Early Miocene remains of *Melissiodon* from Mokrá-Quarry (Moravia, Czech Republic) shed light on the evolutionary history of the rare cricetid genus

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Abstract

Background. *Melissiodon* is a rare cricetid genus endemic to Europe, known from the early Oligocene to the early Miocene. It is usually a very rare find, and even in the few localities where *Melissiodon* remains are found, those are scarce and fragmented. Only a few Central European localities have yielded rich remains of the genus. Currently, two species are known from the early Miocene: *Melissiodon schlosseri,* which is based on two teeth from the MN2 German locality of Haslach and only found in two other sites of similar age (Ulm-Uniklinik and La Chaux, from Germany and Switzerland respectively); and *Melissiodon dominans,* found in MN3 and MN4 localities across Europe, even though the scarce and fragmentary remains make some of these attributions dubious. For that reason, *Melissiodon dominans* has become a catch-all species. However, Mokrá-Quarry represents one of the best documented findings of *Melissiodon* remains from MN4 localities of Europe.

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Methods. The *Melissiodon* assemblage from Mokrá-Quarry has been studied thoroughly, providing metrics and detailed descriptions of all teeth positions, as well as complete comparisons with other MN3 and MN4 localities bearing *Melissiodon* remains.

Results. In this work, new remains of *Melissiodon* have been identified as a new morphotype that clearly differs from *Melissiodon dominans* by its unique m1 morphology but still shows some resemblance with *Melissiodon schlosseri.* Based on that, we here propose the hypothesis of an evolutionary line starting from *Melissiodon schlosseri*, diverging from the lineage leading towards *Melissiodon dominans.* With this finding, there are at least two different taxa of *Melissiodon* known during the latest early Miocene, prior to the genus extinction. This study arises the certainty that the evolution history of the genus is more complex than previously thought and that more studies are necessary to elucidate the evolutionary history of the genus, including a complete revision of the type material of *Melissiodon dominans* and *Melissiodon schlosseri* in the light of current knowledge of the genus, which will help to elucidate the attribution of the populations form Mokrá-Quarry. For the time being, the assemblage presented here is referred as *Melissiodon* aff. *schlosseri*.

Subjects Vertebrate Paleontology, Taxonomy

Keywords Melissiodontinae, *Melissiodon schlosseri, Melissiodon dominans*, Burdigalian, Carpathian Foredeep Basin, Moravian Karst.

Introduction

The extinct genus *Melissiodon*, originally described by Schaub, 1920 is a rare fossil cricetid that ranged from the early Oligocene (MP23) to the early Miocene of Europe (MN4). However, more recent research on the biostratigraphy in the Vallès-Penedès Basin (Catalonia, Spain) date the Miocene site of Sant Mamet, from which *Melissiodon* remains were recovered (Jovells-Vaqué & Casanovas-Vilar 2018), to the beginning of the MN5 (Jovells-Vaqué 2020; Jovells-Vaqué & Casanovas-Vilar 2021). To date, *Melissiodon* includes nine species (Hrubesch 1957; Mödden 1999). Its genus name, meaning “honeycomb tooth”, refers to its peculiar molar morphology, which is characterized by slender crests enclosing numerous pits. In the few European localities where this genus has been recovered, the remains are very scarce and mostly fragmentary. According to de Bruijn et al. (2013), outside of Europe *Melissiodon* sp. is only known from the Anatolian assemblage of Kargi-2 (latest Oligocene-earliest

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Miocene in age), although only a complete M3 and a fragmented m1 have been reported.

Over the Oligocene, up to six different species of *Melissiodon* are recognized in Europe (Schaub 1920, 1925; Freudenberg 1941; Hrubesch 1957). The most extensive work regarding the genus *Melissiodon* during this epoch was carried by Hrubesch (1957), who reviewed most of the available material of the genus and erected three new taxa: two new species and one subspecies. During the Oligocene, *Melissiodon* was much more diverse than it was during the early Miocene, including four different lineages (see Hrubesch 1957).

Regarding the Miocene, only two species, *Melissiodon schlosseri* and *M. dominans*, have been identified. *Melissiodon schlosseri*, the type species of the genus, was established long ago by Schaub (1925) based on two lower molars (i.e., m1 and m3) from Haslach (Germany, MN2). Later, Hrubesch (1957) suggested that an m3 from La Chaux (Swiss Molasse Basin, MN2) could belong to the same species. Moreover, Werner (1994) and Engesser & Mödden (1997) identified very small assemblages belonging to *M.* aff. *schlosseri* from MN2 localities of Ulm-Uniklinik and La Chaux 7: Germany and Switzerland respectively. In fact, only a faunal list was published from the second site.

The second species, *Melissiodon dominans*, was erected by Dehm (1950) from a rich collection from the fissure filling of Wintershof-West (Germany, MN3). This exceptional assemblage constitutes one of the largest collections recovered of the taxa, including: 40 M1, 36 M2, 8 M3, 36 m1, 39 m2 and 30 m3. Shortly after, it was studied in detail by Hrubesch (1957), who assessed the intraspecific variation of the species from this locality, as well as other German MN3 sites (i.e., Wintershof-Ost, Wüterich, and Schnaitheim), which were not as rich as the type locality. In the slightly younger

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The subfamily Cricetopsinae was originally stablished by de Buijn & Koenigswald (1994), but Mckenna & Bell (1997) corrected it to Cricetopinae (terminology followed in this paper). As for the phylogeny, Maridet & Ni (2013) recovered *Melissiodon* into this subfamily, being *Melissiodon* the sister of *Selenomys*, and the two would constitute the sister group of *Mirrabella*: the monophyletic group including the former three genera was called *Melissiodon* clade. Maridet & Ni (2013) included other genera into Cricetopinae (e.g., *Cricetops*, *Meteamys*, and *Selenomys*), however, the most remarkable relocation was that *Edirnella* was recovered into subfamily Pseudocricetodontinae, and consequently, more tightly related to the genera *Pseudocricetodon*, *Adlomyarion* and *Rericricetodon*. This proposal was not followed by ...

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locality of Schnaitheim, significantly larger remains than the type population (i.e., Wintershof-West) were found and referred to *M. dominans*. Remains of this species have also been found in other European MN3 localities, including: Austria (Mein 1989); Switzerland (Bolliger 1992); Spain (Crusafont et al. 1955; Agustí 1981; Sesé 1987; Jovells-Vaqué & Casanovas-Vilar 2018); and France (Aguilar et al. 2003; Bulot et al. 2009). As for the Czech Republic, the only record of *M. dominans* comes from the MN3 site of Ahníkov I, so far published without detailed description (see Fejfar et al. 2003 for details).

Regarding the MN4, very few sites have been found with the level of richness as the MN3 localities. Despite this, some sites yielding *Melissiodon dominans* remains have been identified. Ziegler & Fahlbusch (1986) described *Melissiodon* material from the Upper Freshwater Molasse sites (Germany; Rembach and Fortshart), which despite showing differences in size and morphology, were attributed to *M. dominans*. The same authors also studied remains of the much richer sites of Erkertshofen 1 and Petersbuch 2, but no figures of the remains were provided. Mein & Freudenthal (1981) and Bulot et al. (2009) described scarce remains of *Melissiodon* from the French sites of Vieux-Collonges (Rhône) and Beón 2 (Montreal du Gers). Similarly, the Spanish sites of Montalvos 2 (Hordijk et al. 2015), Barranc de Campisano and Mas d'Antolino (Crespo 2017), and Sant Mamet (Jovells-Vaqué & Casanovas-Vilar 2018) have also yielded scant elements referred to *M. dominans*. Regarding Czech sites, Fejfar (1990) published measurements and drawings of some upper and lower first molars from the early Miocene localities of Dolnice 1, 2, 3 and Ořechov, although no descriptions or data regarding the rest of the molars were provided. Mokrá-Quarry (early Miocene, MN4), a karstic site located close to Brno (Moravia, Czech Republic; Figure 1), constitutes the latest fossil site from which *Melissiodon* remains have been recovered (see Ivanov et al.

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2006 for a detailed geological setting; Bonilla-Salomón et al. 2021a for a discussion on its age based on the small mammal association). The genus *Melissiodon* has been identified in 1/2001 Turtle Joint, 2/2003 Reptile Joint from the Western Quarry (hereinafter MWQ 1/2001 and MWQ 2/2003, respectively); and 3/2005 from the Central one (MCQ 3/2005 from here after). At the species level, a small association of *M. dominans* from MWQ 1/2001 has been published by Bonilla-Salomón et al. (2021a).

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However, *Melissiodon dominans* has become a "waste-basket". Most of the remains found in Europe in MN3 and MN4 localities are referred to this species, despite its attribution being dubious due to the scarcity of remains in most assemblages. The species shows a set of morphological characters that varies significantly between localities (for instance, populations from Forsthart and Rembach compared with the type population), but also in the slightly younger localities (in most MN4 sites *Melissiodon dominans* remains are notably smaller than the type population; see remarks section below for a complete discussion). In that sense, several authors have identified populations which can be referred to different forms of *Melissiodon*, but the scarcity of the remains prevented them to erect a new species (see Mein & Freudenthal 1981; Bulot et al. 2009).

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The assemblage from Mokrá-Quarry is exceptional, since it constitutes one of the best documented findings of the genus among MN4 localities. In this work, we describe all available material of *Melissiodon* aff. *schlosseri* from two karst fissures from Mokrá-Quarry (i.e., MWQ 2/2003 and MCQ 3/2005), and the morphological differences between MN3 and MN4 European assemblages are assessed. Moreover, the evolution of the genus during the early Miocene is discussed and new hypotheses are proposed.

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Material & methods

The micromammal fauna from MWQ 2/2003 and MCQ 3/2005 was discovered during the field campaigns lead by M. Ivanov and R. Musil from the Masaryk University (Brno, Czech Republic) during the years 2002–2005. Fossil remains, mixed in sand and clays, were obtained by washing in sieves of 0.5 mm mesh (Ivanov et al. 2006). Field campaigns were approved by the Masaryk University under the project number: MUNI/31 8016 ("Systematic survey of sediments of karst fissures in the area of the Mokrá Quarry"). The material is currently housed in the collections of the Department of Geological Sciences (Faculty of Science, Masaryk University) under the inventory numbers SMM/009-09-11/ 372009, Pal. 3000–3910. Upper cheek teeth are indicated by upper case letters (M1, M2, M3), whereas lower cheek teeth by lower case (m1, m2, m3). Dental terminology follows Jovells-Vaqué & Casanovas-Vilar (2018), with some modifications (Figure 2). Additional crests and cristids are named based on their position relative to the main cusp or cuspid from which they run (e.g., anterior labial arm of entoconid).

Measurements were taken with the Carl Zeiss Stemi 305 microscope and the Carl Zeiss W-PI 10x/23 Microscope Focusable Eyepiece, providing cheek teeth occlusal surface maximum length and width (L × W). All measured data are given in millimeters (mm). Micrographs were taking using the Quanta FEG 250 Scanning Electron Microscope (SEM) at the Institute of Electrical Engineering of the Slovak Academy of Sciences (SAS) in Bratislava (Slovakia). All teeth are figured as left elements. Miocene time scale and biostratigraphy is based on International Chronostratigraphic Chart (Cohen et al. 2020), Central and Eastern Paratethys boundaries follow Gozhyk et al. (2015) and Kováč et al. (2018); MN-zonations for Western (left) and Central (right) Europe follow Steininger (1999) and Hilgen et al. (2012). Age and chronological position of the localitites mentioned in the text and figures are based on works of

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Bolliger (1992); Steininger (1999); Bulot & Ginsburg (1996); Aguilar et al. (2003); Bulot et al. (2009); Reichenbacher et al. (2013); Ruiz-Sánchez et al. (2013); Hordijk et al. (2015); Prieto et al. (2018, 2022); Jovells-Vaqué & Casanovas-Vilar (2021).

SYSTEMATIC PALEONTOLOGY

Order: RODENTIA Bowdich, 1821
Family: CRICETIDAE Fischer [von Waldheim], 1817
Subfamily: CRICETOPINAE Matthew & Granger, 1923
Tribe: MELISSIODONTINI Schaub, 1925
Genus: ***Melissiodon*** Schaub, 1920
Melissiodon aff. *schlosseri* Schaub, 1925

Remarks on the systematics:

Though Schaub (1920) pointed out that the clade deserved a family rank, it was not until five years later that its formal definition as family level (i.e. Melissiodontidae) was published (Schaub 1925). Many studies hesitated to include the genus *Melissiodon* into the family Muridae (e.g., Freudenthal et al. 1992; Kristkoiz 1992) based on aberrant features in the skull and its derived morphology of the cheek teeth. Therefore, this genus was the only member of the subfamily Melissiodontinae for most of the last century. That was until Ünay-Bayraktar (1989) erected the genus *Edirnella* based on a few isolated upper cheek teeth from the middle Oligocene (MP25) locality of Kocayarma (Thrace Basin, Turkey). This genus was accommodated into the subfamily Melissiodontinae mainly because it shares with *Melissiodon* the character of having a cusp between the anterocone complex and the protocone (protostyle in this work,

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following Jovells-Vaqué & Casanovas-Vilar 2018). In the same publication, Ünay-Bayraktar grouped both subfamilies (i.e. Melissiodontinae, with *Melissiodon* and *Edirnella*; and Paracricetodontinae, with *Paracricetodon* and *Trakymys*) into the family Melissiodontidae, which was strongly criticized and not followed by subsequent works (e.g., Freudenthal et al. 1992; Kristkoiz 1992; Kalthoff 2006). New remains from the late Eocene deposits of Süngülü (Lesser Caucasus, Turkey) were considered as belonging to *Edirnella* and included in the subfamily Melissiodontinae (see de Bruijn et al. 2003). The third genus belonging to Melissiodontinae, i.e., *Mogilia* Wessels et al., 2018, contains two species of the Eocene-Oligocene of Serbia: *M. miloshi* and *M. lautus* (Wessels et al. 2018).

The subfamily Cricetopsinae was originally established by de Buijn & Koenigswald (1994), but McKenna & Bell (1997) emmended it to Cricetopinae (terminology followed in this work). As for the phylogenetic analyses, Maridet & Ni (2013) recovered *Melissiodon* into this subfamily, being *Melissiodon* sister species of *Selenomys*, and both of them sister group of *Mirrabella*: the monophyletic group including the former three genera was called *Melissiodon* clade. Maridet & Ni (2013) included other genera into Cricetopinae (e.g., *Cricetops*, *Meteamys*, and *Selenomys*), however, the most remarkable reallocation was the inclusion of *Edirnella* in the subfamily Pseudocricetodontinae, and consequently, more closely related to the genera *Pseudocricetodon, Adelomyarion* and *Raricricetodon*. This proposal was not followed by Wessels et al. (2018), as they placed all the three genera, i.e., *Edirnella*, *Melissiodon* and *Mogilia*, into subfamily Melissiodontinae mainly based on the enamel microstructure, a key character omitted by Maridet & Ni (2013) in their phylogenetic study. Despite the debate regarding its phylogenetic position, Melissiodontinae

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represent one of the first muroids that have been recorded outside of Asia, and yet, these are still poorly known.

Measurements: see Table 1

(Fig. 3A–AB)

Studied material:

MWQ 2/2003: fragment of left maxilla with M1-M2 (Pal. 3381); fragment of right maxilla with M1-M2 (Pal. 3382); fragment of left maxilla with M1 (Pal. 3490); fragment of right maxilla with M1 (Pal. 3488); four left M1 (Pal. 3371, Pal. 3491, Pal. 3492, Pal. 3493); two right M1 (Pal. 3380, Pal. 3489); one left M2 (Pal. 3496); four right M2 (Pal. 3372, Pal. 3383, Pal. 3495); one left M3 (Pal. 3377); one left m1 (Pal. 3373); two right m1 (Pal. 3374, Pal. 3494); one left m2 (Pal. 3375); two right m2 (Pal. 3497, Pal. 3498); two left m3 (Pal. 3501, Pal. 3502); three right m3 (Pal. 3376, Pal. 3499, Pal. 3500).

MCQ 3/2005: one right M1 (Pal. 3931); one fragment left m1 (Pal. 3903); one left m2 (Pal. 3930).

Description

M1 (Fig. 3A–K): The teeth show five cylindrical roots, the two larger ones situated below the anterocone complex and the protocone. There are two slimmer roots below the metacone and the hypocone. The fifth root is conspicuously thinner than the others, and is situated below the paracone. The anterocone complex is massive and protrudes anteriorly. It presents two cusps, the largest one placed in a centro-lingual position. Both cusps are separated by deep and narrow notch, which is almost enclosed anteriorly in Pal. 3492 (Fig. 3I). The lingual anterocone is connected to the anterolophule. This

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cusp also has a lingual spur that merges with a distolabial crest running from the protostyle. Furthermore, it connects to the anterolophule, dividing the protosinus in 8 out of 11 teeth (Pal. 3491, Fig. 3H): in Pal 3492 (Fig. 3I), this lingual spur merges with the anterolophule before the anterolophule cusp, leaving the protostyle isolated and the protosinus complete; in Pal. 3489 (Fig. 3G), it ends before reaching the spur from the protostyle, and in Pal. 3382 (Fig. 3B), it reaches the anterolophule cusp without connecting to the protostyle. In addition, Pal. 3493 (Fig. 3J) shows a large spur from the protostyle that reaches the labial spur of the lingual anterocone. The anterior spur of the protostyle connects to a spur running lingually from the lingual anterocone enclosing a small sinus in 7/11 teeth (Pal. 3371, Fig. 3E); this crest is specially developed in Pal. 3490 (Fig. 3C). The rest of the specimens show a different degree of development of the spurs without fully enclosing the small sinus (i.e., Pal. 3491, Fig. 3H). The labial anterocone is also large: it connects to the lingual anterocone through a lingual spur and to the two anterior paracone spurs, enclosing the anterosinus. The anterior lingual paracone spur shows a short crest running labially in Pal. 3380 (Fig. 3F). In Pal. 3489, 3491 and 3493 (Fig. 3G, H, J) it shows a short crest running lingually towards a short labial spur from anterolophule but without connecting to it. A small anterostyle is present in Pal. 3381, 3382, 3371 and 3493 (Fig. 3A, B, E, J); it is very strong and isolated from the other cusps in Pal. 3492 (Fig. 3I). Pal. 3931 shows a short transverse crest between the paracone and the labial anterocone (Fig. 3H). The protolophule is defined by a labial spur of the protocone, which is slightly longer than the lingual one of the paracone. The mesocone is well-developed and connected to the protolophule through a short anterior arm (10/11) or isolated from it (1/11; Pal. 3490, Fig. 3C). The posterior arm of the mesocone runs labially and connects to the entoloph, except for Pal. 3490 (Fig. 3C), in which it seems to be isolated.

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Although the morphology of the mesoloph is also variable, it always runs oblique towards the labial end of the tooth. It connects to the posterior arm of the mesocone, and in three specimens, the it is long enough to reach the anterior arm of the mesocone (Fig. 3E, F, G). The entoloph runs labially and joins the metalophule. The mesoloph area is highly variable. In Pal. 3382 and 3488 there is a single connection to the mesoloph, but closer to the mesocone (Fig. 3B, D). In Pal. 3488, the extra metalophule spur runs distolabially and connects to the metacone (Fig. 3D) however; this crest is much shorter in Pal. 3491 and Pal. 3931(Fig. 3H, K) in anteroposterior direction. The remaining teeth (7/11) show an extra metalophule spur that is joined to the mesoloph, enclosing a small pit that can be narrow (Pal. 3381, Fig. 3A) or wide (Pal. 3371, Fig. 3E). Pal. 3382 (Fig. 3B) is the only tooth that does not show an extra metalophule spur. A small mesostyle is present at the connection between the labial crests. Both paracone and metacone show labial spurs that connect with the mesoloph labially. This connection protrudes labially and is specially marked in Pal. 3382 (Fig. 3B). The sinus is partially open. The posteroloph is low and connects to the posterior spur of the metacone. In 7/11, teeth it runs labially surpassing the posterior spur of the metacone (Fig. 3F). In 9/11 teeth a hypoconule is present (Fig. 3F). All specimens show a short lingual posteroloph from the hypocone.

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M2 (Fig. 3L–O): All molars have a rectangular outline. There are four roots, the anterolabial being the thinner one. The lingual anteroloph is short but very robust, anterocone-like in 6/7 teeth, and being very thin in Pal 3383 (Fig. 3M). The anterolophule reaches the anterior lingual spur of the paracone. In half of molars there is a distinct anterolophule cusp. Additionally, Pal. 3381 shows a small bump where the anterolophule meets the anterior lingual spur of the paracone (Fig. 3A). The labial anteroloph connects to the labial anterior spur of the paracone in 6/7 teeth: Pal. 3381 shows an incomplete labial anteroloph, leaving the anterosinus open (Fig. 3A). The protolophule is straight. The posterior lingual spur of the paracone is long in all teeth except for Pal. 3381 (Fig. 3A). It reaches the protolophule (3/6; Fig. 3L) or ends right before it (3/6; Fig. 3N). In Pal. 3381, 3382, and 3495 the protolophule merges with the mesoloph (Fig. 3A, B, N). The mesoloph and mesocone are show high variability within the assemblage of Mokrá-Quarry. The mesocone is round. The anterior arm of the mesocone turns anteriorly and connects to the protolophule in two specimens (Fig. 3L, O). It runs labially and connects to the mesoloph in Pal. 3383 (Fig. 3M). However, in Pal. 3381 and 3495 the anterior arm of the mesocone runs labially and splits in two, connecting to the protolophule and to the mesoloph (Fig. 3A, N). Only in Pal. 3382 (Fig. 3B) the anterior arm of the mesocone is reduced to a short spur that does not reach the mesoloph or the protolophule. In all specimens, the posterior arm of the mesocone connects to the entoloph, except for Pal. 3372, in which is connected to the metalophule (Fig. 3L). As seen in Pal. 3495-3496 (Fig. 3N, O) there is an extra spur from the posterior arm of the mesocone that reaches the mesoloph. This extra spur does not fully connect to the mesoloph in Pal. 3381 (Fig. 3A) but there is a double connection to the entoloph. The metalophule is always connected to the mesoloph. A mesostyle is absent. The ectoloph connects to the metalophule (Fig. 3L). The sinus is open in all teeth. The posteroloph reaches the posterior spur of the metacone. All teeth show a lingual posteroloph running from the hypocone (Fig. 3M).

M3 (Fig. 3P): This molar shows three roots: two labially located and one lingual, which is thicker than the other two. Pal. 3377 has a rounded outline and is narrow. The labial anteroloph is thin and without reaching the labial spur of the paracone (Fig. 3P).

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A very low lingual anteroloph that does not reach the base of the protocone is preserved. Both protocone and paracone are high and well-developed. The anterolophule is straight and reaches the anterior lingual spur of the paracone. The protolophule is fused with the metalophule, which runs from a very small metacone. The lingual paracone spur does not reach the protolophule. The entoloph is somewhat short and therefore does not reach the metalophule. The posterior arm of the hypocone connects with the metacone. All the sinuses are open.

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m1 (Fig. 3Q–T): Both lingual and labial anteroconids are well-developed and separated by a deep anterior groove (clearly visible in Pal. 3373; Fig. 3Q). Despite its fragmentary preservation, Pal. 3494 has a short cristid running lingually from the labial anteroconid towards the lingual one, without fully attaching to it (Fig. 3S). The lingual anteroconid is massive and located slightly posterior to the labial anteroconid. It is connected to the metaconid through a short posterior spur. The metaconid lacks a well-developed anterolingual cristid, which leaves the anterosinusid open. The anterolophulid connects to both anteroconids and to the protoconid in all teeth. The anterolophulid connects to the labial anteroconid posteriorly. The anterolophulid cuspid is large. A short spur developed towards the metaconid is preserved, but without connecting to it. The labial anteroconid is large and bulge-like, and protrudes anteriorly: it is isolated from the protoconid as the protosinusid is open. The protoconid is large and its hind arm connects to the labial posterior spur from the metaconid, and reaches the lingual edge of the tooth (Fig. 3R). The anterior arm of the mesoconid connects to the protoconid hind arm in all specimens, showing a small bulge in Pal. 3374 (Fig. 3R). The mesolophid always starts at the anterior arm of the mesoconid, showing different degrees of development: in Pal. 3373 it is divided but does not reach the anterior arm of

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the entoconid (Fig. 3Q); in Pal. 3374 it turns slightly anterior, connecting to the protoconid hind arm and enclosing a small pit (Fig. 3R); in Pal. 3494 (Fig. 3S) it runs parallel to the protoconid hind arm towards the labial anterior spur of entoconid; in Pal 3903, the anterior arm of the mesoconid appears to run labially and the mesolophid is reduced to a short spur that ends next to the anterior arm of the entoconid without attaching to it (Fig. 3T). The ectolophid is short and attached to the mesoconid. The entoconid has the labial cristids much better developed than the lingual ones, which are almost absent. The labial posterior cristid reaches the posterolophid. There is a well-developed posteriorly oriented spur running from the posterolophid (Fig. 3S). The sinusid is open labially. Pal 3494 (Fig. 3S) has a well-developed ectomesolophid that almost reaches the mesoconid. However, in Pal 3903 there is a small bump instead (Fig. 3T).

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m2 (Fig. 3U–X): Pal. 3498 is damaged anteriorly and lingually (Fig. 3W). The four teeth preserve a very short labial anterolophulid. The protosinusid is open. The lingual anterolophid is well-developed and connects to an anterior labial spur running from the metaconid. There is no anterior lingual cristid from the metaconid, leaving the anterosinusid open. The protoconid hind arm is long and runs distolingually reaching the labial edge. The posterior spurs of the metaconid and the anterior one from the entoconid attach to the protoconid hind arm. The mesoconid is well-developed and its short anterior arm runs anterolabially to connect to the protoconid hind arm. The mesolophid preserves different configurations: in Pal. 3375, a very short spurs starts from the protoconid hind arm but does not reach the mesoconid (Fig. 3U); in Pal. 3497, a short mesolophid starts from the centre of the mesoconid and merges with the protoconid hind arm (Fig. 3V); in Pal. 3498, a long mesolophid, starting from the centre of the mesoconid runs parallel to the protoconid hind arm and links to the anterior labial spur of the entoconid (Fig. 3W); in Pal. 3930 (Fig. 3X), the short mesolophid merges with the protoconid hind arm as seen in Pal. 3497. The ectolophid is short and preserves a short spur in 3375 (Fig. 3U), whereas in Pal. 3390 (Fig. 3X) it is large. The posterolophid is very low and connects to the two posterior spurs of the entoconid. The sinusid is open.

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m3 (Fig. 3Y–3AB): The molars are elongated with a rounded posterior side. There are two roots, the posterior one being much broader than the anterior one. The protoconid connects to an anterior labial spur which departs from the metaconid through a well-developed anterolophulid that runs straight. Eventhough some teeth have a thickening on the anterolophulid (Pal. 3376, 3502; Fig. 3Z, AB) there is no distinct anteroconid. The protosinus is open. The protoconid hind arm reaches the labial edge; the lingual posterior spur of the metaconid and the anterior one from the entoconid connect to it. Pal. 3376 and 3501 also have a posterior labial spur of the metaconid (Fig. 3Z, AA). The mesoconid is again where the most variability occurs. Pal. 3376 and 3502 (Fig. 3Z, AB) present a small but distinct mesoconid, whereas in the rest of the teeth a distinguishable bulge is absent. The hypolophulid is short and directed distolingually (Fig. 3Y). Pal. 3501 shows a division of the hypolophulid into two very short spurs (Fig. 3AA). The posterolophid gets progressively lower, attaching to the base of the entoconid; there is no posterior spur running from this cuspid. The sinusid is open.

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DISCUSSION

The *Melissiodon* remains from Mokrá-Quarry described here show clear differences with *Melissiodon dominans* from all MN3 and MN4 localities. For instance, one of

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these differences lies on the smaller side of the size range of *M. dominans* from MN3 sites (including the type population of Wintershof-West; Fig. 4). When compared with MN4 sites, the population from Mokrá- Quarry is smaller than most of them, except for Rembach and Forsthart. Besides differences in size between populations there are marked morphological differences. Hrubesch (1957) already noticed that *Melissiodon* shows a wide range of morphological variability, especially in the first upper and lower molars, where the stronger morphological differences occur. However, our study evidences clear differences regarding not only the first upper and lower molars, but also the second and third ones.

The assemblage of *Melissiodon* from Mokrá-Quarry resembles the scarce remains of *M. schlosseri* from Haslach (one m1 and one m3) and *M.* aff. *schlosseri* (one mandible with m1-m3) from Ulm-Uniklinik (both from Germany, MN2) in having on the m1 a large cuspid-like labial anteroconid that protrudes anteriorly. However, while the connection of this cuspid to the anterolophid is posterior in the population from Mokrá-Quarry, it is placed more lingually in the *Melissiodon* sample from these German sites (see Schaub 1925: plate 4, fig. 16; and Werner 1994: fig. 27a). Yet, due to the under sampling of the populations attributed to *M. schlosseri* and *M.* aff. *schlosseri*, it cannot be addressed whether it is a morphological difference or rather just intraspecific variability. Moreover, the overall robustness pattern of cuspids in the available m1, not only anteroconids, but also main cuspids as well as mesoconid, is a shared feature between the *Melissiodon* population from Mokrá and *M. schlosseri* from the MN2 sites. The single m2 recovered of *Melissiodon* aff. *schlosseri* resembles the overall morphology of the population from Mokrá-Quarry. However, while the posterior labial cristid of the metaconid always connects to the protoconid hind arm in all teeth recovered from Mokrá, it connects to the lingual posterior cristid of the metaconid in the

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single tooth from Ulm-Uniklinik (Werner 1994: fig. 27b). Regarding the m3, there are no marked differences between both populations.

The type population of *M. dominans* from Wintershof-West presents a small labial anteroconid that is connected lingually to the anterolophulid and labially to the protoconid (Hrubesch 1957), which differs with the anterior morphology of the m1 in the population from Mokrá-Quarry. The m1s from Mokrá-Quarry have a clearly developed labial anteroconid, cuspid-like, which protrudes anteriorly and is only connected to the anterolophulid through a posterior spur (Fig. 3Q; see also Bonilla-Salomón et al. 2021a: fig. 3A). Moreover, the labial posterior cristid of the entoconid always reaches the posterolophid in the *Melissiodon* teeth from Mokrá-Quarry, while it never reaches the posterolophid in the type population. The m2 of *M. dominans* from Wintershof-West are somewhat larger, and the mesolophid, when present, develops from the anterior arm of the mesoconid in the majority of the population, whereas it always starts from the mesoconid in *Melissiodon* from Mokrá-Quarry. The m3s of *Melissiodon dominans* from the type locality are larger than those from Mokrá-Quarry. Two m3s of *Melissiodon* from Mokrá-Quarry show a posterior labial spur of the metaconid, character that is absent in all populations of *M. dominans* along the early Miocene. The anterocone complex in the M1 of *Melissiodon* remains from Mokrá-Quarry is massive and protrudes anteriorly compared with the type population and other MN3 sites. Moreover, the furrow between labial and lingual anterocones is narrower than any population of *M. dominans*. In addition, the lingual anterocone has a second posterior spur, which runs lingually and connects with a posterior spur of the protostyle and an anterior one from the anteroloph, thus dividing the protosinus. This feature, present in the vast majority of M1 from Mokrá-Quarry is only present in a single tooth from the type locality and single specimens from other MN3 sites: Ramblar 7 (Sesé

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1987); and Turó de les Forques 1 (Jovells-Vaqué & Casanovas-Vilar 2018). Regarding the M2, the material from Mokrá-Quarry also has some clear differences with *M. dominans* from the type locality. Firstly, it is narrower than the type population (Fig. 4). Secondly, *Melissiodon* assemblage from Mokrá-Quarry has a long posterior lingual crest from the paracone, which either connects to the protolophule or ends right before it. On the contrary, *M. dominans* from Wintershof-West shows a very short posterior lingual spur of the paracone (Hrubesch 1957: plate 3, fig. 8-11) that never reaches the protolophule. Concerning the M3, besides the smaller size compared with the type locality (Fig. 4), the protolophule does not reach the paracone, and furthermore it turns posteriorly merging with the metalophule towards a very small metacone.

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Melissiodon dominans from Forsthart and Rembach (Germany, MN4) preserves an isolated, cristid-like, labial anteroconid (see Ziegler & Fahlbusch 1986: plate 10, fig. 4-6). This morphology of the anterior part of the m1 differs already from what it is observed in *M. dominans* from the type locality, and even more when compared with the robust cuspid-like labial anteroconid that show the populations of *Melissiodon* from Mokrá-Quarry. Unfortunately, Ziegler & Fahlbusch (1986) did not consider this morphological character different enough to erect a new species. Although Mokrá-Quarry, Forsthart and Rembach sites yielded alike small mammal assemblages (i.e., *Democricetodon* and *Megacricetodon*), the morphology of this character displayed in *Melissiodon* from these sites is completely different, suggesting that the development of more robust labial and lingual anteroconids in the evolutionary history rather represent different evolutionary lines within the genus. Moreover, the presence of already well-developed anteroconids in the lower molars in older populations of *Melissiodon* (i.e., Haslach and Ulm-Uniklinik: Schaub 1925 and Wermer 1994, respectively) could indicate that this trend developed on different lineages at different moments. The m2 of

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Melissiodon from Mokrá-Quarry has a connection of the posterior labial cristid of the metaconid to the protoconid hind arm. However, in *M. dominans* from Rembach and Forsthart this cristid never reaches the protoconid hind arm. In addition, the mesolophid starts at the center of the mesoconid, whereas in *M dominans* from these and other MN4 localities always starts at the anterior arm of the mesoconid. Concerning the m3, in *M. dominans* from Rembach and Forsthart the anterolophulid is straight, whereas in *Melissiodon* from Mokrá-Quarry it is oblique and reaches a well-developed anterior labial spur of the metaconid. Ziegler & Fahlbusch (1986) considered the presence of a labial spur of the mesoconid in all m3 to be a derived character of *Melissiodon dominans* from MN4 sites. However, this feature is absent in all m3 recovered from Mokrá-Quarry, and since the assemblages share a very similar age with the German sites, the absence of this character would point to the presence of a different form of *Melissiodon* in Mokrá-Quarry sites. Regarding the upper molars, the M1 of *M. dominans* from Rembach and Fortshart appear to show a much more developed labial anterocone, which is placed more labially than the *Melissiodon* assemblage from Mokrá-Quarry. In the M1s from these German populations, the second posterior spur of the lingual anterocone is also absent (see above). The M2 from Rembach and Fortshart besides having a shorter posterior lingual spur of the paracone, show no connection between the protolophule and the mesocone, while this feature is preserved in 5/7 teeth in Mokrá-Quarry (Fig. 3L-O). As for the M3, the assemblages of Rembach and Fortshart show the same differences with *Melissiodon* from Mokrá-Quarry as the type population (see above).

Compared with Western European *Melissiodon* assemblages, a well-developed labial anteroconid cuspid-like displayed by the population from Mokrá-Quarry sites resembles the conditions of the single m1 reported from the MN5 site of Vieux-Collonges, (Mein

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& Freudenthal 1981: plate 2, fig. 12), and the older and larger m1 from Sant Andreu de la Barca 1 (Jovells-Vaqué & Casanovas-Vilar 2018; fig. 2c). It is noteworthy that the connection with the anterior spur of the anterolophulid is lingual in these sites, whereas in *Melissiodon* remains from Mokrá-Quarry it is posterior. However, a cristid-like labial anteroconid is clearly visible in the single m1 available from Montalvos 2 (Hordijk et al. 2015: fig. 2e), resembling the MN4 populations of Rembach and Fortshart. The recently published material of *M. dominans* from Echzell show a cristid-like labial anteroconid as well, but connected lingually to the anterolophulid (Jovells-Vaqué & Mörs 2022). As for the M1s, the single specimens recovered from Sant Mamet (Jovells-Vaqué & Casanovas-Vilar 2018) and Montalvos 2 (Hordijk et al. 2015), besides being larger, show no second posterior spur from the lingual anterocone. Compared with other Czech sites (i.e., Dolnice 1, 2 ,3 and Ořechov), within the populations there are specimens that also possess a bulgy labial anteroconid (see Fejfar 1990), and therefore resemble those from Mokrá-Quarry more than *M. dominans* from other MN3 and MN4 sites. Regarding M1, most of the assemblage depicted by Fejfar (1990) also show a second posterior spur of the lingual anterocone, dividing the protosinus. However, the short study published by Fejfar (1990) only included the first upper and lower molars, so there is no information regarding the rest of the tooth row.

The single M3 and the preserved portion (posterior side) of one m1 from the Turkish locality of Kargi 2 attributed to *Melissiodon* sp. show strong differences with the population from Mokrá-Quarry. For instance, the M3 shows a much more rounded outline and absence of connection between protolophule and metalophule, which is present in *Melissiodon* from Mokrá-Quarry.

Overall, the *Melissiodon* remains recovered from Mokrá-Quarry show more resemblance with *M. schlosseri* than with *M. dominans*, especially in the anterior half of the m1. However, *M. schlosseri* was erected based on a single m1 and m3 from the MN2 locality of Haslach, and therefore, it is poorly known. On the other hand, *M. dominans* populations across MN3 and MN4 localities show a wide array of morphological variability. For that reason, it is complicated to establish the set of features characteristic of the species. Based on our current knowledge and all the stated above, the material described here is referred to *Melissiodon* aff. *schlosseri.* Furthermore, the previously described material from MWQ 1/2001 ascribed to *M. dominans* (Bonilla-Salomón et al. 2021a) is here referred to *M.* aff. *schlosseri* as well.

Evolutionary history of *Melissiodon* during the early Miocene

The first phylogenetic hypothesis of the genus *Melissiodon* was proposed by Hrubesch (1957: fig. 125), in which he suggested the existence of various lineages during the Oligocene, whereas during the early Miocene only two branches persisted. Even though the author also considered *Melissiodon arambourgi* to be a completely different lineage, the species has been proven to be a synonym of *M. dominans* (see Agustí 1981; Jovells-Vaqué & Casanovas-Vilar 2018). During the early Miocene, *M. dominans* would be the most abundant species, known in MN3 and MN4 localities, and reaching the Burdigalian before its extinction during the latest early Miocene. The second lineage present in the early Miocene led to *M. schlosseri.* Although the recovered material was very scarce, Hrubesch (1957) considered *M. schlosseri* from Haslach (MN2) to be different to any other species of the genus, based on the specialization of the anterior part of the m1, and more specifically in having stronger cuspids and well-developed bulge-like anteroconids. According to the author, the material was singular enough to represent a different lineage with no connection to *M. dominans*. Given no other related remains to Haslach material were found, this species

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The *Melissiodon* remains from Mokrá-Quarry described here show clear differences with *Melissiodon dominans* from all MN3 and MN4 localities. For instance, it lies on the smaller side of the size range of *M. dominans* from MN3 sites (including the type population, Wintershof-West; Fig. 4). When compared with MN4 sites, the population form Mokrá-Quarry is smaller than most of them, with the exception of Rembach and Forsthart. Despite being about the same size as *M. dominans* from the above mentioned German localities, there are strong morphological differences between these populations and Mokrá-Quarry. Hrubesch (1957) already noticed that *Melissiodon* shows a wide range of morphological variability, and more specifically the first and lower molars are where the stronger morphological changes occur. However, our study focused on *Melissiodon* remains from Mokrá reveals marked differences in first upper and lower molars, as well as in second and third ones.¶
Regarding the m1, the type population of *M. dominans* always presents a small labial anteroconid that connects with the protoconid and anterolophulid (see Hrubesch 1957). Instead, the *M. dominans* from Forsthart and Rembach preserve an isolated, cristid-like, labial anteroconid (see Ziegler & Fahlbusch 1986: plate 10, fig. 4-6), but the authors did not consider it different enough to erect a new species. This feature is also clearly visible in the single m1 available from Montalvos 2 (Hordijk et al. 2015: fig. 2e). Neverthelss, the m1s from Mokrá-Quarry have a clearly developed labial anteroconid, cuspid-like, which protrudes anteriorly and is only connected to the anterolophulid through a posterior spur (Fig. 3Q; see also Bonilla-Salomón et al. 2021a: fig. 3A). As far as we know, this character is not present in any population of *M. dominans.* Among MN3-MN4 *Melissiodon* assemblages, a well-developed labial anteroconid cuspid-like displayed by the population from Mokrá-Quarry sites is only present in the single m1 reported from the MN4 site of Vieux-Collonges, (Mein and Freudenthal 1981: plate 2, fig. 12), and the older and larger m1 from Sant Andreu de la ...

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Deleted: in other localities during the early Miocene represents a completely isolated branch in European localities, i.e., with unknown origin and no continuation along the early Miocene. More recently, Werner (1994) described a partial left mandible with m1-m3 from Ulm-Uniklinik (MN2), a slightly younger locality than Haslach, which was referred to *Melissiodon* aff. *schlosseri*. He also pointed out a small difference in the size of the labial anteroconid, which although large, it was only somewhat smaller than the type species. In fact, as the type species was based on very few remains (and only one m1) it could not be discarded that the small difference in size could be explained by intraspecific variability. Shortly after, Engesser & Mödden (1997) reported two different *Melissiodon* taxa from La Chaux 7, an MN2 site from Switzerland with similar age to Haslach. The remains were attributed to *M.* aff. *schlosseri* and *M.* cf. *dominans,* but no metrics nor descriptions of either taxa were provided. Indeed, La Chaux 7 constitutes up to date the only site from which two different taxa of the genus have been recorded. However, no other remains of *Melissiodon* that related to *M. schlosseri* or this lineage of the genus (*sensu* Hrubesch 1957) have been found at MN3 or MN4 localities.

Melissiodon aff. *schlosseri* from Mokrá-Quarry shows a high degree of development of both lingual and labial anteroconids on the m1, more developed than in *M. dominans* from the MN3 type locality and differently arranged than in *M. dominans* from other MN4 Central European localities. The poorly known *Melissiodon schlosseri* from Haslach shows morphology of the anteroconids in the m1 that resemble the size and development of *M.* aff. *schlosseri* from Mokrá-Quarry. That, together with the overall differences of the assemblage from Mokrá-Quarry with *M. dominans* (see Discussion section above), imply that the material presented here could represent a younger species derived from *M. schlosseri*. However, our knowledge on *M. schlosseri* is still very limited, reduced to a very few teeth, and we concur that a revision of the type material

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will be required before the erection of new species. Even though the high diachrony between regions in Europe prevent a more straightforward correlation, in Figure 5 the biochronologic distribution of *Melissiodon* taxa during the early Miocene in Europe, is shown. If *Melissiodon* aff. *schlosseri* from Mokrá-Quarry is, in fact, closely related to *M. schlosseri*, this would imply that the lineage survived until the latest early Miocene. However, the evolution and distribution of this lineage at MN3 localities still remains unclear. The single m1 from the MN3 site of Sant Andreu de la Barca (Jovells-Vaqué & Casanovas-Vilar 2018: fig. 2C) also shows a similar pattern in the development of anteroconids, despite it being larger than *M.* aff. *schlosseri* and *M. schlosseri* (see Fig. 4). The taxonomical assignment at the species level of this single molar within the evolution of the genus is still uncertain, but also could indicate the existence of more taxa besides *M. dominans* at MN3 localities.

As for MN4 sites, the assemblages of *Melissiodon* are smaller in size compared with the type population. Besides the size decrease, the *Melissiodon* populations from Germany sites (Zielger & Falhbusch 1986) show a completely different arrangement of the anteroconid area in m1 (see Discussion section above). The increase in size of the anteroconid area, a common trend in the *M. dominans* lineage already noticed by several authors (e.g., Hrubesch 1957), together with the complete lack of a labial anteroconid could also indicate a different taxon. Additionally, our recent inspection of the material from Dolnice sites and Ořechov attributed to *M. dominans* by Fejfar (1990) reveals two different m1 morphotypes in that MN4 populations: the cuspid-like labial anteroconid of *Melissiodon* aff. *schlosseri* from Mokrá-Quarry and the cristid-like labial anteroconid of *M. dominans* from German sites, with clear predominance of the latter. It is noteworthy that the morphotype of the m1 present in Mokrá-Quarry and other Czech localities is not only restricted to Central Europe or to the MN4 sites, since there is a

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single m1 recovered from Vieux-Collonges, France (Mein & Freudenthal 1981; MN5) that clearly resembles *M.* aff. *schlosseri* from Mokrá-Quarry. Mein & Freudenthal (1981) noticed that the morphological differences where distinct enough among *Melissiodon* spp., but the scarcity of the material prevented them to erect a new species. At any rate, the morphological variability of the genus during the latest early Miocene, prior to its extinction, seems higher than previously thought.

Besides the complicated alpha-taxonomy of *Melissiodon* populations in MN4 sites, the lineage leading to *Melissiodon dominans* is still poorly known. The existence of a tendency towards size increase between the type locality (Wintershof-West) and younger MN3 sites has been confirmed by several publications: Ramblar, Bañon and Turó de les Forques 1 sites in Spain (Sesé 1987; Jovells-Vaqué & Casanovas-Vilar 2018) and Beaulieu 2B and Jauquet in France (Aguilar et al. 2003; Bulot et al. 2009, respectively). However, *M. dominans* from MN4 assemblages are usually smaller than those of the type locality (see Figure 4), which was also noticed by other authors (see Ziegler & Falhbusch 1986; Bulot & Ginsburg 1996; Bulot et al. 2009, for complete discussions). In fact, both Rembach and Fortshart have yielded remains of *M. dominans* clearly smaller than those from MN3 localities (Fig. 4). These sites are undoubtedly MN4 in age, according to the presence of both *Democricetodon* and *Megacricetodon* genera. Overall, there are only a few exceptions in MN4 localities in which *Melissiodon dominans* is larger than in other coeval sites. One of them is Montalvos 2, in which *M. dominans* is larger than those from most MN4 localities where *Democricetodon* and *Megacricetodon* are also found (see also Hordijk et al. 2015). These remains fit well within the size range of *M. dominans* from Wintershof-West, however, the population from Montalvos 2 shows an m1 morphotype that is similar to those from MN4 sites in Germany. In Dolnice 1 there are two m1 that are clearly larger than the rest of the

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assemblage and further similar size like the m1 from Montalvos 2. Nevertheless, Dolnice material has a cuspid-like labial anteroconid, instead of a cristid-like labial anteroconid like the one in Montalvos 2.

The stated above confirms the complexity of the evolutionary history of *Melissiodon*. Thus, the coexistence of two different lineages within *Melissiodon* genus during the latest early Miocene cannot be discarded: one that slightly increases in size along the MN3 (as proposed by Aguilar et al. 2003); and a second one, smaller, that replaced the large one in most of the MN4 localities across Central and Western Europe. Whether it represents different populations within the *M. dominans* lineage or even different species is out of the scope of the present work. The scarcity of localities of the European fossil record of the early Miocene, together with the small populations that compose *Melissiodon dominans*, have turned *M. dominans* into a catch-all species. Therefore, a complete revision of all Miocene localities bearing *Melissiodon* remains is needed to elucidate and better comprehend the relationships between the different forms and the two species found across Europe during the early Miocene.

Paleoecological implications

Historically, the presence of *Melissiodon* has been linked to wooden areas and somewhat humid conditions (van der Weerd & Daams 1978). According to Sesé (1987), *Melissiodon* enters the Iberian Peninsula during a change from a relatively dry to a relatively wet climate (zone Z; Daams & van der Meulen 1984), and it is no longer recorded in the Calamocha area beyond zone A, when the climate is supposed to become relatively dry again. Mokrá-Quarry sites are characterized by its karstic conditions, together with patches of forest and swampy areas (Ivanov 2008; Ivanov et al. 2006, 2017, 2020; Sabol et al. 2007; Luján et al. 2017, 2021; Bonilla-Salomón et al.

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2021a), which agree with the conditions that presumably favored the presence of *Melissiodon*. Moreover, Jovells-Vaqué & Casanovas-Vilar (2018) argued that rich collections of *Melissiodon* from the Vallès-Penedès Basin come from localities where forest-dwelling rodents (dormice and tree-squirrels) are diverse and abundant. We concur with this premise as in Mokrá-Quarry several genera of sciurids adapted to arboreal lifestyle have been recovered (Bonilla-Salomón et al. 2021b).

The existence of different lineages of *Melissiodon* during the early Miocene could also imply the preference of certain palaeoecological conditions. However, there is no known locality during the latest early Miocene where two different species were undoubtedly proven. The only record of two coexistent *Melissiodon* taxa comes from the MN2 site of La Chaux 7 (Switzerland), where Engesser & Mödden (1997) identify *Melissiodon* aff. *schlosseri* and *M* cf. *dominans*. The high degree of specialization of the first upper and lower molars, together with the clear difference between morphotypes, is likely to be related to slightly different feeding behaviors and, consequently, the preference towards certain habitats as well.

As for feeding adaptations, Mein & Freudenthal (1981) suggested frugivorous diet for *Melissiodon* and ventured that the genus may be arboreal. However, Hordijk et al. (2015) hypothesized than *Melissiodon* was a ground-dweller genus that fed on invertebrates (mainly earthworms), based on the morphological similarity of the teeth with the extant shrew rats from Sulawesi and Philippines. This assumption was also supported by Wessels et al. (2018), suggesting that subfamily Melissiodontinae (sensu Wessels et al. 2018) would feed on small invertebrates. Yet, the scarcity of localities where *Melissiodon* is found represents the main obstacle to interpret its feeding behaviors and palaeoecological preferences.

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Conclusions

New remains of *Melissiodon* from Mokrá-Quarry (MWQ 2/2003 and MCQ 3/2005), attributed here to *M.* aff. *schlosseri*, are presented: the remains constitute one of the best documented assemblages of this genus among MN4 localities known so far. This population, characterized by having the first lower molars with strong cuspids and well-developed labial and lingual anteroconids, differs from all *Melissiodon* assemblages known from MN3 and MN4 localities. In fact, the morphology of the molars of *M.* aff. *schlosseri* soundly recalls that of the poorly known *M. schlosseri* from MN2 localities.

Besides, *Melissiodon dominans* from some MN4 assemblages from Germany are lacking labial anteroconid while others still have this feature developed. This characteristic disrupts the evolutionary trend of *Melissiodon* species shown along the late Oligocene and the early Miocene of increasing the size of the anteroconids. Therefore, its assignation to *M. dominans* is dubious, and demands for a new revision of all material.

Moreover, the apparent trend in size increase shown in *M. dominans* along MN3 localities (with special relevance in the population from Schnaitheim) is abruptly interrupted in MN4 assemblages. Thus, the existence of different lines along the early Miocene cannot be discarded.

The apparent diversity of poorly recorded taxa that lived during the Miocene suggests a more complex evolutionary history than previously thought. A complete revision of the genus is needed to help clarify its diversification and the relationships between the species during the early Miocene. Moreover, some of the already known assemblages that yielded *Melissiodon* remains from the Czech Republic call for a detailed study (i.e. Ahníkov I and II, Dolnice sites and Ořechov), to better comprehend

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the diversity of the genus. The presence of several species in Central Europe along the early Miocene could indicate preference for different ecological conditions.

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Figure captions

Figure 1. Location of Mokrá-Quarry in Moravia, Czech Republic. A – Geographical position of Mokrá-Quarry. B – Position of Mokrá Western and Central Quarries, as well

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as the location of MWQ 1/2001, MWQ 2/2003, MCQ 3/2005, MWQ 4/2018 sites. Source: Mapy.cz (modified); © Seznam.cz, a.s., under license (CC-BY-SA 4.0).

Figure 2. Interpretative drawings and terminology of the upper and lower first molars of *Melissiodon* aff. *schlosseri* from Mokrá-Quarry. A – M1 (Pal. 3380). B – m1 (Pal. 3373). **Abbreviations**: **Alpl**, anterolophule; **Alplc**; anterolophule cusp; **Alpld**, anterolophulid; **Alpldc**, anterolophulid cuspid; **Ast**, anterostyle; **E Mtl**; Extra Metalophule spur; **Ecld**, Ectolophid; **Enl**, Entoloph; **Etcd**, Entoconid; **Hc**, Hypocone; **Hpc**, Hipoconule; **Hpcd**, Hypoconid; **La Ac**; Labial Anterocone; **La Atcd**, Labial anteroconid; **Li Ac**, Lingual Anterocone; **Li Atcd**; Lingual anteroconid; **Li Postl**; Lingual Posteroloph; **Msc**, Mesocone; **Mscd**, Mesoconid; **Msl**, Mesoloph; **Msld**, Mesolophid; **Msst**, Mesostyle; **Mtc**, Metacone; **Mtcd**, Metaconid; **Mtl**, Metalophule; **Pac**, Paracone; **Postl**, Posteroloph; **Postld**, Posterolophid; **Posts**, Posterosinus; **Postsd**, Posterosinusid; **Prc**, Protocone; **Prl**, Protolophule; **Prs**, Protosinus; **Prst**; Protostyle; **Prtsnsd**, Protosinusid; **Ptcd**, Protoconid; **Ptcd h arm**, Protoconid hind arm; **S**, Sinus; **Sd**, Sinusid. Modified from Jovells-Vaqué & Casanovas-Vilar (2018). Scale bar equals 1 mm.

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Figure 3. Scanning electron micrographs of *Melissiodon* aff. *schlosseri* from MWQ 2/2003 and MCQ 3/2005 in occlusal view. A – fragment of left mandible with M1-M2 (Pal. 3381); B – fragment of right mandible with M1-M2 (Pal. 3382); C – fragment of left mandible with M1 (Pal. 3490); D – fragment of right mandible with M1 (Pal. 3488); E – left M1 (Pal. 3371); F – right M1 (Pal. 3380); G – fragment of right M1 (Pal. 3489); H – left M1 (Pal. 3491); I – left M1 (Pal. 3492); J – left M1 (Pal. 3493); K – right M1 (Pal. 3931); L – right M2 (Pal. 3372); M – right M2 (Pal. 3383); N – right M2 (Pal. 3495); O – left M2 (Pal. 3496); P – left M3 (Pal. 3377); Q – left m1 (Pal. 3373); R –

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right m1 (Pal. 3374); S – right m1 (Pal. 3494); T – fragment left m1 (Pal. 3903); U – left m2 (Pal. 3375); V – right m2 (Pal. 3497); W – right m2 (Pal. 3498); X – left m2 (Pal. 3930); Y – fragment of right m3 (Pal. 3499); Z – right m3 (Pal. 3376); AA – right m3 (Pal. 3501); AB – left m3 (Pal. 3502). Scale bar represents 1 mm.

Figure 4. Scatterplot (length and width) size of the upper and lower molars of different *Melissiodon* taxa from various localities during the early Miocene. Measurements of *Melissiodon* taxa were obtained from the following publications: Hrubesch 1957; Mein & Freudenthal 1981; Ziegler & Falhbusch, 1986; Fejfar 1990; Werner 1994; Hordijk et al. 2015; Jovells-Vaqué & Casanovas-Vilar 2018.

Figure 5. Biochoronologic distribution of *Melissiodon* remains across Europe during the early Miocene. Black squares represent localities in which *Melissiodon* remains have been found, while white squares denotes localities in which *Melissiodon* remains with a cuspid-like labial anteroconid have been found. In the Dolnice 1-3 and Ořechov, m1 with both cuspid-like and cristid-like labial anteroconid have been found. The positions of MN4 Czech localities are speculative, since no biostratigraphic data for all localities is available. Age and chronological position of the localitites mentioned in the text is based on works of Bolliger (1992); Steininger (1999); Bulot & Ginsburg (1996); Aguilar et al. (2003); Bulot et al. (2009); Reichenbacher et al. (2013); Ruiz-Sánchez et al. (2013); Hordijk et al. (2015); Prieto et al. (2018, 2022); Jovells-Vaqué & Casanovas-Vilar (2021). *Melissiodon* data was obtained from the following works: Hrubesch 1957; Mein & Freudenthal 1981; Ziegler & Falhbusch, 1986; Werner 1994; Hordijk et al. 2015; Jovells-Vaqué & Casanovas-Vilar 2018; and personal observations.

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