars from Echzell, Petersbuch 7, 36, and 38 (Germany) and Beaulieu 2 (France). The ellipses show the 95% confidence interval for *Melissiodon dominans* speciemens from different localities from MN3, MN4, and for the already published material from Beaulieu 2 (Aguilar et al. 2003) and Petersbuch 2 (Ziegler and Fahlbusch 1986) .

Petersbuch 7, 36, and 38 *M. dominans* has been already described from Peterbusch 2 in Ziegler and Fahlbusch (1986). Beaulieu 2 is a site in southern France from which *Melissiodon* aff. *dominans* has been described earlier by Aguilar et al. (2003).

Order RODENTIA Bowdich 1821
Family CRICETIDAE Fischer von Waldheim 1817
Subfamily CRICETOPINAE Matthew and Granger 1923
Tribe MELISSIODONTINI Schaub 1925
MELISSIODON Schaub 1920
MELISSIODON DOMINANS Dehm 1950

Echzell (Germany) MN4

We studied a total of 36 complete specimens from Echzell along with 28 molar fragments that had not been considered for measurements and descriptions due to their poor preservation. Therefore, there are 6 M1 (HLMD-Ez-2163, HLMD-Ez-2164, HLMD-Ez-2165, HLMD-Ez-2166, HLMD-Ez-2183, HLMD-Ez-2165); 7 M2 (HLMD-Ez-2167, HLMD-Ez-2168, HLMD-Ez-2169, HLMD-Ez -2170, HLMD-Ez-2171, HLMD-Ez-2172, HLMD-Ez-2185); 6 M3 (HLMD-Ez-2167, HLMD-Ez-2182, HLMD-Ez-2186, HLMD-Ez -2187, HLMD-Ez-2188); 6 m1 (HLMD-Ez-2174, HLMD-Ez-2175,

HLMD-Ez-2176, HLMD-Ez-2177, HLMD-Ez-2189, HLMD-Ez-2190); 6 m2 (HLMD-Ez-2174, HLMD-Ez-2178, HLMD-Ez-2179, HLMD-Ez-2191, HLMD-Ez-2192, HLMD-Ez-2193); 4 m3 (HLMD-Ez-2174, HLMD-Ez-2180, HLMD-Ez-2181, HLMD-Ez-2194). For collection numbers and measurements see Table 1.

M1

There are six complete specimens in Echzell (see Figure 3d-g). These specimens have four roots, two posterior ones below the metacone and hypocone, another in a lingual position below the protocone, and the last one in a labial position below the anterocone.

The anterocone complex of all the specimens is well developed and occupies a centrolabial position to the main body of the M1. This complex presents two cusps; the larger one has a centrolingual position while the smaller one is located more labially. They present a narrow ridge between them. The protostyle presents a lingual position and has approximately the same size as the labial cusp of the anterocone. The protostyle shows two connections, the first one connects with the anteroloph forming a small cusp and the second one connects directly to the centrolingual anterocone cusp, forming the anteroloph. The protosinus is closed in all specimens, but it is especially notable in specimen HLMD-Ez-2165 (Figure 3f). In the same way, the anterosinus is closed by a cingulum that emerges from the paracone. Emerging from the labial cusp of the anterocone, a small ridge connects directly with the paracone. The mesocone is as large as the other cusps in the molar but somewhat shorter. The protolophule is simple and connects the labial part of the protocone with the lingual part of the paracone. They both connect with the anterior part of the mesocone.

The mesoloph is long and well developed, reaching the labial margin of the molar. Two small cingula, one emerging from the posterior part of the paracone and the other one from the anterior part of the metacone merge with the mesoloph at the labial margin of the teeth forming the mesostyle. The metalophule is double, the labial arm connects directly to the mesoloph and the lingual arm connects right to the mesocone. The entoloph is well developed and connects the posterior part of the mesoloph with the hypocone. The sinus is closed by a low ridge that connects the paracone and the hypocone. The posteroloph is well developed and connects with a posterior arm of the metacone. The hypocone presents at its torn a spur that originates from the lingual wall of the hypocone and curves into a posterior-labially position defining a posterolingual valley. This spur is present in all specimens but slightly developed in HLMD-Ez-2166 (Figure 3d).

M2

There are seven complete specimens and three identifiable molar fragments ascribed to M2 (see Figure 3h-m). These molars present four roots, each of them below each main cusp of the tooth.

The anteroloph is very well developed in all specimens. The labial arm of the anteroloph merges with the paracone, closing the anterosinus. The lingual anteroloph also merges with the protocone, closing the protosinus. The protocone has a lingual spur that is lingually directed but does not reach the hypocone, leaving the sinus open. This is the situation in all molars except for HLMD-Ez-2170 (Figure 3k), in which the sinus is closed by a low ridge. The protolophule is double with one anterior arm that connects with the labial arm of the anterolophid and the posterior arm that is posteriorly oriented but shows no connection. The mesoloph is long and well-developed reaching the labial mesostyle. The mesocone is also well developed and shows a similar size as the rest of the other cusps present in the molar. The metaloph is double with the anterior arm connecting with the entoloph and the base of the mesoloph and the posterior arm connecting with the posteroloph. The postreloph is well developed and connects with the posterior arm of the metaloph enclosing the posterior margin of the molar, but leaving a small open platform at the postero-labial margin of the tooth. The hypocone presents the same postero-labial arm that delimitates a small postero-lingual valley as in the M1 specimens.

M3

There are six complete M3 specimens (see Figure 3h, n, o for the figured specimens). These specimens present three roots. As in other cricetid species, the upper M3 are highly reduced. M3 show a button shape general morphology, with many similarities with the M2 with a reduced posterior part. The anteroloph is well developed enclosing the anterosinus and the posterosinus. The two major cusps of the M3 are the paracone and the protocone. There is no mesoloph and the sinus is open. The metacone occupies the posterior labial margin of the teeth connecting with the labial ridge of the paracone. The metacone is present but reduced and it is connected with the protocone by the protolophule and with the metacone by the metalophule as shown in HLMD-Ez-2182 (Figure 3o).

m1

There are six complete m1 (see Figure 3s-u). These specimens have two roots. The anterior one is circular and thinner than the posterior one, which is more robust and occupies the space below the hypoconid and entoconid.

Table 1. Collection numbers and measurements in millimetres of *Melissiodon dominans* cheek teeth from Echzell. Only complete specimens are considered for measurements. [] indicate approximate measurement.

| Locality	Number	Element (L/R)	Length	Width
Echzell	HLMD-Ez-2163	M1L	3,25	2,46
Echzell	HLMD-Ez-2164	M1R	3,03	2,4
Echzell	HLMD-Ez-2165	M1L	3,12	2,28
Echzell	HLMD-Ez-2166	M1R	3,09	2,18
Echzell	HLMD-Ez-2183	M1L	3,06	2,18
Echzell	HLMD-Ez-2184	M1R	3,25	2,12
Echzell	HLMD-Ez-2167	M2-M3 (M2L)	2,22	2,02
Echzell	HLMD-Ez-2167	M2-M3 (M3L)	1,85	2,05
Echzell	HLMD-Ez-2168	M2L	2,22	1,87
Echzell	HLMD-Ez-2169	M2L	2,27	1,95
Echzell	HLMD-Ez-2170	M2R	2,27	2,00
Echzell	HLMD-Ez-2171	M2L	2,07	1,85
Echzell	HLMD-Ez-2172	M2R	2,22	1,92
Echzell	HLMD-Ez-2185	M2L	2,22	1,97
Echzell	HLMD-Ez-2173	M3R	1,87	1,92
Echzell	HLMD-Ez-2182	M3L	1,82	2,09
Echzell	HLMD-Ez-2186	M3L	1,85	1,72
Echzell	HLMD-Ez-2187	M3L	1,82	1,85
Echzell	HLMD-Ez-2188	M3R	1,87	1,97
Echzell	HLMD-Ez-2174	m1-m3 (m1R)	2,54	2,14
Echzell	HLMD-Ez-2174	m1-m3 (m2R)	2,29	2,09
Echzell	HLMD-Ez-2174	m1-m3 (m3R)	-	[1,60]
Echzell	HLMD-Ez-2175	m1L	2,46	2,02
Echzell	HLMD-Ez-2176	m1R	2,56	1,87
Echzell	HLMD-Ez-2177	m1L	2,41	1,97
Echzell	HLMD-Ez-2189	m1L	2,37	1,82
Echzell	HLMD-Ez-2190	m1R	2,67	2,02
Echzell	HLMD-Ez-2178	m2R	2,27	1,8
Echzell	HLMD-Ez-2179	m2R	2,32	1,82
Echzell	HLMD-Ez-2191	m2L	2,27	1,77
Echzell	HLMD-Ez-2192	m2R	2,46	2,02
Echzell	HLMD-Ez-2193	m2L	2,32	1,8
Echzell	HLMD-Ez-2180	m3R	2,41	1,92
Echzell	HLMD-Ez-2181	m3R	2,46	1,72
Echzell	HLMD-Ez-2194	m3R	2,22	1,77
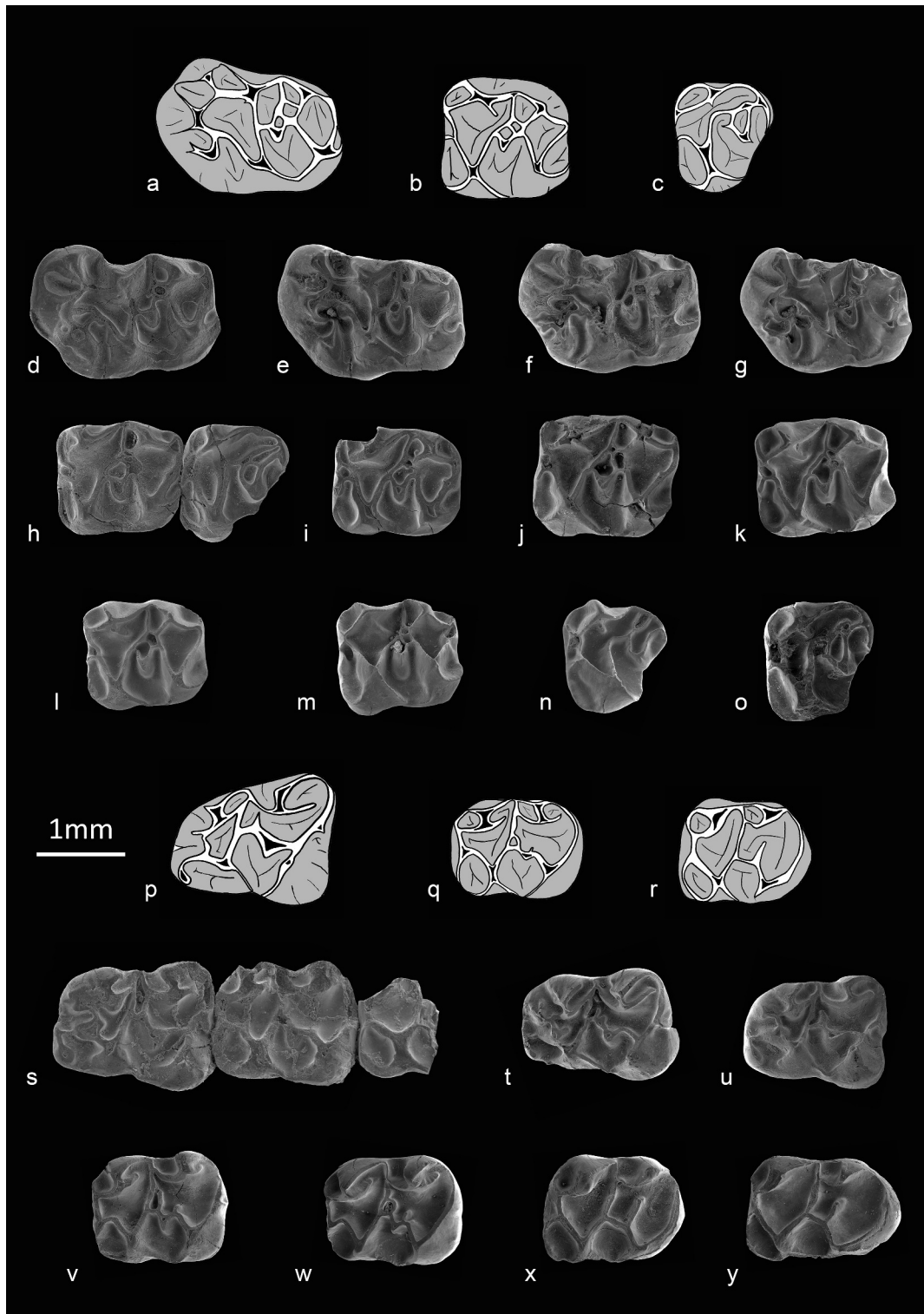
Figure 3. Scanning electron microscope (SEM) micrographs (d-o, s-z) and interpretative drawings (upper molars a-c, and lower molars p-r) of *Melissiodon dominans* molars from Echzell. d, HLMD-Ez-2163 left M1; e, HLMD-Ez-2164 right M1 (reversed); f, HLMD-Ez-2165 left M1; g, HLMD-Ez-2166 right M1 (reversed); h, HLMD-Ez-2167 left M2-M3; i, HLMD-Ez-2168 left M2; j, HLMD-Ez-2169 left M2; k, HLMD-Ez-2170 right M2 (reversed); l, HLMD-Ez-2171 left M2; m, HLMD-Ez-2172 left M2; n, HLMD-Ez-2173 right M3 (reversed); o, HLMD-Ez-2182 left M3; s, HLMD-Ez-2174 left m1-m3; t, HLMD-Ez-2176 left m1; u, HLMD-Ez-2177 right m1; v, HLMD-Ez-2178 left m2; w, HLMD-Ez-2179 right m2 (reversed); x, HLMD-Ez-2180 right m3 (reversed); y, HLMD-Ez-2181 left m3.

The anterior part of the teeth is narrower than the posterior part. The anteroconid is divided into two cusps by a deep valley. Another interpretation for this feature is that the anteroconid would be single and located in a lingual position, while the other labial cusp would be in its turn the protostylid. The lingual anteroconid presents two spurs. The lingual merges directly to the antero-labial spur of the metaconid, thus resulting in the metalophulid. The labial spur of the anteroconid merges with the anterolophulid. The labial anteroconid cusp is round-shaped and shows one poster-ior spur that merges directly to the anterolophulid, which is well

developed. Both anterosinusid and protosinusid are open. The protoconid and the metaconid show no direct connection between them. The entolophid is long and the mesoconid is small compared to the upper molars. Anterior to the mesoconid there are two lingually directed ridges; the first one, which would correspond to the protoconid hind arm, is long and reaches the cingulid that closes the mesosinusid reaching also the mesotylid. The second spur corresponds to the mesolophid which is medium-sized and does not reach the margin of the teeth as shown in HLMD-Ez-2177 (Figure 3u). The sinusoid is closed by two cingula that emerge one from the protoconid and the other from the hypoconid. The entoconid has two posterior spurs. The labial one is posteriorly directed but does not reach the posterolophid. The lingual one curves labially following the posterior margin of the teeth and merging with the posterolophid. The posterolophid shows a small hypoconulid–like spur near the hypoconid.

m2

There are six complete m2 and three identifiable fragments (see Figure 3s, v, w for the figured specimens). The m2 has two roots, the posterior one being more robust than the anterior one. There is a small anteroconid in a labial position and presents two well anterolophids that close the anterosinusid and protosinusid. The protosinusid is closed by the labial anterolophid and the anterior labial spur of the protoconid. The metaconid shows three spurs, one anterolabial spur that merges with the lingual anterolophid. The lingual posterior spur of the metaconid curves and reaches the margin of the tooth merging with the mesostylid. On the contrary, the labial posterior spur is shorter and posteriorly directed. There is no connection between the protoconid and the metaconid. The entolophid is long and well developed. The mesoconid is present but smaller compared to the upper molars. Anterior to the mesoconid, there are two lingually directed ridges; the first one would correspond to the protolophid hind arm, which is long and reaches the cingulid that closes the mesosinusid. The second one would correspond to the mesolophid and is short and does not reach the margin of the tooth. In HLMD-Ez-2179 (Figure 3w), the mesoloph curves anteriorly, merging with the protolophid. HLMD-Ez-2178 (Figure 3v) shows a longer mesolophid that reaches the anterior labial spur of the entoconid. Posterior to the mesoconid a small spur is directed to the entoconid without reaching it. This would correspond to an incomplete hypolophulid. The entoconid shows an anterior labial spur that merges with the mesostylid. There are also two posterior spurs from the entoconid. The lingual one merges with the posterolophid while the labial one is shorter and posteriorly directed and shows no connection with any other element. The posterolophid is well developed and does not show the hypoconid-like spur that appeared in the m1. The sinusid is closed in all specimens by merging two cingulids, one emerging from the protoconid and the other from the hypoconid.

m3

There are three complete m3 and one fragment (Figure 3s, x, y). The size of the m3 can be variable, they are normally longer than m2, but narrower. They present two roots one located in an anterior position and the other in a posterior position.

Contrary to most cricetids, the m3 is not reduced, showing a similar morphology as the m2, with the four main cusps similar in size (protoconid, metaconid, entoconid, and hypoconid). The anteroconid and mesoconid are reduced and not present. The lingual and labial anterolophids close the anterosonusid and protosinusid respectively. The protosinusid is larger compared to the anterosinusid. The ectolophid presents two lingually directed ridges. The first one would be the protoconid hind arm that is long and reaches the lingual margin of the

tooth, enclosing the mesosinusid. The second ridge is parallel to the first one and directed to the entoconid without reaching it. This would correspond to an incomplete hypolophulid as in the m2 specimens, see HLMD-Ez-2181 (Figure 3y). Therefore, the m3 lacks a mesolophid. The posterior part of the tooth is closed by a well-developed posterolophid. The sinusid is also closed by a low cingulid.

Petersbuch 36 (Germany) MN3

One maxillar fragment with M1-M3 (NRM-PZ M8158); one mandibular jaw with m1-m3 (NRM-PZ M8159); one mandibular fragment with m1-m2 (NRM-PZ M8160). For collection numbers and measurements see Table 2.

The Petersbuch 36 material is well preserved and offers the possibility to see the cheek teeth in their natural position thanks to the preservation of a maxillary fragment and two mandibular jaws with the teeth displayed in it (NRM-PZ M8159, Figure 4 b1, b2). Regarding the molars, they do not show any substantial morphological difference from the Echzell specimens described above despite the Petersbuch 36 material is younger. As for the size, they fit with the Echzell material and with the specimens from Petersbuch 2 previously studied by Ziegler and Fahlbusch (1986) (see Figure 2).

The lower jaw exhibits a well-expressed bulb in the labial part of the mandible (NRM-PZ M8159, Figure 4 b1, b2). This bulb has no relationship with the molar row or the incisor; instead, it represents a deep muscular insertion for the masseter muscle. This bulb has also been detected in the Echzell specimen HLMD-Ez-2174 (see Figure 4 a1, a2) and in the Petersbuch 38 specimen NRM-PZ M8163.

Petersbuch 38 (Germany) MN4

One M2 (NRM-PZ M8161); one m1 (NRM-PZ M8162); one m2 (NRM-PZ M8163); one m3 (NRM-PZ M8164). For collection numbers and measurements see Table 3.

The Petersbuch 38 material shows no morphological differences from the Echzell material described above. However, the m1 NRM-PZ M8162 is markedly smaller than the m1 from Echzell, other Petersbuch sites, and from Beaulieu 2 (Figure 2). Despite this size difference, this tooth lies well within the other MN4 *Melissiodon dominans* material compiled to perform the MN4 ellipse in Figure 2. Since there is no morphological difference, we attribute this difference in size as variability within the species.

The lower m2 (NRM-PZ M8163) is attached to a mandibular fragment. This mandibular fragment shows the same bulb in its labial part below the m2, as the mandibular jaw from Echzell (HLMD-Ez-2174, Figure 4 a1, a2) and Petersbuch 36 (NRM-PZ M8159, Figure 4 b1, b2).

Table 2. Collection numbers and measurements in millimetres of *Melissiodon dominans* cheek teeth from Petersbuch 36. Only complete specimens are considered for measurements.

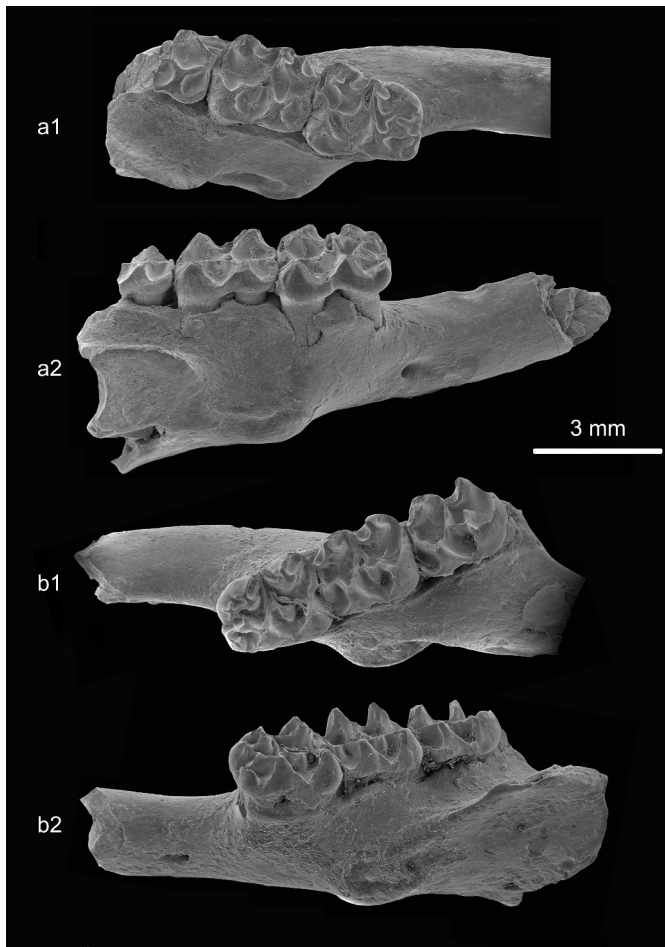| Locality	Number	Element (L/R)	Length	Width
Petersbuch 36	NRM-PZ M8158	M1-M3 (M1R)	3,12	2,25
Petersbuch 36	NRM-PZ M8158	M1-M3 (M2R)	2,03	1,87
Petersbuch 36	NRM-PZ M8158	M1-M3 (M3R)	1,65	1,9
Petersbuch 36	NRM-PZ M8159	m1-m3 (m1L)	2,37	1,87
Petersbuch 36	NRM-PZ M8159	m1-m3 (m2L)	2,18	1,87
Petersbuch 36	NRM-PZ M8159	m1-m3 (m3L)	2,34	1,81
Petersbuch 36	NRM-PZ M8160	m1-m2 (m1L)	2,62	2,18
Petersbuch 36	NRM-PZ M8160	m1-m2 (m2L)	2,56	2,03

Figure 4. Scanning electron microscope (SEM) micrographs of *Melissidon dominans* mandibles. a1, a2, from Echzell (HLMD-Ez-2174), a1, occlusal view, a2, buccal view; b1, b2 from Petersbuch 36 (NRM-PZ M8159), b1, occlusal view, b2, buccal view.

Table 3. Collection numbers and measurements in millimetres of *Melissiodon dominans* cheek teeth from Petersbuch 38. Only complete speciemens are considered for measurements.

Locality	Number	Element (L/R)	Length	Width
Petersbuch 38	NRM-PZ M8161	M2R	2,02	1,87
Petersbuch 38	NRM-PZ M8162	m1R	2,27	1,7
Petersbuch 38	NRM-PZ M8163	m2L	2,46	2,02
Petersbuch 38	NRM-PZ M8164	m3L	2,46	1,9

Petersbuch 7 (Germany) MN4

Two M2 (NRM-PZ M8165; NRM-PZ M8170 almost complete, but metacone cusp broken); one M3 (NRM-PZ M8166); two m1 (NRM-PZ M8167, NRM-PZ M8168); one m2 (NRM-PZ M8169); one m3 (NRM-PZ M8171 posterior fragment). For collection numbers and measurements see Table 4.

These materials show many similarities with the Echzell specimens in tooth morphology and dimensions (Figure 2). Regarding the M2, they are morphologically similar to the Echzell material. We would like to highlight the presence of a well-developed postero-lingual valley in both specimens. The M3 has also this general button-shape morphology with the posterior part of the tooth reduced. It also lacks the mesoloph, being the protocone and paracone the main cusps in the tooth. Regarding the lower molars, the m1 show no differences between them. Similarly, as the Echzell specimens, the mesolophid is parallel to the protoconid hind arm. It

Table 4. Collection numbers and measurements in millimetres of *Melissiodon dominans* cheek teeth from Petersbuch 7. Only complete specimens are considered for measurements.

Locality	Number	Element (L/R)	Length	Width
Petersbuch 7	NRM-PZ M8165	M2L	2,24	1,95
Petersbuch 7	NRM-PZ M8166	M3R	1,83	1,97
Petersbuch 7	NRM-PZ M8167	m1L	2,59	1,85
Petersbuch 7	NRM-PZ M8168	m1R	2,41	1,85
Petersbuch 7	NRM-PZ M8169	m2L	2,29	1,97

Table 5. Collection numbers and measurements in millimetres of *Melissiodon dominans* cheek teeth from Beaulieu 2. Only complete specimens are considered for measurements.

Locality	Number	Element (L/R)	Length	Width
Beaulieu 2	NRM-PZ M8175	M2L	2,46	2,07
Beaulieu 2	NRM-PZ M8176	M3L	1,97	2,07
Beaulieu 2	NRM-PZ M8177	m1L	2,71	2,09
Beaulieu 2	NRM-PZ M8178	m2L	-	-

is also medium-sized and does not reach the margin of the tooth or the mesostylid. The m2 (NRM-Pz M8169) shows no particular differences from the general morphology of the lower m1, with the anterior part of the tooth reduced. The m3 shows the elongated general morphology, with many shared features of the lower m2.

Beaulieu 2 (France) MN3

One M2 (NRM-PZ M8175); one M3 (NRM-PZ M8176); one m1 (NRM-PZ M8177); one m2 fragment (NRM-PZ M8178) and several molar fragments were not considered for measurements and description due to their poor preservation state. For collection numbers and measurements see Table 5.

These materials show many similarities with the Echzell specimens; however, some morphological differences can be spotted. Moreover, these specimens are a bit larger than the Echzell specimens (Figure 2).

The M2 (NRM-PZ M8175) shows the same morphological characteristics as the M2 from Echzell. Some differences can be spotted in the central region of the tooth, where the Beaulieu M2 shows a long mesoloph, and the entoloph does not connect directly with the mesoloph. The M3 shows no substantial morphological difference to the Echzell material.

The lower m1 (NRM-PZ M8177) presents several morphological differences. The anteroconid cusps present a narrow deep valley between them. There is also no connection between the labial spur of the lingual anteroconid and the anterolophulid. This results in a continuous narrow deep valley in the anterior part of the tooth that is not present in the m1 from Echzell. The lingual posterior spur of the paracone does not connect with the mesoloph or the mesostyl. In the same way, the labial posterior spur does not connect to the mesoloph either, resulting in an open mesosinus.

Discussion and conclusions

The specimens studied from the German sites (Echzell, Petersbuch 7, 36, and 38) and the French site Beaulieu 2 fit dimensionally and morphologically to the type material of *Melissiodon dominans* from Wintershof-West described in Dehm (1950) and Hrubesch (1957). Some of these characteristics consist of the M1, a large anterocone complex, which is more developed in the labial part of the teeth, resulting in a sinuous labial outline, rather than straight in *M. schaubi* for example. The anterocone complex is also divided

into two main cusps separated by a narrow valley. Moreover, the M1 show a pronounced protostyle that connects with the lingual cusp of the anterocone by a small ridge. Regarding the lower molars, they have a reduced mesolophid present in all teeth except for m3 specimens. The m1 show robust anteroconid cusps, but they are smaller than the protoconid. All m1 specimens show a well-defined labial anteroconid. There is some variability in this feature with some *M.* aff. *dominans* having a cristid-like labial anteroconid (currently under study by authors in this work) instead of the cuspid-like morphotype that we observe in the material studied in this work. Beaulieu 2 specimens show both morphotypes (Aguilar et al. 2003). An in-depth study of *Melissiodon* populations through the early Miocene in Europe would enlighten the understanding of this genus and give more insight into intraspecific variation, such as the variation of the m1 anterconid morphology, and if different species within what we now call *Melissiodon dominans* should be considered. Apart from dental morphological features, we also compared the tooth dimensions of the specimens studied with the already published data from different MN3 and MN4 localities across Europe. Despite the MN system can be imprecise due to differences of the faunistical association between different regions (De Bruijn et al. 1992; Van Dam et al. 2001; Van Dam 2003; Van der Meulen et al. 2011, 2012), we use it to have a general view of the distribution of *M. dominans* across Europe during the early Miocene.

The specimens from Echzell, Petersbuch 7, 36, 38, and Beaulieu 2 have been compared with MN3 and MN4 material from different localities (for localities and references see Material and Methods, Figure 2). Moreover, our Petersbuch and Beaulieu specimens have also been compared with the previously published specimens from these sites (Ziegler and Fahlbusch 1986; Aguilar et al. 2003).

The Echzell material studied in this work is the richest and fits in size with the specimens from other MN4 localities used for comparison. It is also morphological similar to the Petersbuch 7, 36 and 38 materials. However, some differences can be seen between the Echzell specimens and Beaulieu 2 material, such as a long mesoloph in the M2 and the missing connection between the entoloph and the mesoloph. The Beaulieu 2 specimens fit in size with the already published material from this same site by Aguilar et al. (2003), and also fits within the range of the other MN3 specimens from other localities (Figure 2). However, Beaulieu 2 specimens seem to be a bit larger compared to those studied from Echzell and Petersbuch 7, 36, and 38 (Figure 2). Regarding the Petersbuch 7, 36, and 38 materials, it fits in size with the specimens from Petersbuch 2 already published by Ziegler and Fahlbusch (1986). This material also is similar in size to the Echzell specimens and also to the MN4 localities used for comparison (Figure 2).

The unusual tooth morphology of *Melissiodon dominans* can give us some clues regarding its possible diet preferences. The mandible morphology together with tooth morphology would indicate a more insectivorous diet. Insectivorous diet has evolved several times in Rodentia. Hordijk et al. (2015) suggested the murine shrew rats from South-East Asia as an analogue for *Melissiodon*. Shrew rat genera seem to have independently evolved long diastema and slender incisors and all of them feed on soft invertebrates like earthworms. *Paucidentomys* from Sulawesi is even edentulous except for the incisors (Esselstyn et al. 2012). We would like to highlight here *Onychomys leucogaster*, a species from North America as an analogue. The lower jaw of these neotomine grasshopper mice remarkably resembles mandibular morphology of *Melissiodon*. The central African insectivorous deomyine murid *Deomys* has evolved tweezer-like mandibles with slender incisors that end under the m2 like in *Melissiodon* (Figure 4). The lower incisors of *M. dominans* are

characterised by a remarkable thin enamel band that shows a buckle in the middle of teeth, according to Kalthoff (2000) a unique feature in Cricetidae that represents a reminiscence of three enamel ribs in that position, present in early Oligocene *Melissiodon*. Surprisingly, and contrary to the highly derived molar morphology, the enamel microstructure of the lower incisors in all *Melissiodon* species is underived in contrast to the highly derived enamel microstructure in other Palaeogene Cricetidae, thus reconsidering the phylogenetic relationship of *Melissiodon* (Kalthoff 2000).

Concerning the habitat, Hordijk et al. (2015) pointed out that *Melissiodon* is invariably rare in lacustrine deposits and more common in fissure fillings, and interpreted *Melissiodon* species to be inhabitants of dry limestone plateaus. Taking into account that *M. dominans* is also quite abundant in Echzell, which is not a fissure fill deposit, it appears to us that this species generally avoided wet lowland habitats and instead preferred less wet upland habitats, but not necessary dry karst plateaus.

In conclusion, the *Melissiodon* specimens studied from the French and German localities fits in size with the *Melissiodon dominans* from the type locality; therefore, we ascribe this new material as *Melissiodon dominans*. This species of cricetid is noteworthy for its rare cheek teeth and mandible morphology which have prompted discussions regarding its diet. Regarding the palaeoecological preferences of *M. dominans*, it seems to prefer upland habitats with seasonal wet conditions. The paleoenvironmental reconstructions for central Europe's early Miocene are consistent with these results.

ORCID

Sílvia Jovells-Vaqué 🔵 http://orcid.org/0000-0003-0358-0840
Thomas Mörs 🔵 http://orcid.org/0000-0003-2268-5824

References

Aguilar JP, Clauzon G, Goer de Herve A, Maluski H, Michaux J, Welcomme J. 1996. The MN3 fossil mammal-bearing locality of Beaulieu (France): biochronology, radiometric dating, and lower age limit of the Early Neogene renewal of the mammalian fauna in Europe. Newsl. Stratigr. 34:177–191. doi:10.1127/nos/34/1996/177.

Aguilar JP, Crochet JY, Antoine PO, Martínez NL, Métais G, Welcomme JL, Michaux J. 2003. Les mammifères du Miocène inférieur de Beaulieu (Bouches-du-Rhône, France), comparaison avec Wintershof-West et le problème de la limite MN3/MN4. [Mammals from the lower Miocene of Beaulieu (Bouches-du-Rhône, France), comparison with Wintershof-West and the problem of the MN3/MN4 boundary] Col. Paleontol. 1: 1–24. French.

Aguilar JP, Escarguel G, Crochet JY, Sigé B, Sudre J. 1997. Nouveaux sites d`âges variés dans les remplissages karstiques du Miocène inférieur de Bouzigues (Hérault, Sud de la France). Partie II: faunes 2 (rongeurs), biochronologie et corrélations. [New sites of varying ages in the karstic fills of the lower Miocene of Bouzigues (Hérault, southern France. Part II: faunas 2 (rodents), biochronology and correlations]. Geobios M.S. 20: 485–491. French.

Antunes MT, Mein P. 1992. Les plus anciens mammifères terrestres du Miocène marin de Lisbonne - le gisement du Km 10. [The oldest land mammals from the marine Miocene of Lisbon - the km 10 deposit]. Ciencia da Terra (UNL). 11: 127–140. French.

Bolliger T. 1992. Kleinsäugerstratigraphie in der miozänen Hörnlischüttung (Ostschweiz). [Small mammal stratigraphy of the Miocene Hörnli fan (Eastern Switzerland). Docum. Nat. 75: 1–296. German.

Bolliger T, Rummel M. 1994. Säugetierfunde aus Karstspalten - Die komplexe Genese am Beispiel eines Steinbruches bei Petersbuch, Südliche Frankenalb (Bayern). Mitt. Bayer. Staatsslg. Paläont. Hist. Geol. 34: 239–264. German.

Bonilla-Salomó I, Čermák S, Luján ÀH, Horáček I, Ivanov MA, Sabol M. 2021. Early Miocene small mammals from MWQ1/2001 Turtle Joint (Mokrá-Quarry, South Moravia, Czech Republic): biostratigraphical and palaeoecological considerations. Bull Geosci. 96:99–122. doi:10.3140/bull.geosci.1801.

Bowdich TE. 1821. An analysis of the natural classifications of mammalia for the use of students and travellers. Smith J. Paris IV. 115.

Bulot C, Antoine PO, Duranthon F. 2009. Rongeurs et lagomorphes du Miocène inférieur de Béon 2 (MN4, Montréal-du-Gers, SW France). [Rodents and lagomorphs from the lower Miocene of Béon 2]. Ann de Paléontol. 95 (4):197–215. French. doi:10.1016/j.annpal.2009.09.003.

Crespo Roures VD 2017. Los mamíferos del Mioceno inferior de la Cuenca de Ribesalbes-Alcora (Castelló,España). [The mammals of the lower Miocene of the Ribesalbes-Alcora Basin (Castellón, Spain)] [Dissertation]. Universitat de València. Spanish.

Daams R, Freudenthal M. 1989. The Ramblian and Aragonian: limits, subdivision, geographical and temporal extension. In: Lindsay EH, Fahlbusch V, Mein P, editors. European Neogene mammal chronology. New York: Springer US; p. : 51–59.

Dawson MR. 2003. Paleogene rodents of Asia. Deinsea. 10: 97–126.

De Bruijn H, Daams R, Daxner-Höck G, Fahlbusch V, Ginsburg L, Morales J, Heinzmann E, Mayhew DF, Van der Meulen AJ, Schmidt-Kittler N, et al. 1992. Report of the RCMNS working group on fossil mammals, Reisenburg 1990. Newsl. Stratigr. 26(2/3):65–118. doi:10.1127/nos/26/1992/65.

De Bruijn H, Ünay E, Hordijk K. 2013. Chapter 26. A review of the Neogene succession of the Muridae and Dipodidae from Anatolia, with special reference to taxa known from Asia and/or Europe. In: Wang X, Flynn L, Fortelius M, editors. Fossil mammals of Asia. New York Chichester, West Sussex: Columbia UNiversity Press. p. 566–582.

Dehm R. 1937. Neue tertiäre Spaltenfüllungen im südlichen Fränkischen Jura. [New Tertiary fissure fillings in the southern Franconian Jura]. Zbl. Miner. Geol. Paläont. B. 1937(9):349–369. German.

Dehm R. 1939. Über neue tertiäre Spaltenfüllungen im Fränkischen und Schwäbischen Jura. [About new Tertiary fissure fillings in the Franconian and Swabian Jura]. Zbl. Miner. Geol. Paläont. B. 1939(4):113–124. German.

Dehm R. 1950. Die Nagetiere aus dem Mittel-Miocän (Burdigalium) von Wintershof-West bei Eichstätt in Bayern. [The rodents from the middle Miocene (Burdigalian) of Wintershof-West near Eichstätt in Bavaria]. Neues Jahrb. Geol. Paläontol. Abh. 91: 321–428. German.

Esselstyn JA, Achmadi AS, Rowe KC. 2012. Evolutionary novelty in a rat with no molars. Biol. Lett. 8:990–993. doi:10.1098/rsbl.2012.0574.

Fahlbusch V. 1989. European Neogene rodent assemblages in response to evolutionary, biogeographic, and ecologic factors. papers on fossil Rodents in honor of Albert Elmer Wood. Nat. Hist. Mus. LA County, Sci. Ser. 33:129–138.

Fejfar O. 1990. The Neogene VP sites of Czechoslovakia: a contribution to the Neogene terrestric biostratigraphy of Europe based on rodents. In: Lindsay EH, Fahlbusch V, Mein P, editors. European Neogene mammal chronology. NATO ASI series. Series A (Vol. 180). New York (NY): Plenum Press; p. 211–236.

Fejfar O, Dvorák Z, Kadelecová E. 2003. New record of early Miocene (MN3a) mammals in the open brown coal pit Merkur, North Bohemia, Czech Republic. Deinsea. 10:163–182.

Fejfar O, Kalthoff DC. 1999. Aberrant cricetids (Platacanthomyines, Rodentia, Mammalia) from the Miocene of Eurasia. Berliner geowiss. Abh. E. 30:191–206.

Fischer von Waldheim G. 1817. Adversaria zoologica. [Zoological Adversary]. Mem.Soc.Nat.Moscou. 5: 357–471. Latin.

Freudenthal M, Hugueney M, Moissenet E. 1994. The genus *Pseudocricetodon* (Cricetidae, Mammalia) in the upper oligocene of the province of Teruel (Spain). Scripta Geol. 104:57–114.

Freudenthal M, Lacomba JI, Sacristán MA. 1992. Classification of European Oligocene cricetids. Rev Esp Paleontol Extra 1992. 49–57.

Hordijk K, Bosma A, De Bruijn H, Van Dam J, Geraedts G, Van den Hoek Ostende LW, Reumer J, Wessels W. 2015. Biostratigraphical and palaeoecological implications of the small mammal assemblage from the late early Miocene of Montalvos2, Teruel Basin, Spain. Palaeobiodivers Palaeoenviron. 95:321–346. doi:10.1007/s12549-015-0203-2.

Hrubesch K. 1957. Zahnstudien an tertiären Rodentia als Beitrag zu deren Stammesgeschichte. Über die Evolution der Melissiodontidae, eine Revision der Gattung *Melissiodon*. [Dental studies at Tertiary Rodentia as a contribution to their evolution. About the evolution of the Melissiodontidae, a revision of the genus *Melissiodon*]. Bayer. Akad. Wiss. Math.-Natur. Kl. 83: 1–101. German.

Hugueney M, Bulot C. 2011. Les petits Mammifères du Burdigalien (MN3; Miocène) d'Estrepouy (Gers, France): liste faunique actualisée. [The small Mammals of the Burdigalian (MN3; Miocene) of Estrepouy (Gers, France): updated faunal list]. Estud. Geol. 67(2):427–442. French. doi:10.3989/egeol.40584.200.

Jovells-Vaqué S 2020. Early Miocene cricetids from the Vallès-Penedès Basin (Catalonia): taxonomy, biostratigraphy and paleoecological implications. [Dissertation]. Autonomous University Barcelona, Spain.

Jovells-Vaqué S, Casanovas-Vilar I. 2018. A review of the genus *Melissiodon* (Cricetidae, Rodentia) in the Vallés-Penedès Basin (Catalonia). J. Vertebr. Paleontol. 38(5):e1520714. doi:10.1080/02724634.2018.1520714.

Kalthoff DC. 2000. Die Schmelzmikrostruktur in den Incisiven der hamsterartigen Nagetire und anderer Myomorpha .Rodentia, Mammalia. Palaeontogr. A. 259: 1–193. German.

Maridet O, Ni X. 2013. A new cricetid rodent from the early Oligocene of Yunnan, China, and its evolutionary implications for early Eurasian cricetids. J. Vertebr. Paleontol. 33(1):185–194. doi:10.1080/02724634.2012.710283.

Matthew WD, Granger W. 1923. Nine new rodents from the Oligocene of Mongolia. Am. Mus. Novit. 102:1–10.

Mein P. 1989. Updating of MN zones. In: Lindsay EH, Fahlbusch V, Mein P, editors. European Neogene Mammal Chronology. New York: Plenum Press; p. 73–90. [imprint date 1990].

Mein P, Freudenthal M. 1971. Une nouvelle classification des Cricetidae (Mammalia, Rodentia) du Tertiaire de l'europe. [A new classification of Cricetidae (Mammalia, Rodentia) from the Tertiary of Europe]. Scripta Geol. 2: 1–37. French.

Mödden C. 1999. Family Melissiodontidae. In: Rössner GE, Heissig K, editors. The Miocene Land Mammals of Europe. Munich: Verlag Dr. Friedrich Pfeil; p. 343–348.

Mörs T. 2010. Wirbeltiere aus dem Miozän von Homberg/Ohm (Vogelsberg, Hessen). Geol. Jahrb. Hessen. 136: 109–119. German.

Mörs T, Flink T. 2018. Large apeomyine rodents (Mammalia, Eomyidae) from the early Miocene of Echzell, Germany. Hist. Biol. 30:1102–1111. doi:10.1080/08912963.2017.1338695.

Pineker P, Mörs T. 2011. *Neocometes* (Rodentia, Platacanthomyinae) from the early Miocene of Echzell, Germany. Geobios. 44:279–287. doi:10.1016/j.geobios.2010.12.001.

R Core Team. 2017. R: a language and environment for statistical computing. URL. Vienna (Austria): R Foundation for Statistical Computing. https://www.R-project.org/

Rummel M. 2000. Die Cricetodontini aus dem Miozän von Petersbuch bei Eichstätt. Die Gattung *Cricetodon* Lartet 1851. Senck. Leth. 80:149–170. German. doi:10.1007/BF03043668.

Schalk K. 1957. Geologische Untersuchungen im Ries. Das Blatt Bissingen. [Geological investigations in the Ries. Sheet Bissingen]. Geol. Bav. 31: 1–107. German.

Schaub S. 1920. *Melissiodon* nov. gen., ein bisher Übersehener oligocäner Muride. Vol. 2. German: Senckenberg; p. 43–47. [*Melissiodon* nov. gen., a hitherto overlooked oligocene murid].

Schaub S. 1925. Die hamsterartigen Nagetiere des Tertiärs und ihre lebenden Verwandten. Eine systematisch-odontologische studie. [The hamster-like rodents of the Tertiary and their living relatives. A systematic-odontological study]. Abh. Schweiz. Paläontol. Ges. 45(3):1–114. German.

Sesé C. 1987. *Eucricetodon* and *Melissiodon* (Cricetidae, Rodentia) from the Ramblian and Lower Aragonian of the Calamocha area (Calatayud-Teruel Basin, Spain). Scripta Geol. 83:1–17.

Steinthorsdottir M, Coxall HK, de BAM, Huber M, Barbolini N, Bradshaw CD, Burls NJ, Feakins SJ, Gasson E, Henderiks J, et al. 2021. The Miocene: the future of the past. Paleoceanogr Paleoclimatol. 36(4):e2020PA004037. doi:10.1029/2020PA004037.

Tobien H. 1954. Eine miozäne Säugetierfauna aus vulkanischen Tuffen des Vogelsberges . Zeitschr. Dtsch. Geol. Ges.105: 588.

Ünay-Bayraktar E. 1989. Rodents from the middle Oligocene of Turkish Thrace. Utrecht Micropaleontol Bull. Spec Publ. 5:1–119.

Van Dam JA. 2003. European Neogene mammal chronology: past, present and future. Deinsea. 10:85–95.

Van Dam JA, Alcalá L, Alonso Zarza A, Calvo JP, Garcés M, Krijgsman W. 2001. The upper Miocene mammal record from the Teruel-Alfambra region (Spain). The MN system and continental stage/age concepts discussed. J. Vertebr. Paleontol. 21(2):367–385. doi:10.1671/0272-4634(2001)021[0367:TUMMRF]2.0.CO;2.

Van der Meulen AJ, García-Paredes I, MÁ Á-S, van den Hoek Ostende LW, Hordijk K, Oliver A, López-Guerrero P, Hernández-Ballarín V, Peláez-Campomanes P. 2011. Biostratigraphy or biochronology? Lessons from the early and middle Miocene small Mammal events in Europe. Geobios. 44(2–3):309–321. doi:10.1016/j.geobios.2010.11.004.

Van der Meulen AJ, García-Paredes I, Sierra MÁ Á, Van den Hoek Ostende LW, Hordijk K, Oliver A, Pélaez-Campomanes P. 2012. Updated Aragonian biostratigraphy: small mammal distribution and its implications for the Miocene European chronology. Geol. Acta. 10(2):159–179.

Vasilyan D, Čerňanský A, Szyndlar Z, Mörs T. in press. Amphibian and reptilian fauna from the early Miocene of Echzell, Germany.

Wessels W, Van de Weerd AA, De Bruijn H, Marković Z. 2018. New Melissiodontinae (Mammalia, Rodentia) from the Paleogene of south-east Serbia. Paleobiodivers Paleoenviron. 98(3):471–487. doi:10.1007/s12549-017-0311-2.

Ziegler R, Fahlbusch V. 1986. Kleinsäugerfaunen aus der basalen Oberen Süsswasser-Molasse Niederbayerns Zitteliana. 14: 3–58.