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NEW SPECIMENS OF ANTHRACOTHERIIDAE (*BRACHYODUS*, *MASRIMERYX*) FROM EARLY MIOCENE LOCALITIES NEAR EGGENBURG, LOWER AUSTRIA

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Abstract: The Early Miocene anthracotheres from the Austrian Paratethyan Eggenburgian deposits of the Eggenburg Marine Bay have proven to be of great interest for taxonomy and biostratigraphy. The discovery of specimens in the region of Eggenburg led to the erection of the genus *Brachyodus* in 1895, and their association with marine fossils in the subjacent deposits helped to establish their biostratigraphic position within the Eggenburgian stratigraphic interval, which has generally been correlated to the Burdigalian of France and elsewhere in Europe. Even though the quantity of material is limited, the fossils continue to throw light on the morphology and taxonomy of the group, this paper dealing with some undescribed cranial and mandibular fossils that provide evidence concerning the tusk-like teeth of these anthracotheres. The said teeth are incisors, and not canines. The upper tusk-like tooth is the central incisor, whereas the lower one is the second incisor, and it is inserted in the antero-lateral corner of the fully fused symphysis. Metric analysis of the teeth indicates the presence of three species of anthracothere in the Austrian deposits, two of which are attributed to *Brachyodus* and one to *Masrimeryx*. A general revision of all the Austrian dento-gnathic material of these large-bodied hydrophile mammals is provided.

Zusammenfassung: Die Anthracotherien aus dem frühen Miozän der österreichischen Paratethys in der Eggenburger Meeresbucht haben sich für die Taxonomie und Biostratigraphie als äußerst interessant erwiesen. Die Entdeckung von Exemplaren in der Region um Eggenburg führte 1895 zur Errichtung der Gattung *Brachyodus*, und ihr Vorkommen mit marinen Fossilien trug dazu bei, ihre biostratigraphische Position innerhalb der Zeitstufe des Eggenburgium zu klären. Das Eggenburgium wird im Allgemeinen mit dem Burdigalium in Frankreich und anderen Teilen Europas korreliert. Auch wenn die Menge des Materials begrenzt ist, geben die Fossilien weiterhin Aufschluss über die Morphologie und Taxonomie der Gruppe. Dieser Artikel befasst sich mit einigen unbeschriebenen Schädel- und Unterkiefer-Resten, die Hinweise auf die stoßzahnartigen Zähne dieser Anthracotherien liefern. Bei den genannten Zähnen handelt es sich um Schneidezähne und nicht um Eckzähne. Der obere stoßzahnähnliche Zahn ist der mittlere Schneidezahn, der untere der zweite Schneidezahn und dieser sitzt in der anterolateralen Ecke der vollständig verschmolzenen Symphyse. Die metrische Analyse der Zähne weist auf das Vorkommen von drei Anthracotherien-Arten in den österreichischen Lagerstätten hin, von denen zwei *Brachyodus* und eine *Masrimeryx* zugeordnet werden. Es wird eine allgemeine Überarbeitung des gesamten österreichischen Zahn- und Kiefermaterials dieses großwüchsigen, wasserliebenden Säugetiers vorgelegt.

Key words: Anthracothere, dentition, Paratethys, biostratigraphy, taxonomy, systematics, Early Miocene, Eggenburgian

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Introduction

The Early Miocene shallow marine and coastal sedimentary deposits in the Eggenburg "marine bay" of the Paratethys, in Austria, have yielded fossil mammals that have proven to be crucial for throwing light on taxonomic and systematic issues. As concerns the anthracotheres, the subject of this paper, the Eggenburgian specimens yielded to Depéret (1895) the evidence that he was dealing with a new taxon. This prompted him to revise the taxonomy of what used to be called *Anthracotherium onoideum* Gervais, 1859, a taxon first described from Neuville-aux- Bois, in the Faluns de la Touraine (France) which are also shallow marine strata intercalated with fluviatile sands. He erected the new

genus *Brachyodus* Depéret, 1895 for the species, and the combination *Brachyodus onoideus* (Gervais, 1859) has been in use ever since. Among the characters that distinguished this genus from *Anthracotherium* Cuvier, 1822 was the presence of wrinkled enamel in the teeth, and the selenodont cusp morphology of the molars.

The quantity of Early Miocene anthracothere fossils from Austria is still limited, with fewer than 60 teeth in the collections, only a few of which are associated in mandibles, and only one in a maxilla. Exploitation of sands of the Burgschleinitz Formation from eight mostly historical outcrops in the vicinity of Eggenburg has continued to yield fossils among which are a few anthracotheres. The aim of this paper is to describe and analyse the published and unpublished fossils of this family of artiodactyls from the Early Miocene of Austria. It follows the revision by Pickford (2025) of the same family on the basis of nearly 2,000 dental specimens from the French Faluns and the Sables de l'Orléanais. The undescribed anthracothere fossils from Austria include the first associated remains of upper and lower dental rows collected from Maigen, near Eggenburg. The sample consists of two fragments of premaxillae with the upper central incisors in situ, some isolated upper incisors and cheek teeth, a mandible with p/2–m/3 and an isolated lower second incisor. From a nearby site called Gauderndorf, there is a damaged but highly informative mandibular symphysis which preserves the alveoli of the lower second incisors and the anterior premolars.

The outcome of the study is that there are two species of *Brachyodus* in the Eggenburgian deposits, as well as one species of *Masrimeryx* Pickford et Gawad, 2024 on the basis of a partial upper molar from Eggenburg/Wolkenspiegel. Figures of the available dento-gnathic Early Miocene anthracothere fossils (or casts) from Austria, are provided.

Historical background

The history of study of anthracotheres, an extinct superfamily of suoid artiodactyls, has been exceptionally convoluted (Pickford 2025). Some authors (Orliac et al. 2013, Lihoreau et al. 2015) linked the group to Hippopotamidae, whereas others concluded that the relationship between these mammals was remote (Pickford 2008, 2015, 2025). The axial skeleton of *Rusingameryx aequatorialis* (MacInnes, 1951), a species from eastern and southern Africa that is closely related to *Brachyodus onoideus*, indicates that the neck was long, and that the head was habitually carried well above the level of the shoulders (Pickford 2015) much as in large hydrophile mammals such as swamp deer, moose and lechwe (Pickford 2008) and unlike the short necks of hippopotami in which the heads are habitually carried beneath the level of the shoulders. The limb bones of *Brachyodus* are also appreciably longer than those of hippos.

Initially, the fossils that eventually came to be called *Brachyodus* were included in the genus *Anthracotherium*, firstly as "*A*[*nthracotherium*] *Magnum*, de l'Orléanais" by Blainville (1846: pl. III of *Anthracotherium*) and then as *Anthracotherium onoideum* Gervais, 1859. After examining fossils from Eggenburg, Austria, that had been classified as *Hyopotamus* Owen, 1848 by Neumayr (1888), Depéret (1895) erected the genus *Brachyodus* with *Brachyodus onoideus* as the type species. Among the specimens from Austria described by Depéret (1895) there were two tusk-like teeth that he thought were canines. However, both of the teeth are incisors. What he thought were upper canines were in fact lower second incisors. The same category of misattribution was made by Daxner-Hoeck (1971) when she described additional fossils from the same region. Other authors have made similar misattributions, including Mayet (1908) who identified a premaxilla of *Brachyodus onoideus* as a mandible of *Pseudocyon depereti* Mayet, 1908 because he thought the tusk-like tooth in it was a lower canine rather than an upper central incisor. The proper identification of the tusk-like teeth of *Brachyodus* was eventually demonstrated by Cabard et al. (1980) and confirmed by Hellmund (1991). A detailed history of the study of the anterior dentition of *Brachyodus* was published by Pickford (2025).

Thus, even though the anthracothere fossils from Austria were limited in extent, and some were initially misinterpreted they have proven to be of great utility for clarifying the systematics and taxonomy of the group. Their association with marine fossils in the Paratethys stratigraphic sequence has also been of major significance, in that the biostratigraphic relations of the material were clear, indeed much clearer than those of the fossils from the Faluns de la Touraine, many of which have been eroded from their original context and redeposited in younger strata (Dineur and Ginsburg 1986).

Palaeobiogeography

The Early Miocene anthracotheres from the Central Paratethys (Austria) lie geographically midway between those of the western and eastern sectors of the Paratethys and are north of those from the Tethyan Realm. The Austrian taxa show stronger taxonomic affinities with the faunas from the Western Paratethys and the Atlantic sectors of Europe (France, Iberian Peninsula) than they do to those of the Eastern Paratethys, but there are hints of a link to the Tethyan Realm, in particular to the sedimentary succession at Moghara in Egypt.

Anthracotheriidae (*Brachyodus* spp.) are known from the Early Miocene around 19 Ma from Eurasia and Africa (Text-

Text-fig. 1. Early Miocene localities in Europe and North Africa that have yielded fossilised remains of large anthracotheres.

fig. 1). Following the revision of the French anthracotheres by Pickford (2025) there are four species known (*Br. pontigneensis* Pickford, 2025, *Br. onoideus* (Gervais, 1859), *Br. nancrayensis* Pickford, 2025, *Br. depereti* (Fourtau, 1918)). The first three of these species are known from Western Europe: Iberian Peninsula (Portugal, Spain; Pickford 2025), France (Sables de l'Orléanais, Faluns, St. Antoine de Ficalba, Bonrepos-sur-Ausonelle; Pickford 2025), Germany (Elm; Stehlin 1917), Switzerland (Brüttelen; Studer 1895), the Czech Republic (Tuchořice; Fejfar et al. 2003), Austria (Eggenburg; Depéret 1895), Greece (Kalimeriani; Melentis 1965) while the fourth is recorded from Africa – Egypt (Moghara; Fourtau 1918). A species of *Brachyodus* has also been recorded from Thailand (Ducrocq et al. 2003) but the genus does not appear to be present in the deposits of Sind or Bugti in Pakistan (Forster-Cooper 1924) nor in the Kachchh Peninsula, India (Prasad 1964) despite the fact that several authors have reported it from there (Pickford 1987). Madden et al. (1983), recorded a species of *Masritherium* Fourtau, 1918 from Wadi Sabya, Red Sea area, Saudi Arabia, but its affinities remain in doubt: it might represent *Brachyodus* or *Rusingameryx* Pickford, 2022. It is stressed that the small-bodied anthracotheres that were for a long time included in *Brachyodus* (Astre 1926, Geais 1934) are no longer included in the genus, but have been transferred to *Elomeryx* Marsh, 1894b (Hellmund 1991) and other genera.

Chitenaymeryx intermedius (Mayet, 1908) (formerly classified as *Brachyodus intermedius*) is common in France and Portugal, but is unknown elsewhere, except for a possible record at Olkhon, Lake Baikal, Russia (Vislobokova 1994). In particular it is not known from the Central Paratethys deposits nor from those of the Tethyan and Mediterranean realms. Deposits in Kazakhstan (Dmitryeva and Nesmenayov 1982) were reported to have yielded three species of anthracotheres. One of them was named *Brachyodus trofimovi* de Bonis, Brunet, Kordikova et Mavrin, 1997 by de Bonis et al. (1997), but the material does not belong to this genus (mandibular symphysis unfused, even at adult stages of ontogeny). As such the generic attribution of the Askazansor fossils requires revision. They possibly represent a species of *Elomeryx* as suggested by Ducrocq and Lihoreau (2006) but comparisons need to be made to *Chitenaymeryx* Pickford, 2025, *Masrimeryx*, *Mogharameryx* Pickford et Gawad, 2024 and *Aegyptomeryx* Pickford et Gawad, 2024. None of the fossils from China hitherto identified as *Brachyodus*, such as *Brachyodus hui* (Chow, 1958) (Xu 1962) can be confidently attributed to this genus, although Ducrocq et al. (2003) thought that *Sihongotherium* Liu et Zhang, 1993 from Sihong, Jiangsu Province (Liu and Zhang 1993), might belong to it. *Brachyodus japonicus* Matsumoto, 1925 (in Tokunaga 1925), was transferred to the genus *Elomeryx* by Tsubamoto and Kohno (2011) because the mesostylar morphology of the upper molar suggests affinities with *Elomeryx* or a similar bothriodont, as pointed out by Dineur (1982) and Ducrocq and Lihoreau (2006). The same applies to fossils from Nabeshima Island, Yamaguchi Prefecture, Japan, attibuted to *Brachyodus* by Okazaki (2003) but the mesostylar morphology indicates that the species is more likely to belong to *Elomeryx* or a related form, rather than to *Brachyodus* (Ducrocq and Lihoreau 2006).

Material from Moghara, Egypt, previously classified as *Brachyodus africanus* (Andrews, 1899) was attributed to *Jaggermeryx* Miller et al., 2014, by Pickford and Gawad (2024). Fossils from Kenya, Uganda and Namibia that were hitherto included in *Brachyodus aequatorialis* MacInnes, 1951 were classified in a separate genus, *Rusingameryx*, by Pickford (2022). Tsubamoto et al. (2025) opted to retain the species in *Brachyodus* but they recognised that the East African fossils attributed to *Brachyodus aequatorialis* were heterogeneous enough to warrant the creation of a new subspecies *Br. aequatorialis nacholaensis* Tsubamoto, Kunimatsu, Tsujikawa et Nakatsukasa, 2025. The latter subspecies has no lower canines (Tsubamoto et al. 2025), whereas the nominotypical subspecies (*Brachyodus aequatorialis aequatorialis*) retains them (Pickford 2022). European species of *Brachyodus* do not possess lower canines, so it is clear that there are dental differences between *Brachyodus* sensu stricto and *Rusingameryx aequatorialis* from Rusinga. Pickford (2020a) already pointed out the presence of significant differences in dental morphology of material from Napak, Uganda, that suggested the presence of two taxa at the site. The same applies to the remains from Moroto, Uganda (Pickford 2020b). Further study of all the Early Miocene, African large anthracotheres is required.

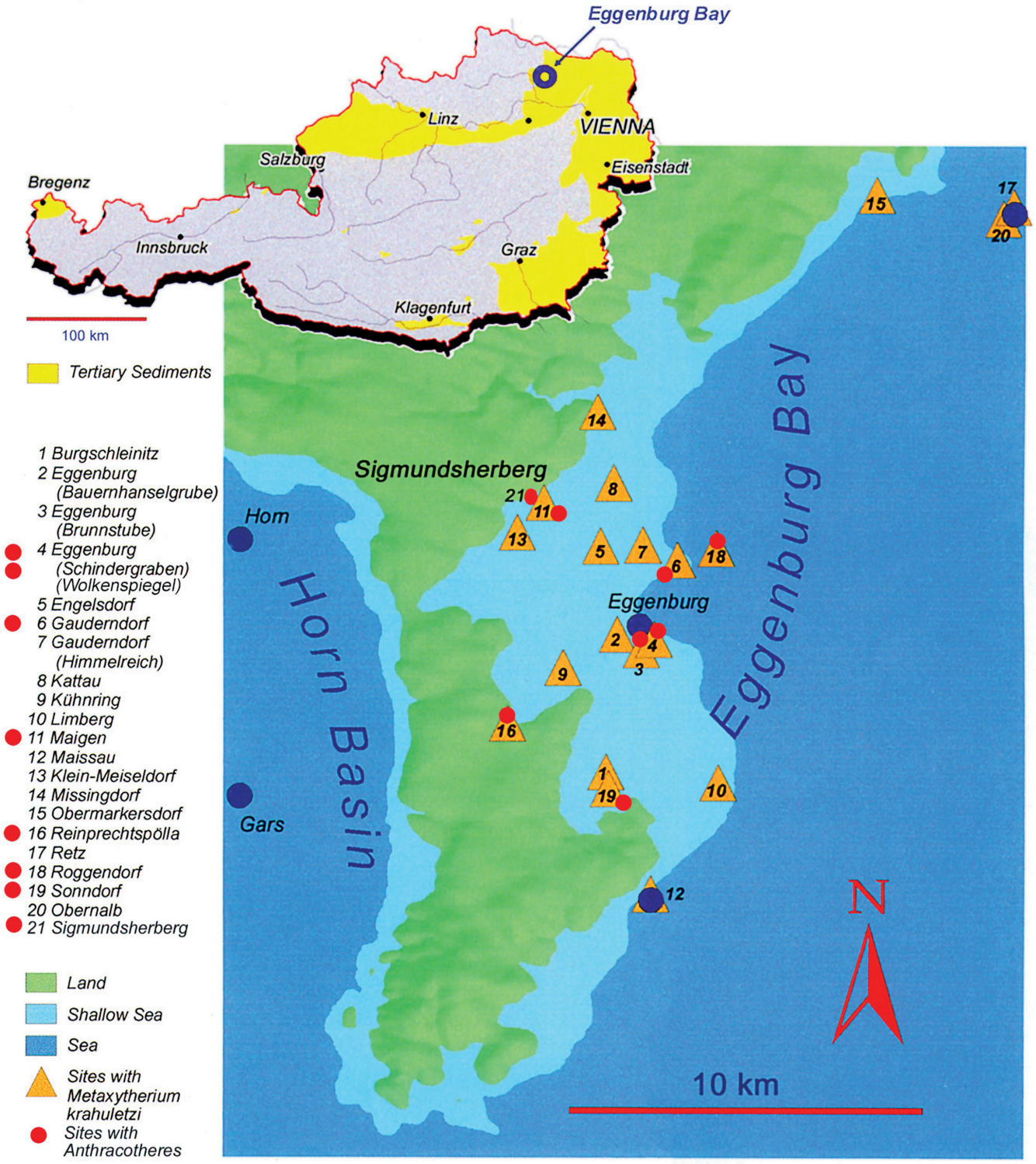
The fossil tooth from Bozovici, Romania, attributed to *Brachyodus onoideus* by Grigorescu (1985) is herein considered to represent *Masrimeryx palustris* (Miller et al., 2014), the type locality of which is Moghara, Egypt. The same species is present at Eggenburg/Wolkenspiegel, Austria.

The Eggenburgian marine biotas from the southern rim of the Bohemian Massif (Fels Formation, Roetzel 2022f) and Horn Basin (Mold Formation, Roetzel 2022h; Loibersdorf Formation, Roetzel 2022g) show clear differences from those from the Eggenburg Marine Bay (Kühnring Member, Roetzel 2022b; Burgschleinitz Formation, Roetzel 2022a; Gauderndorf Formation, Roetzel 2022c; Retz Formation, Roetzel 2022j and Langau Formation, Roetzel 2022i) (Text-fig. 2).

Mammal remains are not known from the sedimentary successions at the southern rim of the Bohemian Massif nor have they been reported from the Horn Basin, in contrast to the Eggenburg Bay, where *Brachyodus* spp. occur in the Burgschleinitz Formation alongside remains of the sirenian *Metaxytherium krahuletzi* Depéret, 1895 and diverse small mammals (Mein 1989). There are also differences in the rich molluscan faunas from the two regions, especially among large cardiids, pectinids and other families (Mandic and Steininger 2003).

Material and methods

The fossils described herein were collected from eight sand pits in the region of Eggenburg, Austria. The specimens are curated at several museums (Krahuletz Museum, Eggenburg; Horn Museum, Horn; the OÖLKG, Linz; the University of Vienna) and casts of some of the historic fossils are in the Naturhistorisches Museum Basel, Switzerland. The fossils from Maigen near Eggenburg, described herein,



Text-fig. 2. Palaeogeographic reconstruction of the Eggenburg region during the Early Miocene with localities that have yielded remains of the Sirenian, *Metaxytherium* (yellow triangles; data from Domning and Pervesler 2001) and anthracotheres (red dots).

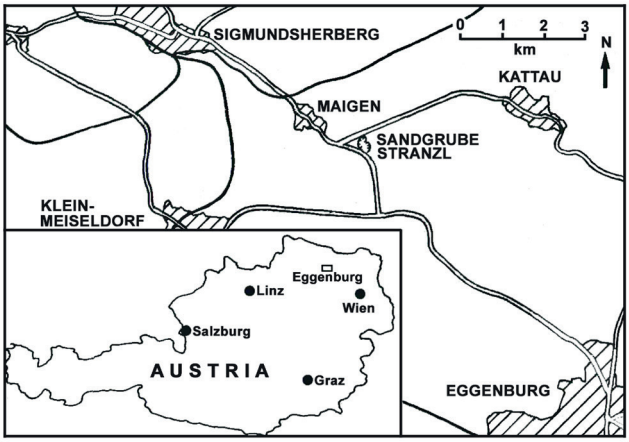
were part of a collection made by Dr Herbert Schaffer, Würting, Upper Austria, now housed in the Geoscientific Collections, Biodiversity Centre Upper Austria (OÖLKG), Linz. For fossils for which precise details of provenience are known, latitude and longitude co-ordinates of localities are provided (WGS 84 grid).

Comparisons were made with Early Miocene anthracothere fossils from France, Portugal, Egypt, Romania, the Czech Republic and Pakistan.

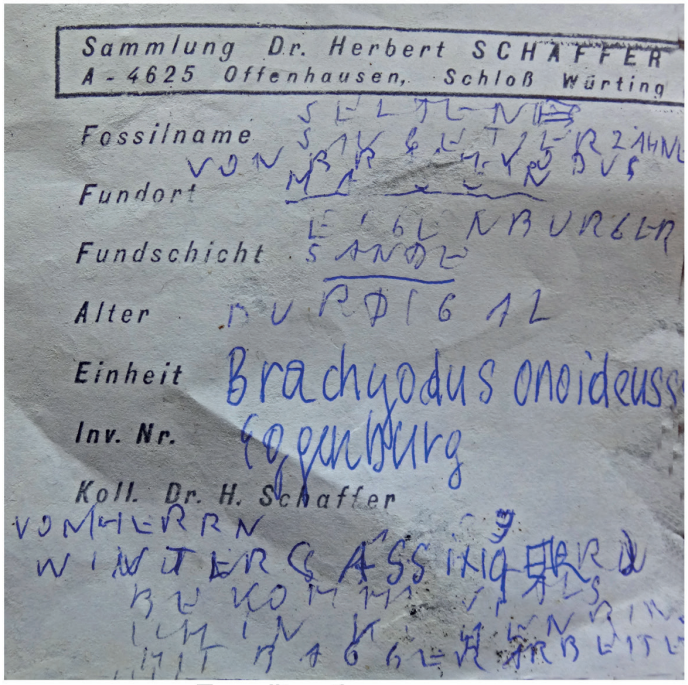
The Maigen anthracothere collection, history and documentation

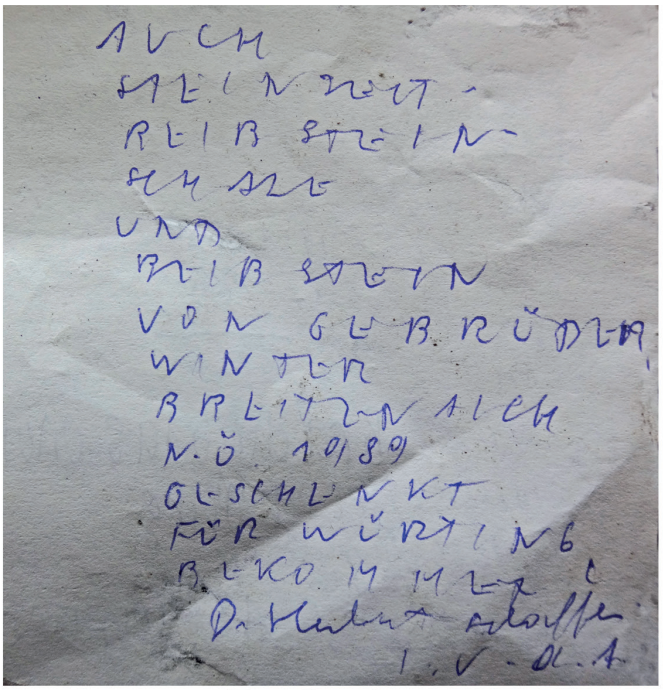
The remains of *Brachyodus pontigneensis* and *Brachyodus onoideus* from Maigen described herein were found in the private collection of Dr Herbert Schaffer, and were previously kept in the castle of Würting in Offenhausen, Upper Austria. The entire fossil collection was purchased by the Cultural Section of the Government of Upper Austria in 2023, and

is now curated in OÖLKG, Linz. The accompanying labels (slips of paper) of the *Brachyodus* remains indicate (Text-figs 4, 5) that Dr Schaffer received these remains in 1989 as a gift from Mr Winter of Breiteneich near Horn. Mr Winter (deceased) was a collector of archaeological objects and his collection is now curated in the Horn Museum. According to one of these labels, Mr Winter found the *Brachyodus* remains in 1977. The location is clearly indicated on the label as "Maigen near Eggenburg" but there is no information about the precise sand pit (at that time, the Stranzl, Wagerer, Rhiel and Western pits were active). Based on other vertebrate finds in the Stranzl pit, it is assumed that the *Brachyodus* fossils were found there.



Text-fig. 3. Location of the Maigen fossil site (Stranzl Sandgrube) northwest of Eggenburg.





Transliteration

Fossilname Seltene Säugetierzähne von Brachyodus
Fundort Maigen
Fundschicht Eggenburger Sande
Alter Burdigal
Einheit Brachyodus onoideuss
Inv. Nr. Eggenburg
Vom Herrn Winter (Assinger) bekommen als
ich in Kühnring mit Bagger arbeitete

Translation

Fossil name Rare mammal teeth of Brachyodus
Locality Maigen
Horizon Eggenburger Sands
Age Burdigal
Gift from Mr Winter (Assinger) when I was working
in Kühnring with my loader excavator

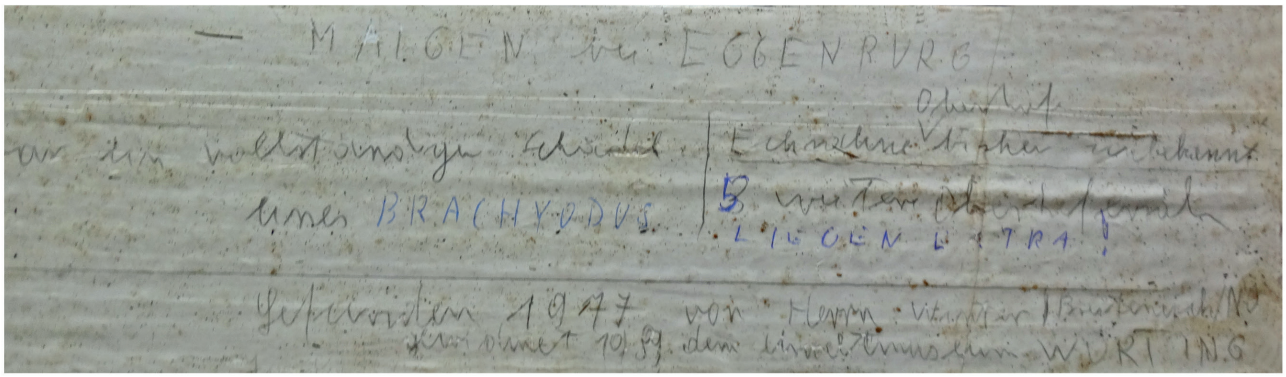
Transliteration

Auch Steinzeit Reibstein-Schale und Reibstein
von Gebrüder Winter
Breitenaich N.O. 1989 geschenkt
für Würting bekommen
Dr. Herbert Schaffer I.V.a.A.

Translation

Also Stone aged Quern-Stone and Quern-bowl gifted
by brothers Winter Breiteneich N.O. 1989 from
Würting
Dr. Herbert Schaffer I.V.a.A.

Text-fig. 4. Recto and verso sides of a label accompanying the fossil anthracothere remains in the Schaffer collection, with transliterations and translations.



Transliteration

MAIGEN BEI EGGENBURG

War in vollständigem Schädel eines Brachyodus. Eckzähne, Oberkiefer bisher unbekannt 5 weitere Oberkieferfragmente liegen extra!

Gefunden 1977 von Herrn Winter Breiteneich NÖ. Gwidmet 1989 dem Urweltmuseum Würting

Translation

MAIGEN NEAR EGGENBURG

Was part of a complete skull of Brachyodus. Canine, upper jaw hitherto unknown 5 more fragments of upper jaw lie separately.

Found 1977 by Mr. Winter Breiteneich NÖ. Dedicated 1989 to the primeval world Museum Würting

Text-fig. 5. Note with faded handwriting accompanying the fossil anthracothere remains in the Schaffer collection, with transliteration and translation.

Institutional abbreviations

CGM	Cairo Geological Museum (now the Egyptian Geological Museum)
HO	Hörn Museum, Horn, Lower Austria
IPUW	Institute of Palaeontology, University of Vienna, Vienna
KM	Krahulez Museum, Eggenburg, Lower Austria (previous inventory numbers are given in parentheses)
LPB	STAR Institute Laboratory of Paleotheriology and Quaternary Geology (Babes-Bolyai University Cluj-Napoca)
MNHN	Muséum National d'Histoire Naturelle, Paris
MSNO	Muséum des Sciences naturelle, Orléans
NHMB	Naturhistorische Museum, Basel
NHMW	Naturhistorisches Museum, Vienna
OÖLKG	Oberösterreich Landes-Kultur GmbH Geowissenschafliche Sammlungen, Linz, Upper Austria

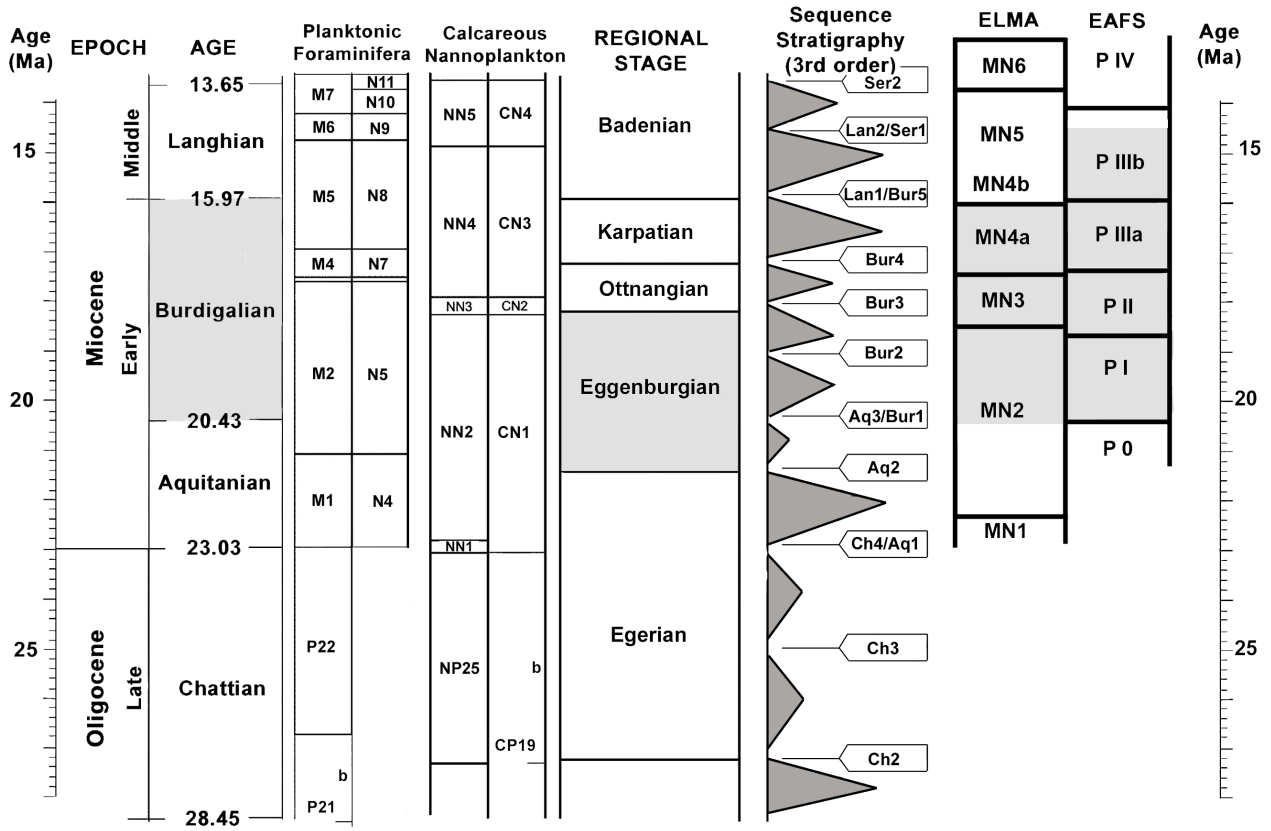
Geological context

The Eggenburgian (Early Miocene) sediments in the Eggenburg area – the "Eggenburgian Miocene Bay" – overlie diverse crystalline rocks of the Bohemian Massif. The basal transgressive Burgschleinitz Formation (Roetzel 2022a) is characterised by an alternation of moderately- to poorly-sorted, coarse to fine sands with gravelly intercalations and a rich fossil fauna, and in places it changes laterally into muddy sands and silts often with layers (the Kühnring Member) that includes oysters and *Mytilus* (Roetzel 2022b). The Burgschleinitz Formation is usually concordantly overlain by the Gauderndorf Formation (Roetzel 2022c) comprised of fine to silty sands with irregular concretions and a rich molluscan fauna. The discordantly overlying Ottnangian Zogelsdorf Formation (Roetzel 2022d) consists of a detritic coralline algal, bryozoan limestone, reworking parts of the Gauderndorf and Burgschleinitz formations. The Zogelsdorf Formation passes up section into clays and marls of the Ottnangian Zellerndorf Formation (Roetzel 2022e).

For a better understanding of older lithological terms used in the literature, we herein provide the various synonyms of lithological terms in the Eggenburg area (see also Fuchs 1900a, b, 1902, 1904; Tab. 1) and the estimated ages of the units (Tab. 2).

Table 1. Early Miocene lithostratigraphic units defined in Austria, and their synonyms (arranged from oldest at the base to youngest at top). (Arranged from Roetzel 2022a–e and Fuchs 1900a, b, 1902 and 1904).

Present terminology	Synonyms
Zogelsdorf Formation	Nulliporenkalk, Molassesandstein, Brunnstubensandstein, Schichten von Eggenburg, Eggenburger Schichten, Pectenschichten von Eggenburg, Zogelsdorfer Stein, Zogelsdorfer Sandstein
Gauderndorf Formation	Schichten von Gauderndorf, Niveau von Gauderndorf, Mugelsande, Tellinensande
Burgschleinitz Formation	Loibersdorfer Schichten, Liegendsande, Liegendschichten, Liegendsandstein, Patellensande von Roggendorf, Grobsandentwicklung von Burgschleinitz, Basale Grobsande
Kühnring Member (base of Burgschleinitz Formation)	Dunkelblauer Tegel or Mergel, Liegendtegel, Molter-Schichten, Crassostreen-Schichten von Kühnring



Text-fig. 6. Geological Time Scale from the upper parts of the Oligocene to Middle Miocene, highlighting the Eggenburgian Regional Stage, the Burdigalian Age, European Land Mammal Ages (ELMA) and East African Faunal Sets (EAFS) that have yielded remains of large-bodied anthracotheres (chart modified from Piller et al. 2022 with addition of ELMA and EAFS from Pickford and Gawad 2024). Anthracothere distribution (light grey background) from Pickford (2025), Tsubamoto et al. (2025) and present study.

The Eggenburgian Stage/Age (synonyms: Horner-Schichten, Erste Mediterranstufe, Eggenburger Serie, Eggenburger Schichten s.l., Eggenburg Formation) with a numerical age at the base of 20.44 Ma, correlates in terms of planktonic foraminiferans to zones N5 and M2, in terms of calcareous nannoplankton zones to NN2 and CN1, in terms of mammal zones to MN 2 and MN 3 (basal Orléanian). According to the chart in Piller et al. (2007: fig. 1, 2022) sea-level lowstand Aq 2 (Aquitanian 2) marks the base of the Eggenburgian, and lowstands Aq 3/Bur 1 (Aquitanian 3/Burdigalian 1), Bur 2 (Burdigalian 2) and Bur 3 (Burdigalian 3) correlate to the middle and upper Eggenburgian.

The small mammal fauna from Maigen (Mein 1989) corresponds to the older part of the MN 3 mammal zone (Basal Orléanian, the basal part of MN 3). The nannoplankton zone NN2/NN3 was identified in the sediments of the Gauderndorf Formation. The rich molluscan fauna corresponds to that from the lower Burdigalian of the Mediterranean region (Steininger et al. 1976).

The base of the Ottnangian Stage has a numerical age of approximately 18.2 Ma (Steininger et al. 1976) (Tab. 2).

There are two distinct areas of deposition of Eggenburgian sediments on the Bohemian Massif: 1) the Horn Basin and the southern rim of the Bohemian Massif in the west and south and 2) the Eggenburg Bay in the east, separated today by a massif of crystalline basement rocks.

In Austria, Early Miocene anthracothere remains have been found in only eight localities in the Early Miocene Eggenburgian fossil bay, all of which are in deposits in the vicinity of Eggenburg, Lower Austria (Tab. 3, Text-fig. 7). Thus far no fossils of *Brachyodus* or *Metaxytherium* de Christol, 1840 have been recorded from the deposits of the Horn Basin or along the southern rim of the Bohemian Massif nor have remains of turtles, dolphins or other mammals been found there.

Table 2. Numerical ages of regional stages in Austria from Steininger et al. (1976).

Stage	Age span	Stratigraphic units
Ottnangian Stage	ca. 18.2 to 17.3 Ma	Zogelsdorf Formation ca. 18.2–17.8 Ma
Eggenburgian Stage	20.44 to 18.2 Ma	Gauderndorf Formation ca. 18.7–18.3 Ma, Burgschleinitz Formation ca. 19.3–18.7 Ma

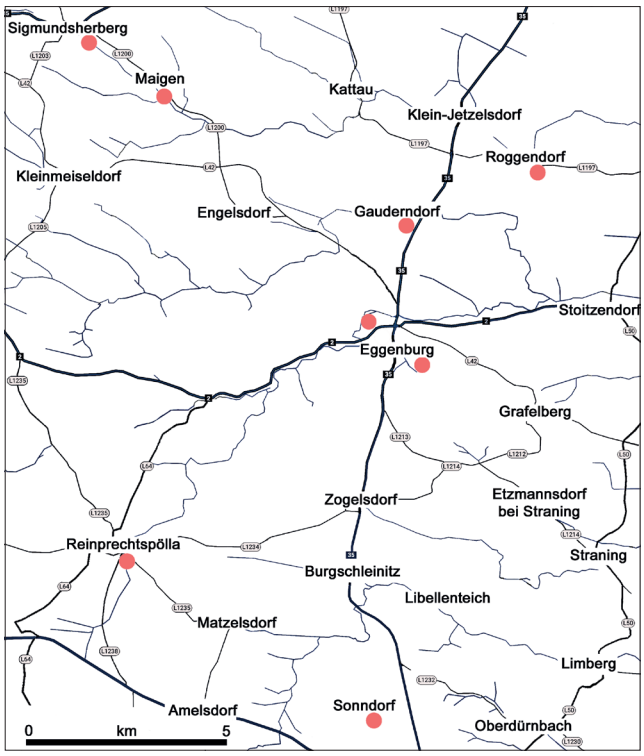
Anthracothere localities in Austria

See Table 3 for summary.

1. Eggenburg, Schindergraben

Taxon: *Brachyodus pontigneensis*, *Brachyodus onoideus*.

According to Neumayr (1888) the remains of *Brachyodus* subsequently described by Depéret (1895) came



Text-fig. 7. Location of the eight Early Miocene (Eggenburgian) fossiliferous localities in the vicinity of Eggenburg that have yielded remains of anthracotheres (red dots).

from the locality "Schindergraben" in the eastern part of the town of Eggenburg and not from the locality "Bauernhanselgrube" as stated by Daxner-Hoeck (1971). In addition to the *Brachyodus* remains, this is the type locality of *Metaxytherium krahuletzi* described by Depéret (1895). From this locality, a rich, typically Eggenburgian molluscan fauna was described. A description of the locality with an idealised section can be found in Schaffer (1914: 12–13, fig. 1) and in Fuchs (1900a, b). Overlying the granite there is a marine, indurated sandstone-like layer, approximately 5 m thick (the so-called "Liegend-Schichten") with granite boulders, which yielded the vertebrate remains described by Depéret (1895). This section of the Schindergraben is no longer exposed today; the site is preserved as a steep overgrown slope. Lithostratigraphically, these basal layers belong to the Burgschleinitz Formation and thus to the middle part of the Eggenburgian Stage (Schaffer 1914).

2. Eggenburg, Wolkenspiegel

Taxon: *Masrimeryx palustris*.

The outcrops at the "Wolkenspiegel" area (in the northwestern part of the town) as described and illustrated by Schaffer (1914: 39–40, pl. 4b) are today under buildings or have been infilled. In the description, alternating layers of clayey and sandy sediments containing *Mytilus* and other bivalves were described as overlying the crystalline basement. This formation extends towards the west almost to the hilltop of the Wolkenspiegel. Schaffer (1914) did not mention any vertebrate remains, but a damaged M3/ of an anthracothere is confirmed by inventory numbers and labels to have originated from these sediments on the eastern slope of the Wolkenspiegel.

3. Gauderndorf

Taxon: *Brachyodus pontigneensis*, *Brachyodus onoideus*.

The formerly well-exposed sand pits (Gemeindesandgrube, Sandgruben Metzger, Zimmermann and Zotter; see Steininger and Seneš 1971) and profiles at the so called "Himmerreich" Road were described in detail with fossils listed by Fuchs (1900a, b, 1902, 1904) and Schaffer (1914: 51–58, figs 14, 15, pl. 5a). Bones of *Metaxytherium krahuletzi* are frequently mentioned in the literature. In general, the sedimentary profiles overlying the crystalline rock comprise coarse sands with oysters and molluscs, the Burgschleinitz Formation, with the Kühnring Member at the base, that grades upwards into the fossil-rich silts with concretions of the Gauderndorf Formation that are unconformably overlain by the Zogelsdorf Formation. In particular, the so-called "Gemeindesandgrube" (Schaffer 1914: pl. 5a) that is rich in molluscs, shark and ray remains, could be the place where the *Brachyodus* remains were recovered.

4. Maigen Sand pit Stranzl (KG Maigen, Parz. 291)

Co-ordinates: 48° 40′ 26.2″ N, 15° 46′ 49.4″ E (Nehyba and Roetzel 2021).

Taxon: *Brachyodus pontigneensis*, *Brachyodus onoideus*.

On the northern and southern sides of the Maigen Valley, there were a number of sand pits, now abandoned, that have been infilled or recultivated. In these pits, the entire sequence of Early Miocene formations characteristic of the Eggenburg area was exposed above the crystalline rocks (phyllites of the Moravian Group). For example, in the now fenced-off Stranzl sand pit, the Kühnring Member, Burgschleinitz Formation, and Gauderndorf Formation of Eggenburgian age are exposed and are transgressively overlain by the Zogelsdorf Formation of Ottnangian age.

At Maigen, the basal Kühnring Member is dominated by green-grey silty, poorly sorted, fossil-rich gravels and coarse sands. In addition to the typical molluscs, there were oyster-, *Mytilus*- and *Pirenella*-bearing horizons and reworked coral fragments. Noteworthy is the rich fish otolith fauna (Brzobohatý 1989) and a biostratigraphically significant small mammal fauna (Mein 1989). The Kühnring Member grades upwards into the coarse- to medium-sandy, partly gravel-bearing, fossil-rich Burgschleinitz Formation with tellinids and turritellids. The coarse sands are characterised by typical tunnel systems of *Ophiomorpha* trace fossils. This horizon is overlain concordantly by the Gauderndorf Formation, green-grey silty fine sands with a rich bivalve infauna.

The base of the Ottnangian Zogelsdorf Formation follows with a distinct transgressive boundary, partly reworking the underlying Gauderndorf Formation. The sediments of the Zogelsdorf Formation are rich in bryozoans with typical pectinids and balanids.

Whereas the sediments of the Kühnring Member correspond to muddy, shallow water deposition in the sublittoral zone, the Burgschleinitz Formation was deposited as a slightly deeper-water, wave-dominated facies. The Gauderndorf Formation corresponds to deeper marine facies with molluscs burrowing in fine sediment in an area of calm water movement. Similar conditions prevailed in the Ottnangian Zogelsdorf Formation, which transgressively overlies the Gauderndorf Formation (Schaffer 1914, Steininger and Roetzel 1991, Domning and Pervesler 2001).

5. Reinprechtspölla Sandpit Pfaller, (KG Reinprechtspölla, Parz. 298)

Co-ordinates: 48° 36′ 59.4″ N, 15° 46′ 35.7 ″ E.

Taxon: *Brachyodus onoideus*, *Brachyodus pontigneensis*.

East of Reinprechtspölla, a road branches off from the L 1234 road (Reinprechtspölla to Zogelsdorf) to the north, leading toward the forest and the Schmida Valley. After a few hundred metres, on the south side of the road, we located a former sand/gravel pit (the Pfaller Sand Pit) that is almost completely buried and overgrown. At the base of the pit, above the crystalline rock, there is a horizon of scree and coarse sands of the Burgschleinitz Formation with oyster debris. Occasionally, *Metaxytherium* remains and crocodile teeth have been found here. It is assumed that this is the location of the *Brachyodus* remains labelled in the collections as "Reinprechtspölla – Pfaller Sandgrube".

6. Roggendorf

Taxon: *Brachyodus onoideus*.

East of Roggendorf, the Maigen Creek flows through a narrow valley eroded into the granite towards Röschitz. To the north, on the flanks of the valley, on the Feldberg Plateau, there are a several abandoned sand pits (Burgschleinitz Formation) and sandstone quarries (Zogelsdorf Formation). The sands on top of the granite were mined from "caves" and used as building and plastering sand. The sands are transgressively overlain by the indurated calcareous sandstones of the Zogelsdorf Formation which forms the roofs of the "caves". Most of the calcareous sandstone roofs collapsed and only in two outcrops are the underlying sands still visible: The two partially accessible "caves" are the so-called "Krampuslucke" ("Patellen Cave") (Steininger and Seneš 1971: 154–157, fig. 18) and the so-called "Fuchsenlucke"; both on property no. 653 of Roggendorf.

In the "Krampuslucke" ("Patella Cave") a thickness of approximately 200 cm of coarse quartz sands of the Burgschleinitz Formation, with a distinct shell layer containing molluscs and pebbles, lies on top of the crystalline rocks. In the wall of the quarry, the sands are overlain by the Zogelsdorf Formation, which includes a layer of redeposited mollusc shells. The Zogelsdorf Formation overlies a deeply incised surface with potholes, marking the base of the transgression, and it grades upwards into quartz siltstones. In addition to remains of *Brachyodus*, those of selachians, *Testudo antiqua noviciensis* and *Metaxytherium krahuletzi* were recovered from the sands of the Burgschleinitz Formation (Schaffer 1914).

7. Sigmundsherberg

Taxon: *Brachyodus onoideus*.

Just north of the railway underpass on the road from Sigmundsherberg to the main road No. L 42 there was a gravel and sand pit, which is now integrated into the farmhouse at Main Road (Hauptstrasse) No. 15 in Sigmundsherberg. The locality is completely overgrown and built over. Here, marly fine sands with large, thick-shelled oysters (*Crassostrea gryphoides*) were exposed. These sediments represent the Kühnring Member of the Burgschleinitz Formation and are probably the site where the *Brachyodus* remains were recovered (Schaffer 1914).

8. Sonndorf Sandpit Deim (KG Oberdürnbach, Parz. 905/2)

Co-ordinates: 48° 35′ 51.3″ N, 15° 49′ 0.9″ E.

Taxon: *Brachyodus pontigneensis*.

The Sonndorf sandpits (Daim, alternatively Hammer Sandpit) are situated 850 m NNE of the village of Sonndorf and 300 m west of the Maissau – Eggenburg road No. B 35. In the bottom of an artificial trench, the Kühnring Member was exposed passing upwards into the sands of the Burgschleinitz Formation (Domning and Pervesler 2001). These beds of the Burgschleinitz Formation contain two bone-bearing layers overlying a hard layer rich in mollusc shells (oysters, scallops and barnacles). Apart from other vertebrates these bone-rich layers yielded a large quantity of *Metaxytherium* skeletal elements (see Domning and Pervesler 2001). We consider that the anthracothere material published by Daxner-Hoeck (1971) and recently by Pickford (2008, 2025) and Pickford and Gawad (2024) could originate from these sandpits.

Systematic palaeontology

Order Artiodactyla Owen, 1848
Family Anthracotheriidae Leidy, 1869

Genus *Brachyodus* Depéret, 1895

Type species. *Anthracotherium onoideum* Gervais, 1859.

Diagnosis. Large anthracotheres with pentacuspidate upper molars, lower molars in which the metaconid has no sign of the premetacristid and mesiolingual metacristid and the entoconid does not have a mesiolingual entocristid, central upper incisors tusk-like, pointing forwards and downwards, lower second incisors foliate-spatulate and tusk-like; I1/ and i/2 sexually dimorphic; elongate diastema between I3/ and P1/ and between i/3 and p/1. Mandibular symphysis completely fused even in juveniles. Canines present in maxilla but absent from mandible. Enamel wrinkling relatively coarse.

***Brachyodus onoideus* (Gervais, 1859)**

Holotype. Musée d'Orléans 05 (2016-0-3-75, 314), right mandible fragment with p/4–m/3 (Cast in MNHN).

Diagnosis. Species of *Brachyodus* smaller than *Br. nancrayensis* and larger than *Br. pontigneensis* and *Chitenaymeryx intermedius*. Serration on mesial and distal crests of lower second incisors weak to absent.

Type locality and age. Neuville-aux-Bois, Loiret, France, Early Miocene, the upper part of MN 3.

Material. See Table 4 for teeth, plus a right talus from Sigmundsherberg (Daxner-Hoeck 1971).

Description. KM F/3710 a (G I-11 + G 592 + G I-12), a reconstituted anthracothere mandibular symphysis and part

Table 3. The eight Early Miocene, Eggenburgian anthracothere localities in Austria (in alphabetical order).

Locality	Main references describing anthracotheres	Taxon (this paper)
1. Eggenburg, Schindergraben	Neumayr 1888, Depéret 1895, Melentis 1965	*Br. pontigneensis*, *Br. onoideus*
2. Eggenburg, Wolkenspiegel	None (Daxner-Hoeck 1971, refers, but the fossils were not from the site)	*Masrimeryx palustris*
3. Gauderndorf	Daxner-Hoeck 1971	*Br. onoideus*, *Br. pontigneensis*
4. Maigen	None	*Br. pontigneensis*, *Br. onoideus*
5. Reinprechtspölla	Daxner-Hoeck 1971	*Br. onoideus*, *Br. pontigneensis*
6. Roggendorf	Daxner-Hoeck 1971	*Br. onoideus*
7. Sigmundsherberg	Daxner-Hoeck 1971	*Br. onoideus*
8. Sonndorf	Daxner-Hoeck 1971	*Br. pontigneensis*

of the left ramus from Gauderndorf, preserves the damaged alveoli of the i/2s, as well as the alveoli of the left p/1 and p/2 (Text-fig. 8). The alveoli of the i/2s are large and deep, extending close to the rear of the symphysis. The mental foramen is beneath the elongate diastema that extends between the alveoli of the i/2 and the p/1. It is slightly anterior to the root of the p/1. The diastema is 73 mm long, and the jaw is 68 mm deep at the middle of the diastema. The alveoli of the i/2s are damaged but the dimensions can be estimated – the labio-lingual diameter is ca. 24 mm and the mesio-distal diameter is ca. 34 mm. These measurements correspond to male lower incisor roots of *Brachyodus onoideus*. The alveolus of the p/1 is larger than the mesial alveolus of the p/2, as in other specimens of the species.

The lower second incisor from Maigen (Text-fig. 9) is a tusk-like tooth with a robust root and a tall foliate crown. The section of the crown is ovoid with an almost flat lingual surface with a slight central ridge, and a convex labial surface. The mesial and distal cristids are sharp and show beaded morphology. There is a small wear facet on the mesial side of the crown close to its apex. The root is larger than the crown, and shows a distinct bend beneath the cervix. The crown is 47.7 mm tall on its buccal side, and the root is 2–3 mm larger than the base of the crown (MDL × BLB of the root are 26.8 × 22.9 mm, and of the crown base are 24.2 × 20.0 mm).

KM F/3710 b (G 594) is the rear part of a left mandible with the roots of the m/3 from Gauderndorf (Text-fig. 10). It probably represents the same individual as the symphysis described above. There is a well-defined buccinator ridge and a relatively long retro-molar space. The dimensions of the roots are compatible with material of *Brachyodus onoideus*.

Discussion. Most of the Austrian specimens herein attributed to *Brachyodus onoideus* (Tab. 3) have already been described (Depéret 1895, Melentis 1965, Daxner-Hoeck 1971). It should be noted that these authors attributed all the Eggenburg material to this species, but some of it belongs to the smaller species, *Brachyodus pontigneensis*, while one specimen from Eggenburg/Wolkenspiegel is attributed to a larger species, *Masrimeryx palustris* (see below).

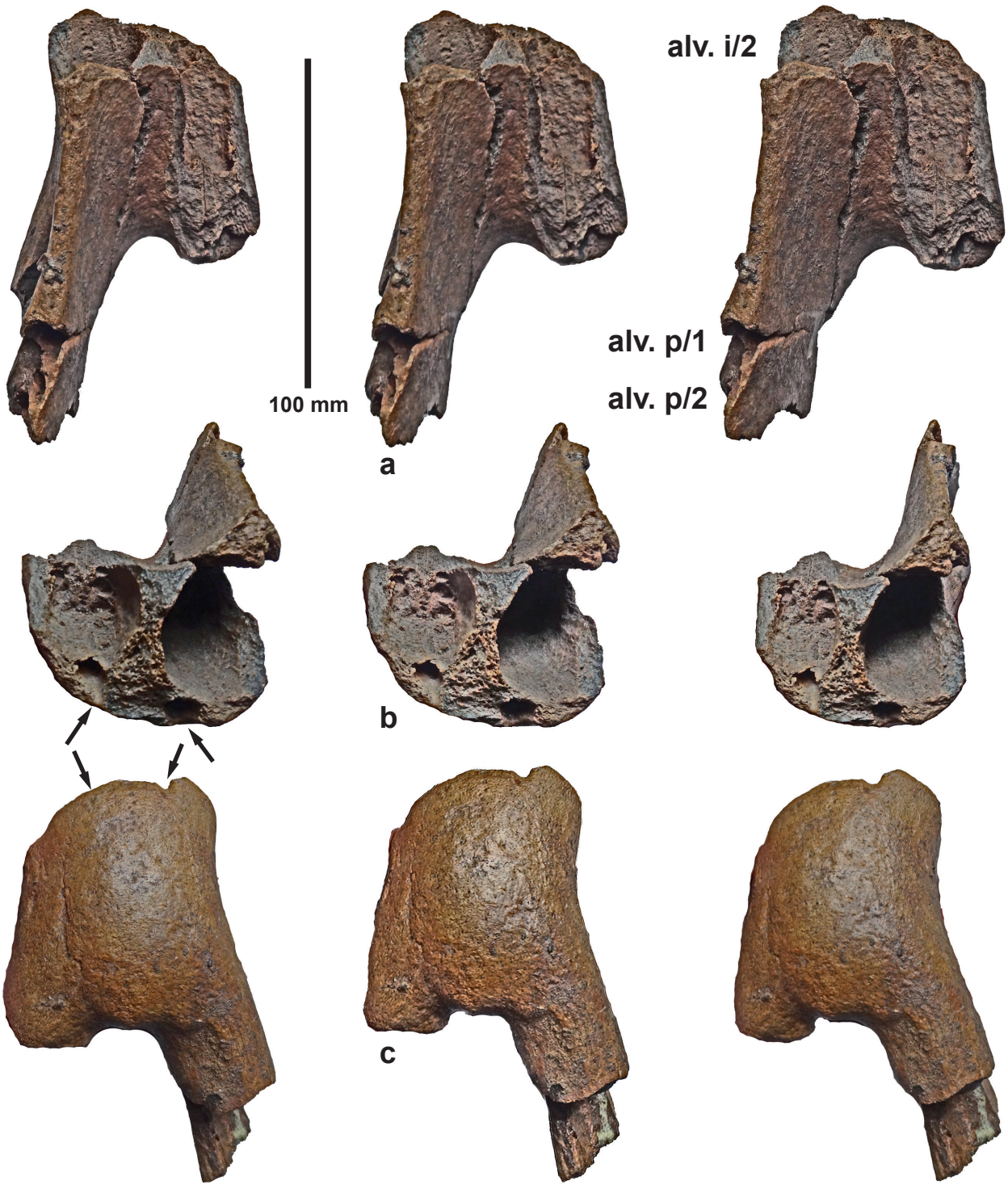
Brachyodus pontigneensis Pickford, 2025

Holotype. MNHN FS 5884, left mandible fragment from Pontigné, France, with p/3–m/1 and alveoli of p/2.

Diagnosis. Species of *Brachyodus* intermediate in size between, on the one hand, *Br. onoideus*, *Br. depereti* and *Br. nancrayensis*, which are larger, and on the other, *Chitenaymeryx intermedius* which is smaller. Marked bend in the root of the upper central incisors of male individuals.

Table 4. Measurements (in mm) of teeth of *Brachyodus onoideus* from Austria. New inventory numbers are in bold (in brackets are old numbers or the register numbers of casts).

Catalogue N°	Tooth	MDL	BLB	Data Source	Locality
KM F/3710 a (NHMB AE 11 cast)	M3/ lt	39.0	41.5	own 2021; Daxner-Hoeck 1971 as 39 × 42	Gauderndorf
KM F/3710 c (NHMB AE 16 cast)	M2/ lt	39.2	42.5	own 2025; Daxner-Hoeck 1971 as 39 × 43	Roggendorf
KM F/3710 e (NHMB AE 9 cast)	P3/ lt	27.3	26.3	own 2021; Daxner-Hoeck 1971 as 25 × 26	Eggenburg
KM F/3710 b (G 594)	m/3 lt	55.5	28.0	own 2025, root only	Gauderndorf
KM F/3710 f (G I-13) (NHMB AE 12 cast)	m/2 lt	39.0	26.0	own 2021; Daxner-Hoeck 1971 as 39 × 26	Reinprechtspölla
KM F/3710 c (G I-6)	m/2 lt	–	30.7	own 2025	Reinprechtspölla
KM F/3710 a (G I-11)	i/2 lt	–	–	own 2025, alveolus in symphysis 34 × 24	Gauderndorf
KM F/3710 d (NHMB AE 14 cast)	i/2 lt	22.3	17.8	own 2021; Daxner-Hoeck 1971 height 49	Sigmundsherberg
OÖLKG 2025/44	i/2 rt	24.2	20.0	own 2025	Maigen

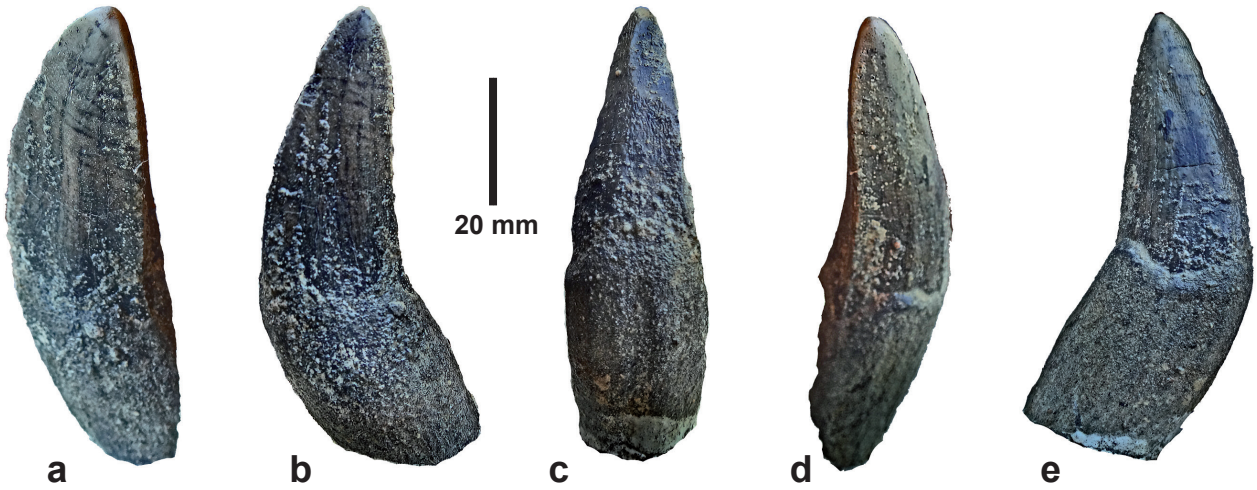


Text-fig. 8. Stereo images of KM F/3710a (G I-11, mandibular symphysis + G 592 + G I-12, parts of left ramus which fit together) of *Brachyodus onoideus* from Gauderndorf. a: superior views, b: anterior views, c: inferior views (black arrows show the foramina on the ventral surface of the symphysis).

Type locality and age. Pontigné, Maine-et-Loire, France, Early Miocene, MN 3.

Material. The dentognathic remains of *Brachyodus pontigneensis* listed in Table 5 plus three tali from Sonndorf and Eggenburg (Depéret 1895, Daxner-Hoeck 1971).

Description. Many of the fossils from Austria herein attributed to *Brachyodus pontigneensis* have already been described by Depéret (1895), Melentis (1965) and Daxner-Hoeck (1971) so it is not necessary to redescribe them, only to point out some features, such as their diminutive dimensions, that indicate that they are smaller than *Brachyodus onoideus*,



Text-fig. 9. OÖLKG 2025/44, right i/2 of *Brachyodus onoideus* from Maigen, Austria. a: oblique postero-lingual view, b: lingual view, c: mesial view (note the wear facet close to the apex), d: distal view, e: labial view.

Text-fig. 10. Superior view of KM F/3710 b (G 594), left mandible fragment with roots of m/3 of *Brachyodus onoideus* from Gauderndorf.

the species to which they were previously attributed. The fossils from Sonndorf (curated at the Horn Museum) were described by Daxner-Hoeck (1971) but she did not publish measurements of the individual teeth.

The anthracothere fossils from Maigen have not been published previously. The archives associated with the specimens indicate that the cranial and mandibular specimens represent a single individual, which, if correct, would be the first such association found in Europe. It includes parts of both premaxillae, three isolated maxillary teeth, a mandible and an isolated lower second incisor. It is noted, however, that the lower second incisor from Maigen appears to be too large to belong to the mandible. Its dimensions indicate that it probably represents a male of *Brachyodus onoideus*, whereas all the cheek teeth in the mandible plot within the range of variation of *Brachyodus pontigneensis*.

The anthracothere premaxillae from Maigen (Text-figs 11–13) retain the upper central incisors in situ, but the other upper incisors were separated from the bone during excavation. They were glued back, but in the wrong positions. There is a small fragment of I2/ with part of its root, plus both I3/s lacking parts of the roots.

There is a diastema between the I1/ and the I2/. It measures 20.5 mm on the left premaxilla and 15.0 mm on the right one.

The upper central incisors are large curved tusk-like teeth, in which the root is enlarged relative to the crown. The crown is ovoid to rounded triangular in section and has two crests, a weak, discontinuous one on the labial (anterior) side, and a prominent one on the lingual (posterior) side, close to its distal edge. There is a wear facet on the lingual side of the crown, where it occluded with the mesial edge of the lower second-incisor. The root is much taller than the crown (root height, distal side: 74 mm, crown height, distal side: 42 mm), and it is bent posteriorly much as in a specimen from Pontigné, France (Pickford 2025).

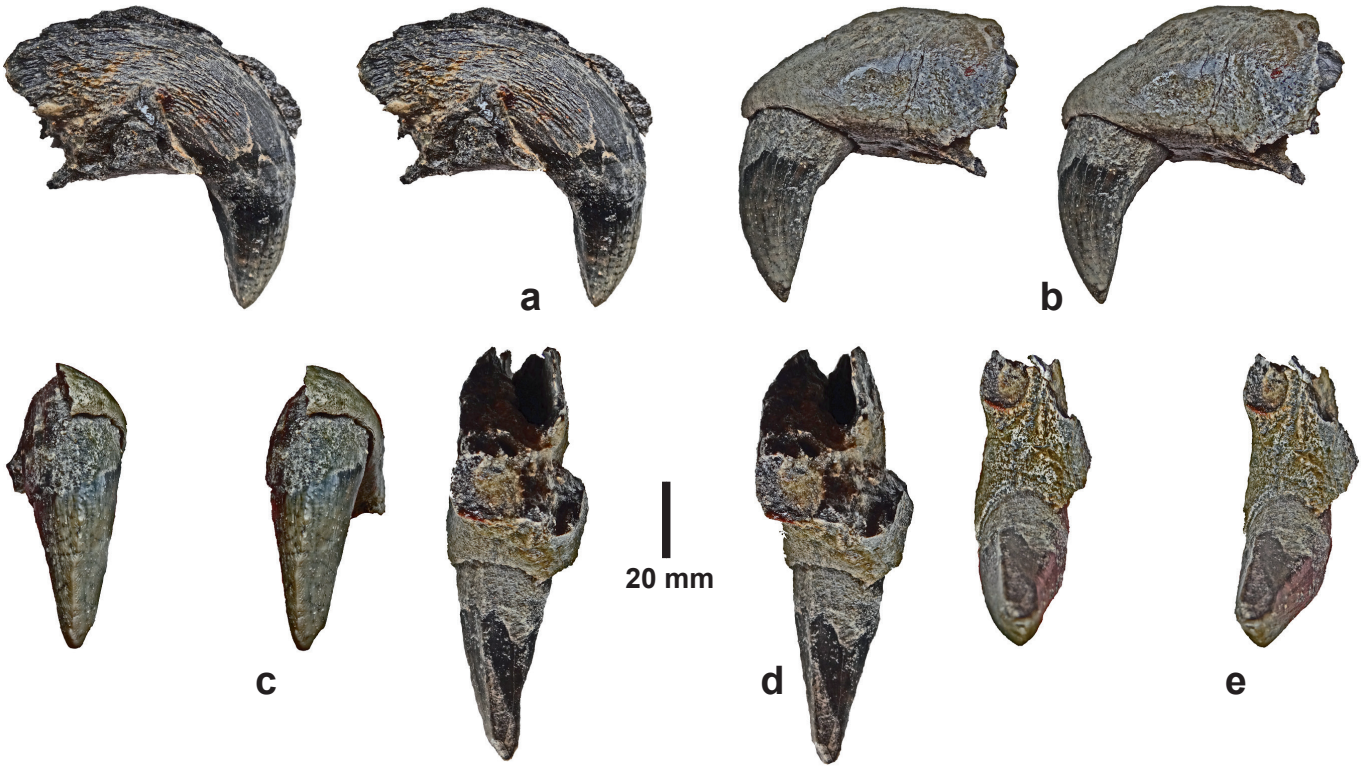
The upper third incisors are small, their crowns are ovoid in section with mesial and distal crests, the distal one being more prominent than the mesial one (Text-figs 14, 15). The lingual surface is concave with a central swelling, the labial surface is convex. There is an apical wear facet. The root is partly preserved, and shows that it was somewhat larger than the crown, and was exposed above gingival level, such that the surface of the root was polished by contact with food items.

In occlusal view the P2/ is rounded triangular in outline, with a tall paracone, from the apex of which two crests descend steeply mesially, and one strong one disto-buccally (Text-fig. 16). The two anterior crests enclose a tall triangular fovea or shallow depression which has a large wear facet where it occluded with the lower premolar. The postparacrista has grooves on its buccal and lingual sides, hinting at the formation of an incipient metacone at the distal end of which is a small metastyle. There is a disto-lingual shelf bordered distally and lingually by a beaded cingulum. The buccal surfaces of the paracone and metacone are partly covered by cementum. The enamel is wrinkled.

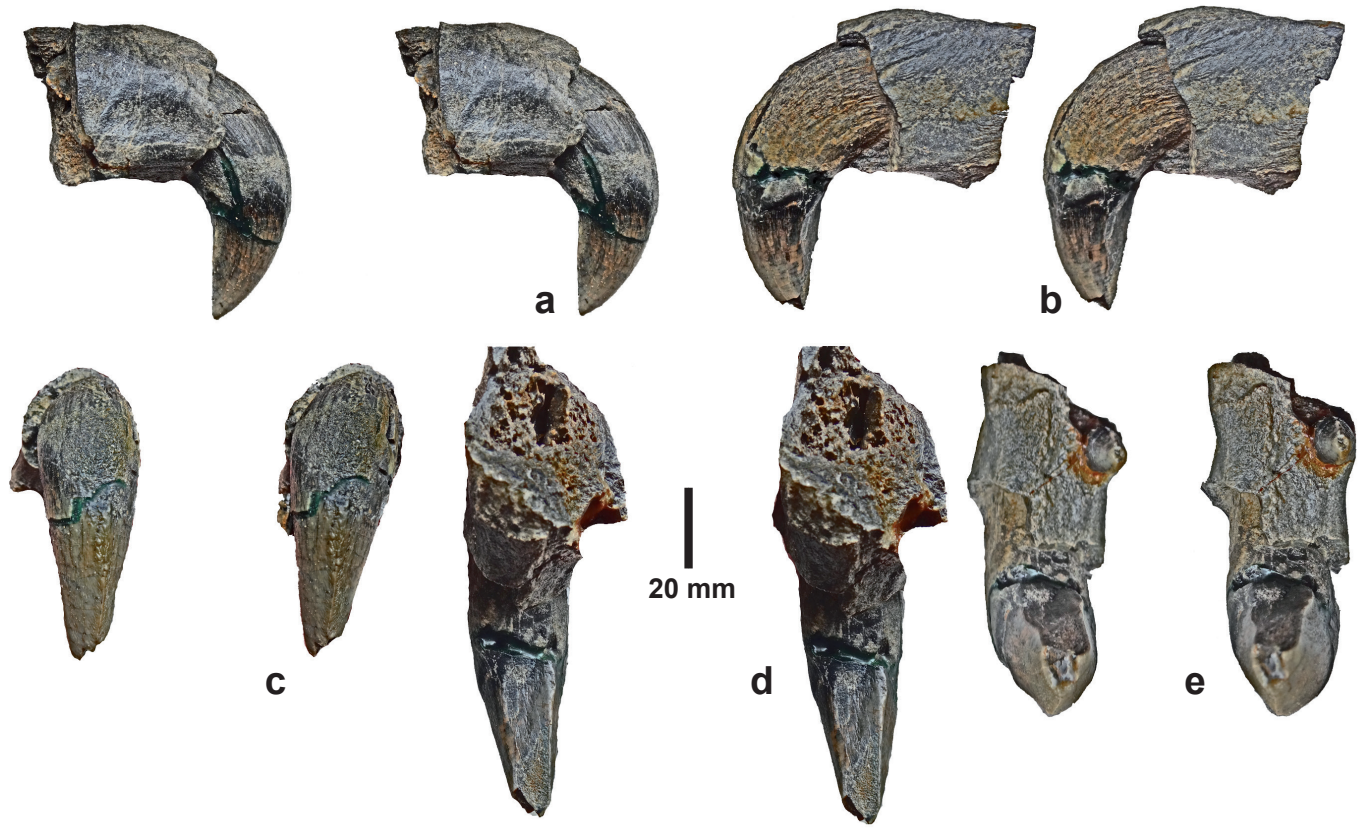
The P4/ from Maigen has two large cusps (paracone, protocone) and a small metaconule at the distal end of the postprotocrista (Text-fig. 17). The protocone is slightly

Table 5. Measurements (in mm) of teeth of *Brachyodus pontigneensis* from Austria. (Note that the left mandible KM/3703 was reported by Daxner-Hoeck (1971), to be from Wolkenspiegel, but the label (with the date 1936) accompanying a cast in the NHMB (AE 15) indicates that it was collected from the Pfaller Sandgrube, Reinprechtspölla).

Catalogue	Tooth	MDL	BLB	Data source	Locality
KM F/3716 (NHMB AE 7 cast)	i/2 lt	–	–	own 2021, base damaged; Depéret 1895: fig.	Eggenburg
KM F/2365 (NHMB AE 6 cast)	i/2 rt	21.0	15.0	own 2021; Depéret 1895: fig.	Eggenburg
IPUW 2629	p/2 lt	23.0	15.0	Depéret 1895, est. from fig. (original fossil damaged)	Eggenburg
IPUW 2629	p/3 lt	25.0	19.0	Depéret 1895, est. from fig. (original fossil damaged)	Eggenburg
IPUW 2629	p/4 lt	26.8	20.1	own 2025; Melentis 1965 as 27.5 × 20.4	Eggenburg
IPUW 2629	m/1 lt	31.7	20.7	own 2025; Melentis 1965 as 33.3 × 21.4	Eggenburg
IPUW 2629	m/2 lt	36.3	25.5	own 2025; Melentis 1965 as 36.8 × 26.4	Eggenburg
IPUW 2629	m/3 lt	48.2	26.2	own 2025; Melentis 1965 as 49.5 × 26.7	Eggenburg
IPUW 6 I 8 (NHMB AE 8 cast)	P4/ rt	23.6	29.9	own 2021; Daxner-Hoeck 1971 as 25 × 31	Gauderndorf
IPUW 6 I 4 (NHMB AE 10 cast)	M2/ rt	36.0	40.7	own 2021	Eggenburg
OÖLKG 2025/43/2	I1/ lt	17.9	22.6	own 2025 (root 23 × 27.2)	Maigen
OÖLKG 2025/43/1	I1/ rt	18.2	21.9	own 2025 (root 23 × 26.5)	Maigen
OÖLKG 2025/43/3	I3/ rt	8.0	6.0	own 2025 (root 9 × 9)	Maigen
OÖLKG 2025/43/4	I3/ lt	8.5	8.9	own 2025	Maigen
OÖLKG 2025/43/5	P2/ rt	22.4	20.2	own 2025	Maigen
OÖLKG 2025/43/6	P4/ lt	23.5	29.7	own 2025	Maigen
OÖLKG 2025/43/7	M2/ rt	35.2	40.0	own 2025	Maigen
OÖLKG 2025/44/8	p/2 lt	21.3	14.2	own 2025	Maigen
OÖLKG 2025/44/8	p/3 lt	23.0	12.0	own 2025	Maigen
OÖLKG 2025/44/8	p/4 lt	27.4	20.9	own 2025	Maigen
OÖLKG 2025/44/8	m/1 lt	–	21.3	own 2025	Maigen
OÖLKG 2025/44/8	m/3 lt	48.5	26.5	own 2025	Maigen
HO 2681	i/2 lt	17.2	16.1	own 2025	Sonndorf
HO 2681	i/2 rt	18.4	15.4	own 2025	Sonndorf
HO 26061	p/1 lt	9.2	6.1	own 2025	Sonndorf
HO 26061	p/2 lt	21.6	12.7	own 2025	Sonndorf
HO 26061	p/2 rt	21.3	13.1	own 2025	Sonndorf
HO 26061	p/3 lt	25.2	15.9	own 2025	Sonndorf
HO 26061	p/3 rt	24.4	16.7	own 2025	Sonndorf
HO 26061	p/4 lt	24.9	18.9	own 2025	Sonndorf
HO 26061	p/4 rt	25.5	19.1	own 2025	Sonndorf
HO 26061	m/1 rt	30.8	21.6	own 2025	Sonndorf
HO 26061	m/1 lt	33.5	21.3	own 2025	Sonndorf
HO 26061	m/2 lt	36.9	24.1	own 2025	Sonndorf
HO 26061	m/2 rt	36.2	24.4	own 2025	Sonndorf
HO 26061	m/3 lt	49.0	23.8	own 2025	Sonndorf
HO 26061	m/3 rt	51.4	24.5	own 2025	Sonndorf
KM 3703 (G 584) (NHMB AE 15 cast)	m/2 lt	37.0	24.5	own 2021 from cast; Daxner-Hoeck 1971 as 37 × 24	Reinprechtspölla
KM 3703 (G 584) (NHMB AE 15 cast)	m/3 lt	45.3	26	own 2021 from cast; Daxner-Hoeck 1971 as 44 × 25	Reinprechtspölla
KM F/3710 d	M2/ lt	35.0	40.0	Daxner-Hoeck 1971	Reinprechtspölla

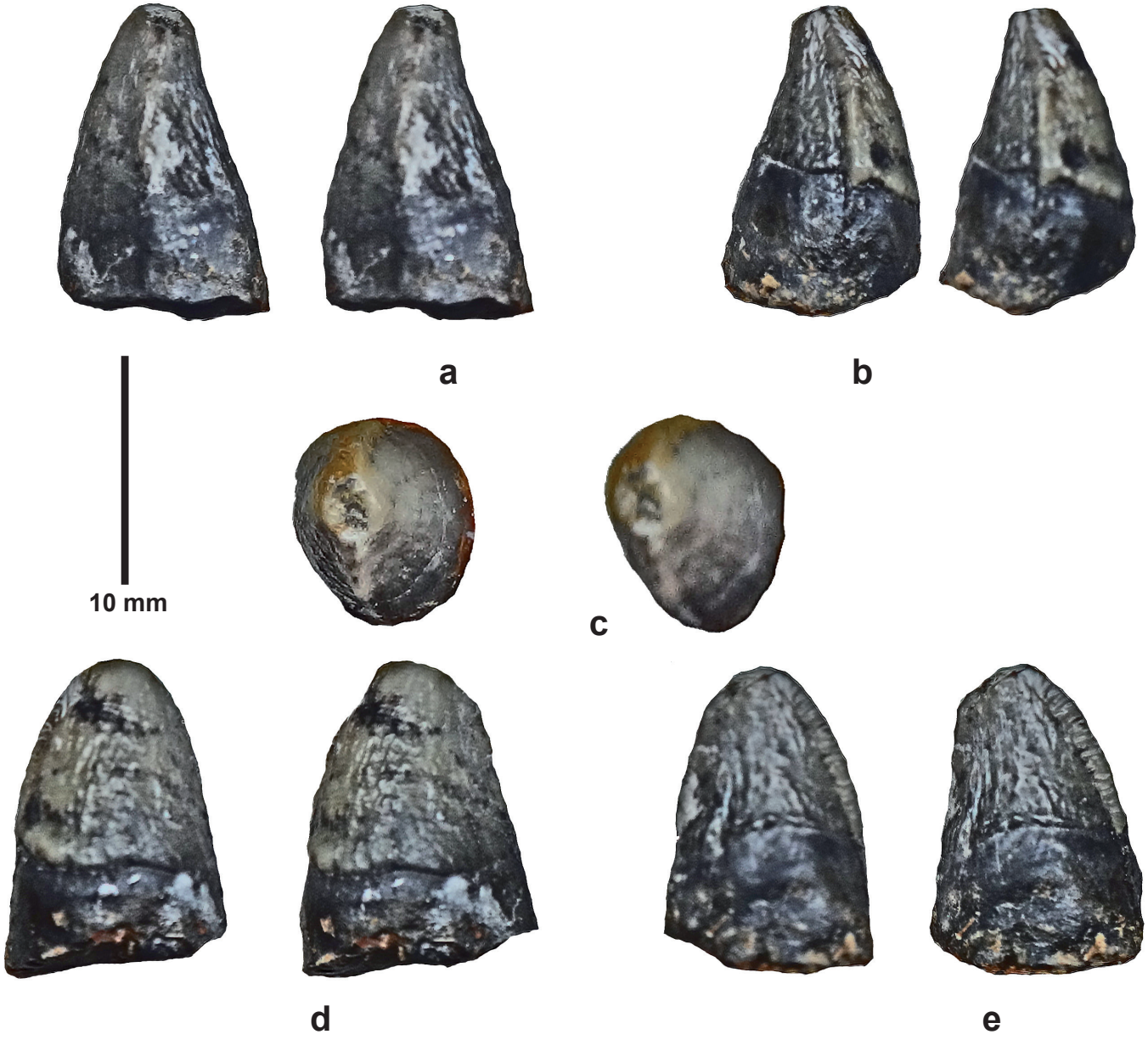


Text-fig. 11. Stereo images of OÖLKG 2025/43/1, left premaxilla with the I1/ in situ, of *Brachyodus pontigneensis* from Maigen, Austria. a: medial view, b: lateral view, c: anterior view, d: posterior view, e: inferior view.

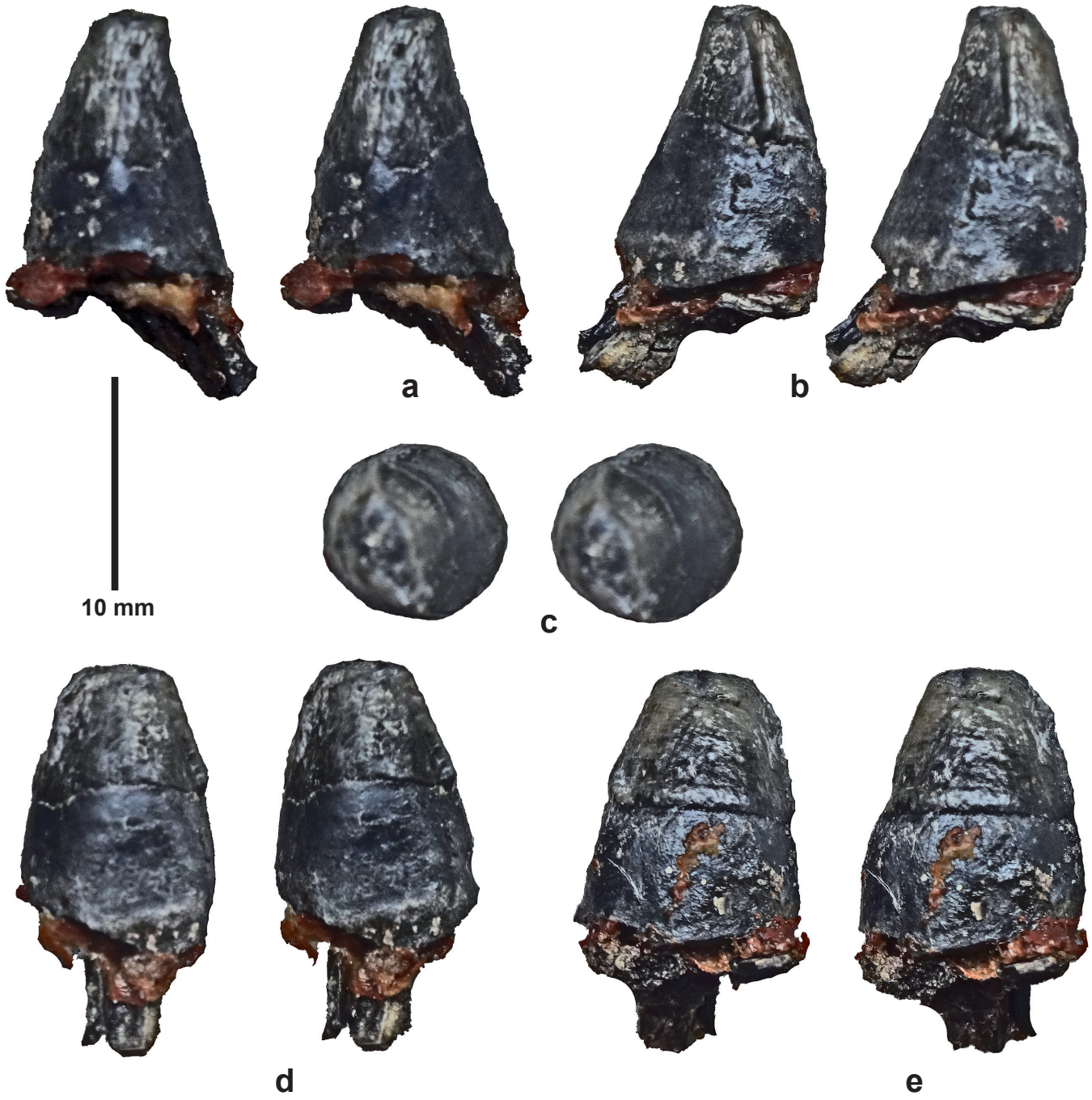


Text-fig. 12. Stereo images of OÖLKG 2025/43/2, right premaxilla with the I1/ in situ, of *Brachyodus pontigneensis* from Maigen, Austria. a: lateral view, b: medial vew, c: anterior view, d: posterior view, e: inferior view.

Text-fig. 13. Stereo inferior views of OÖLKG 2025/43/1 and OÖLKG 2025/43/2 the left and right premaxillae with upper central incisors and partial alveoli of I2/s of *Brachyodus pontigneensis* from Maigen, Austria. The two fragments are arranged approximately in anatomical position relative to each other.



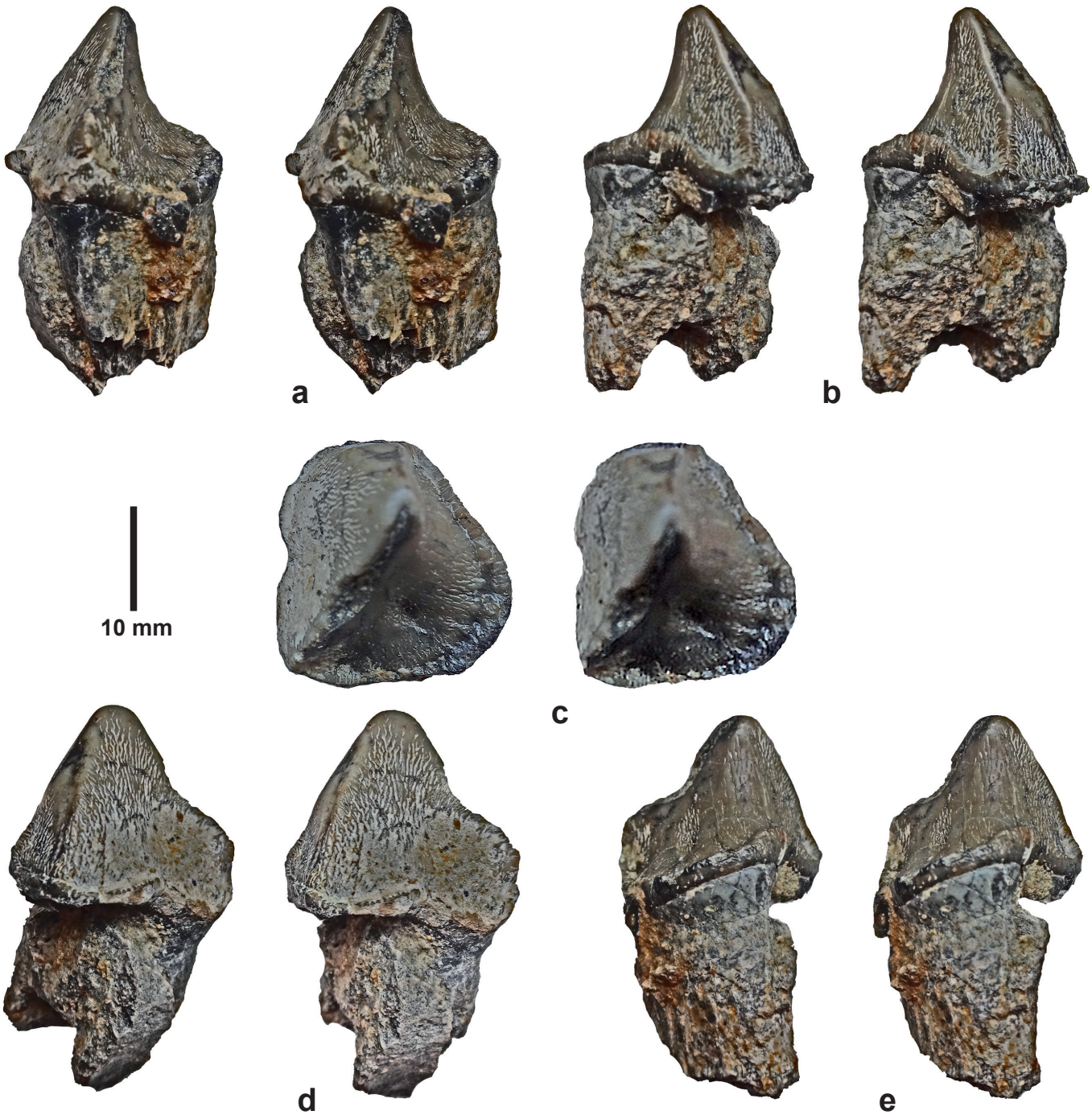
Text-fig. 14. Stereo images of OÖLKG 2025/43/3, right I3/ of *Brachyodus pontigneensis* from Maigen. a: mesial view, b: distal view, c: occlusal view, d: labial view, e: lingual view.



Text-fig. 15. Stereo images of OÖLKG 2025/43/4, left I3/ of *Brachyodus pontigneensis* from Maigen. a: mesial view, b: distal view, c: occlusal view, d: lingual view, e: labial view.

more anteriorly positioned than the paracone. The paracone has a buccal rib, and the shallow depressions either side of it are infilled with cementum. The preparacrista and postparacrista are sharp, and terminate cervically in small styles, the mesial one curving lingually to join the mesial cingulum. The protocone has a precrista and a postcrista, the latter descending cervically towards the small metaconule which appears as a small swelling between the base of the protocone and the distal cingulum. There is a prominent bead of enamel between the metaconule and the distal cingulum. There is a broad cingulum on the mesial, lingual and distal edges of the crown. The enamel is wrinkled.

The right M2/ from Maigen is preserved in a small fragment of maxilla which shows a well-developed buccinator ridge (Text-fig. 18). The molar has five main cusps arranged into two transverse lophs. The mesial loph consists of the paracone and a prominent paraconule close to the protocone. The posterior loph is comprised of the metacone and metaconule, bordered distally by a cingulum. All five cusps possess pre- and post-cristae which curve towards the buccal side of the crown as they descend from the apex towards cervix. The paracone and metacone have weakly expressed buccal ribs, and the shallow depressions either side of the ribs are partly infilled with cementum.



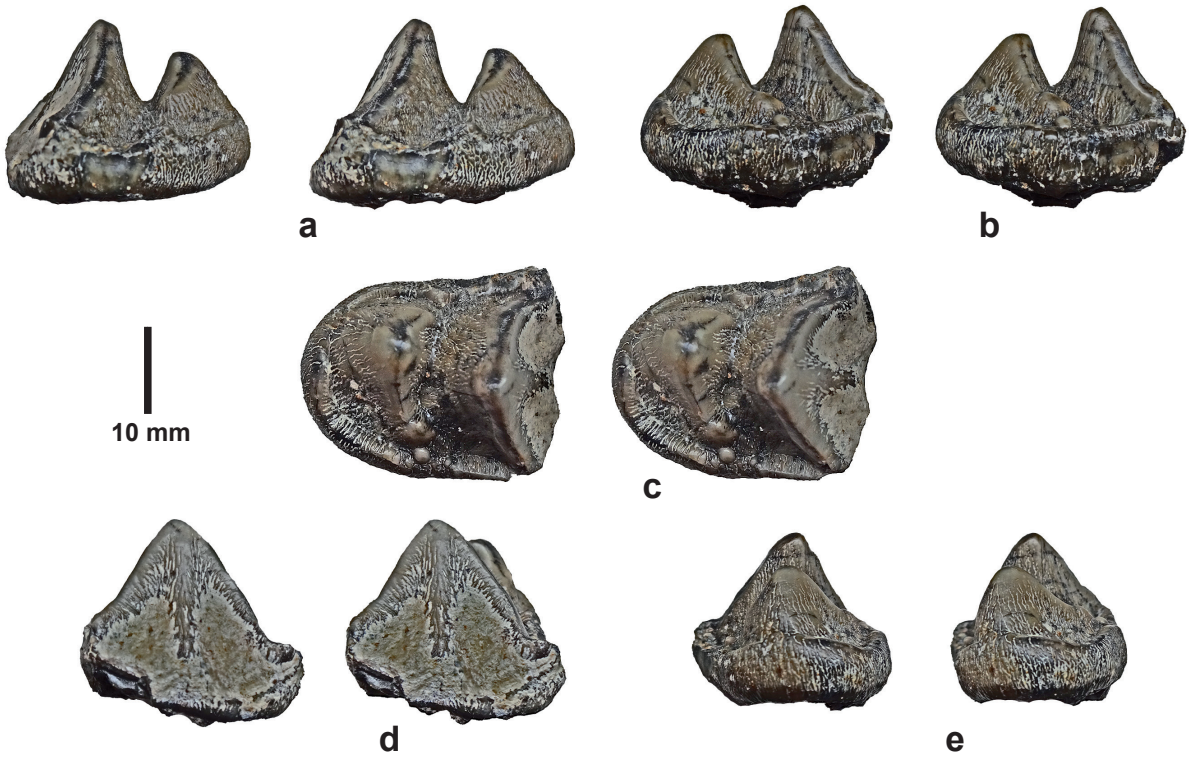
Text-fig. 16. Stereo images of OÖLKG 2025/43/5, right P2/ of *Brachyodus pontigneensis* from Maigen, Austria. a: distal view, b: mesial view, c: occlusal view, d: buccal view, e: lingual view.

The parastyle is prominent and curves anteriorly and then lingually where its crest approaches the end of the preparaconule cristule and where it blends into the mesial cingulum. The mesostyle has broken off, but what remains indicates that the postparacrista and the premetacrista probably met at a centrally positioned junction that closed off the transverse valley on its buccal end. The transverse valley is not obstructed by the crests descending towards it from the protocone, paraconule and metaconule, but it is blocked off at its buccal end by the postparacrista and the premetacrista which form the mesostyle. The metastyle is weak but is confluent with the distal cingulum. There is a well-formed lingual cingulum that blends into the mesial and distal cingula. The enamel is wrinkled.

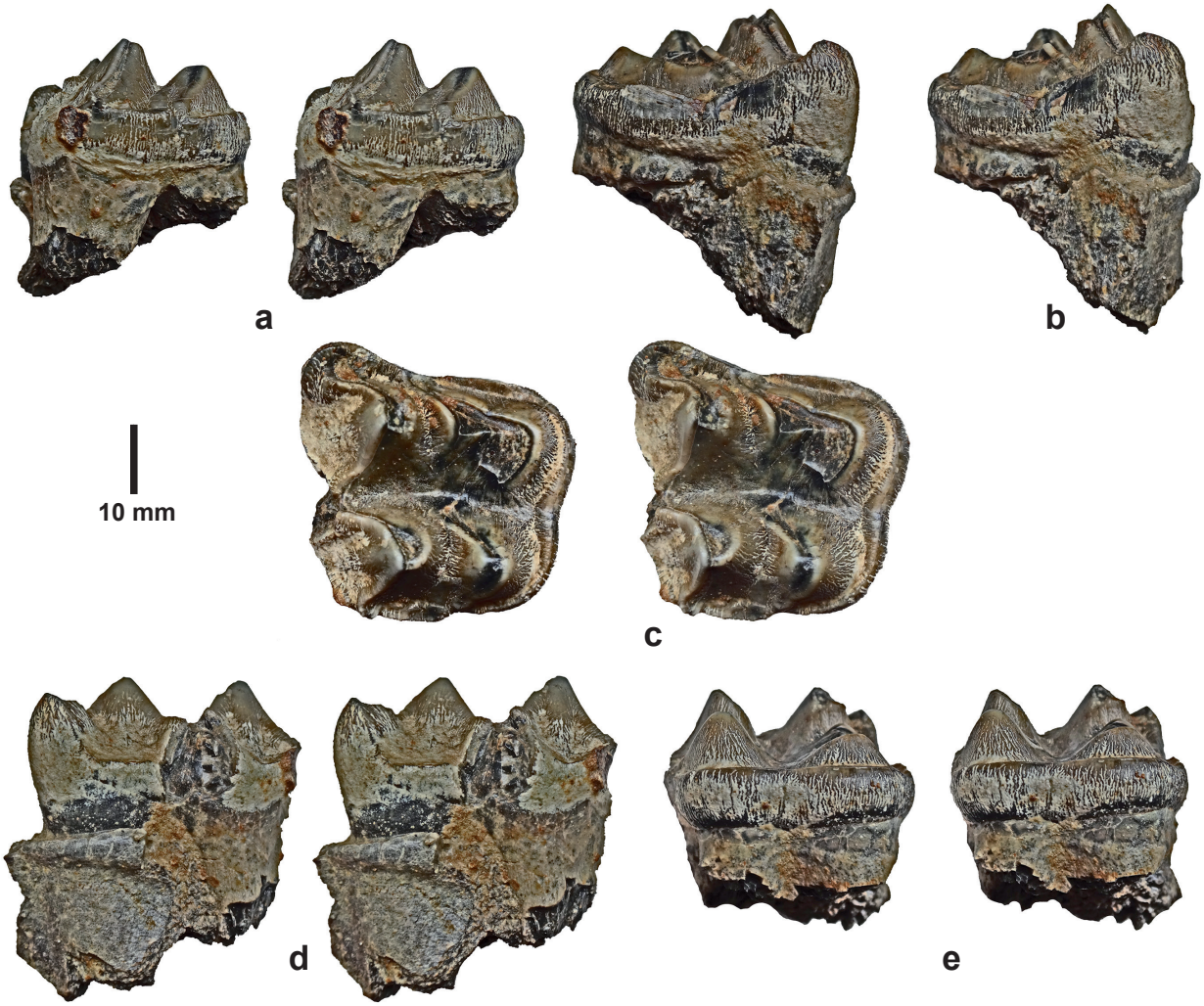
The left mandibular ramus from Maigen is in poor condition, and has been extensively reconstructed (Text-figs 19–21). The m/1 is missing most of the posterior lophid, whereas the other teeth are well preserved but lightly worn.

There is a substantial retromolar space between the hypoconulid of the m/3 and the root of the ascending ramus of the mandible. The buccinator ridge is well defined.

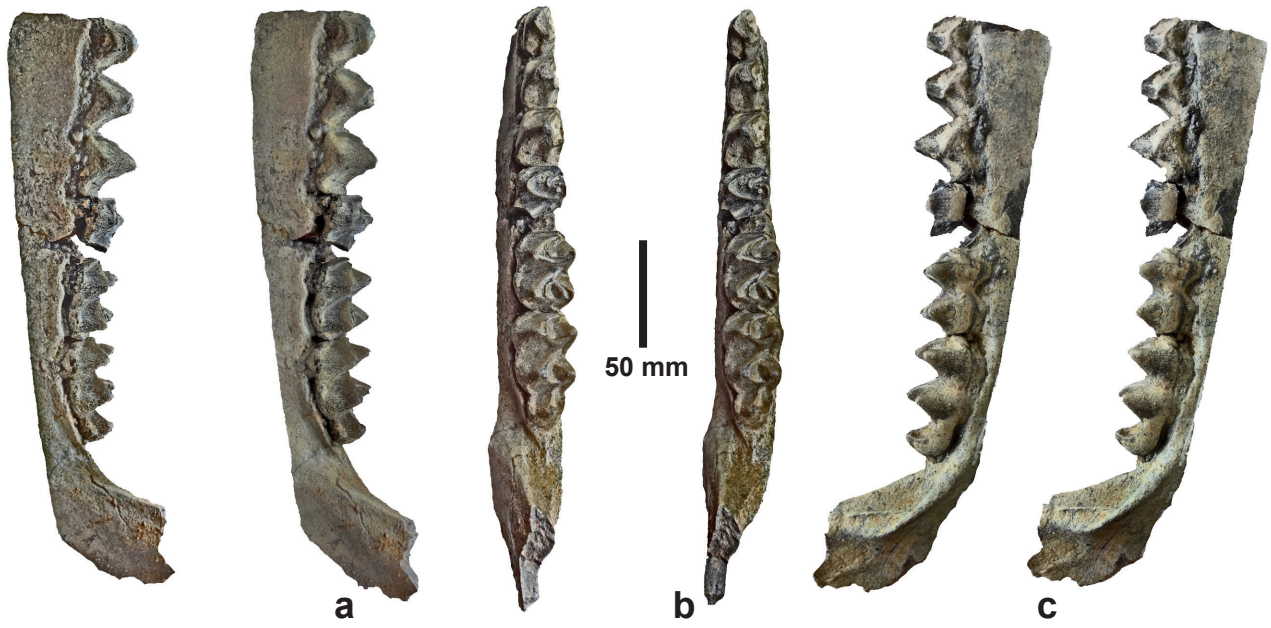
The p/2, p/3 and p/4 are constructed along similar lines, but they increase in dimensions and robusticity from p/2 to p/4. There is a single, tall main cusp (protoconid) from the



Text-fig. 17. Stereo images of OÖLKG 2025/43/6, left P4/ of *Brachyodus pontigneensis* from Maigen, Austria. a: mesial view, b: distal view, c: occlusal view, d: buccal view, e: lingual view.



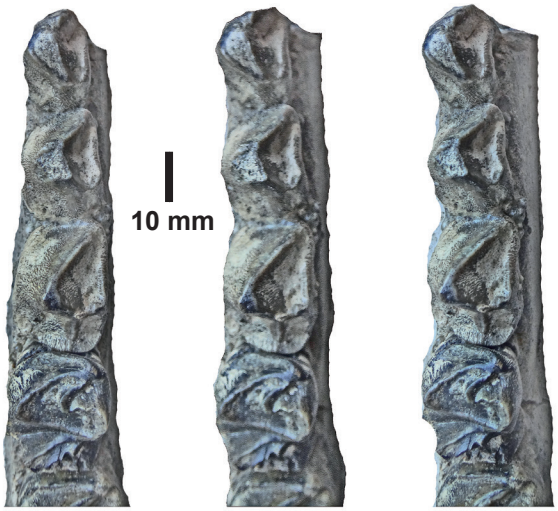
Text-fig. 18. Stereo images of OÖLKG 2025/43/7, right M2/ of *Brachyodus pontigneensis* from Maigen, Austria. a: distal view, b: mesial view, c: occlusal view, d: buccal view, e: lingual view.



Text-fig. 19. Stereo images of OÖLKG 2025/44/8, left mandible with p/2–m/3 of *Brachyodus pontigneensis* from Maigen, Austria. a: lateral view, b: occlusal view, c: medial view.

apex of which robust cristids descend mesio-lingually and disto-lingually where they blend into the lingual cingulum. The lingual surface of the main cusp is shallowly concave, and its buccal surface is strongly convex, thereby giving the tooth a selenodont appearance in occlusal view. Behind the main cusp there is a low shelf-like platform which has a low swelling in its central part (incipient hypoconid). This swelling is joined by a low-relief cristid that descends along the distal side of the main cusp. On the lingual side of the crown, the lingual cingulum is continuous but it rises to meet the postprotocristid of the main cusp. This part of the cingulum forms an incipient metaconid, which becomes more distinct from the p/2 to the p/4.

The enamel is wrinkled, and there is a discontinuous cover of cementum on the lingual and buccal surfaces of the teeth.



Text-fig. 20. Stereo occlusal views of the premolars and m/1 in OÖLKG 2025/44/8, left mandible of *Brachyodus pontigneensis* from Maigen, Austria.

The m/1 and m/2 have four main cusps and a minuscule hypoconulid posteriorly. The m/3 is like the m/2, but its hypoconulid is developed into a large cusp with two cristids that descend anteriorly from its apex, one towards the midline of the tooth, the other towards the base of the entoconid. The following description is of the m/3, but the same description applies to the four main cusps of the m/1 and m/2.

The buccal cingulum is continuous with the mesial cingulum, but it weakens on the buccal surfaces of the protoconid and hypoconid. The preprotocristid is well developed but terminates well before reaching the lingual margin of the crown, and there is a deep groove between it and the metaconid which leaves the mesial fovea open lingually. The metaconid has no precristid, but its postcristid is robust and extends towards the postprotocristid which it joins at about mid-height of the crown, leaving a v-shaped notch between the two cusps. The lingual postmetacristid is weakly developed and is oriented directly distally, being separated from the postmetacristid by a narrow groove.

Text-fig. 21. Stereo occlusal views of the m/3 in OÖLKG 2025/44/8, left mandible of *Brachyodus pontigneensis* from Maigen, Austria.

The base of this groove is where the prehypocristid terminates, forming a low obstruction in the lingual end of the median transverse valley. The preentocristid joins the prehypocristid about half way between the apex of the latter cusp and the median transverse valley. The postentocristid is almost obsolete but at its base it joins the distal end of the posthypocristid, thereby closing off the rear of the fovea between the hypoconid and entoconid. The hypoconulid is almost in line with the protoconid and hypoconid and its two cristids lead anteriorly, the precristid ending beneath the v-shaped notch between the hypoconid and entoconid, the postcristid leading towards the base of the entoconid.

Discussion. The cranial and mandibular remains of anthracotheres from Maigen are of interest because they are reported to belong to a single individual. However, the lower second incisor which has been mounted into a block of plaster-of-paris along with the left mandible, is from the right side of the jaw and judging from its dimensions, it likely belongs to a larger species than the mandible. The mandibular cheek dentition is typical of the species *Brachyodus pontigneensis*, whereas the lower second incisor is compatible with a male individual of the larger species *Brachyodus onoideus*.

Genus *Masrimeryx* Pickford et Gawad, 2024

Type species. *Afromeryx palustris* Miller et al., 2014.

Diagnosis. Brevirostral anthracothere of large dimensions. Mandibular symphysis with approximately equal thickness postero-basally as close to the alveolar margin anteriorly. Presence of large mental foramen beneath the p/4 and several large foramina in the area of the symphysis. Short diastema between the p/1 and the incisors (ca. 19 mm). Mandible relatively shallow anteriorly deepening slightly beneath the molars. Snout narrows markedly in front of the P4/. P1/ present in maxilla.

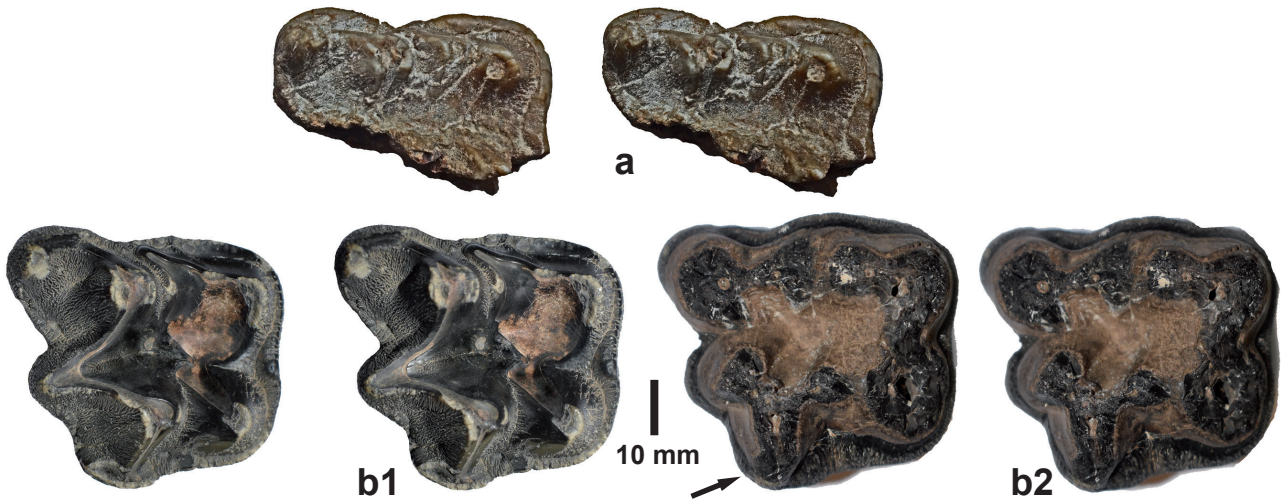
Masrimeryx palustris (Miller et al., 2014)

Holotype. CGM 83751, right mandible fragment with symphysis, alveoli of i/1–p/1, crowns of p/2–p/4.

Diagnosis. "Differs from *A*[*fromeryx*] *zelteni* and *A*[*fromeryx*] *grex* in being much larger (m2 area >70% larger than *A*[*fromeryx*] *zelteni*, m2 area >25% larger than *A*[*fromeryx*] *grex*); further differs from *A*[*fromeryx*] *grex* in having premolars with weaker pustulate crest development, premolars lacking distinct and elevated premolar cingulids, taller and more sharply tapering p2–p3, p2 with better developed anterior crest. All premolar crowns have very finely wrinkled enamel." (from Miller et al. 2014: 974).

Type locality and age. Moghara, Egypt, Early Miocene.

Description. KM F/3716 (G 17) is the mesial loph of a large upper molar, probably an M3/ (Text-fig. 22a). It is lightly worn, and shows well the three main cusps (paracone, paraconule and protocone) together with a prominent parastyle which sends a precrista mesially and then lingually which attains the end of the preparaconule cristule. In the median transverse valley there is a low swelling in the enamel close to the distal end of the postparaconule cristule, which fills in the distal part of the groove between the paracone and the paraconule. The parastyle almost forms a separate cusp, its apex standing slightly higher than the buccal end of the preparacrista to which it is joined. The lingual cingulum is well developed and is continuous with the mesial cingulum. The buccal cingulum is present between the parastyle and mesostyle but it is less well developed than the lingual cingulum. Small parts of the metacone and metaconule are preserved, but they do not reveal much about their morphology. However, they are well separated from the mesial cusps, such that the median transverse valley is not blocked by their precristae, nor is it obstructed by the postcristae of the protocone and



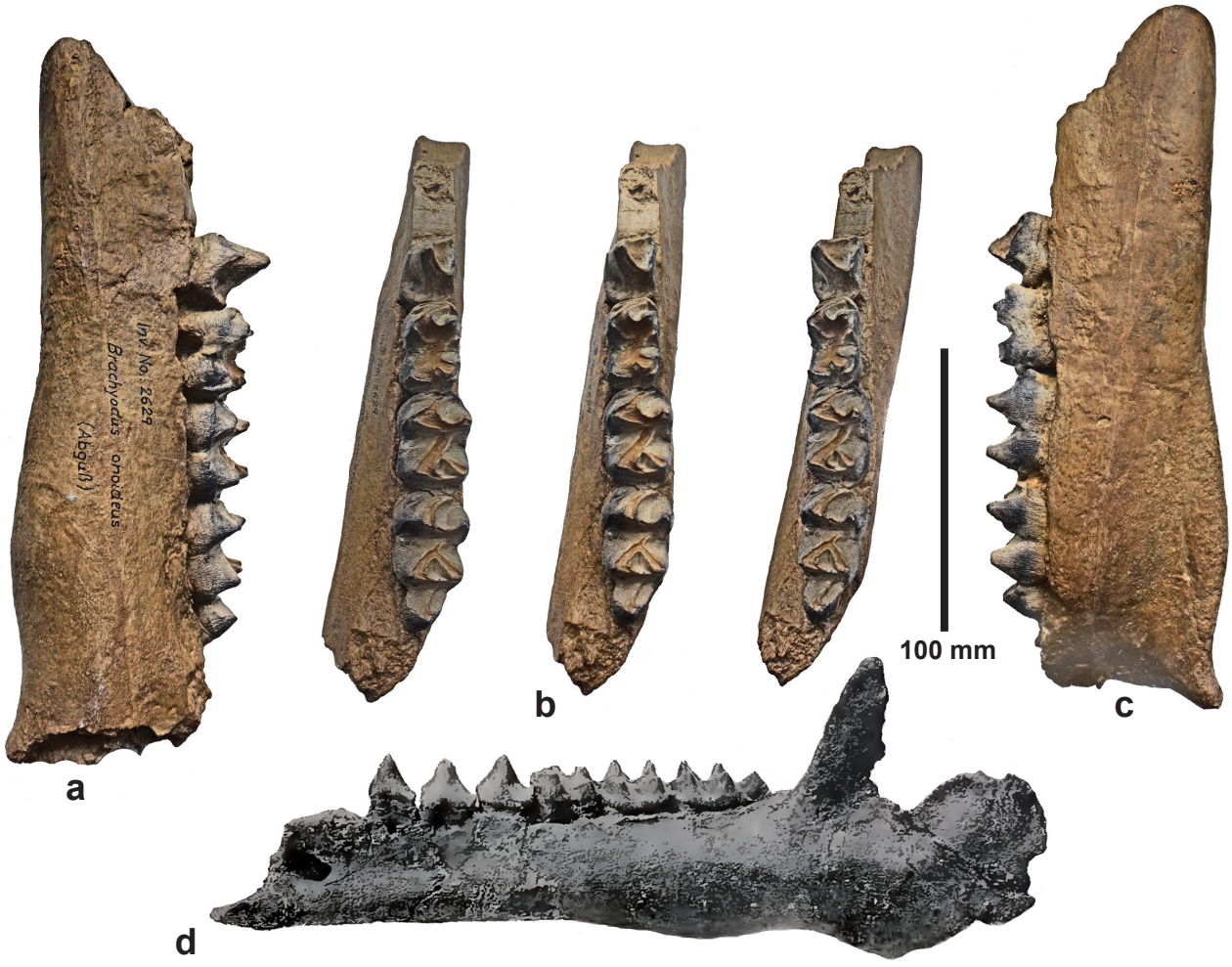
Text-fig. 22. a: Stereo occlusal view of KM F/3716 (G 17), mesial loph of right upper molar (probably M3/) of *Masrimeryx palustris* from Eggenburg/Wolkenspiegel. b: occlusal view of LPB. V 0352, left M3/ of *Masrimeryx palustris* from Bozovici, Romania (photo by Stefan Vasile, Cluj-Napoca), b1 – occlusal view (image reversed), b2 – radicular view (image not reversed); arrow shows the distal root extension that supports the metastyle.

paraconule. The postparacrista reaches towards a remnant of the mesostyle, closing off the buccal end of the transverse valley. The rib on the paracone is of relatively low relief. The enamel is wrinkled.

Discussion. The bucco-lingual breadth of the mesial loph of the large upper molar from Eggenburg/Wolkenspiegel is 49 mm, which is broader than any of the upper molars of anthracotheres known from the French Faluns, but which agrees in dimensions with teeth of *Brachyodus depereti* from Moghara, Egypt (Pickford and Gawad 2024) and other large anthracotheres from the site such as *Masrimeryx palustris*, *Jaggermeryx africanus* Pickford et Gawad, 2024 and *Aegyptomeryx grandis* Pickford et Gawad, 2024. It is slightly broader than a specimen from Bozovici, Romania (Text-fig. 22b), that is 48.4 mm broad mesially (Grigorescu 1985, Codrea et al. 2023). The latter tooth was attributed to *Brachyodus onoideus* by Grigorescu (1985) but there are several morphological differences from upper molars of this species, such as the enlarged parastyle that is almost detached from the paracone, the more lingually positioned paracone and the more sloping buccal surface of the paracone. A point of particular resemblance to the Eggenburg/Wolkenspiegel specimen is the presence of a small cusplet in the median transverse valley at the distal end of the groove between the paracone and the paraconule.

In the Eggenburg/Wolkensiegel specimen, the orientation and angle of the buccal side of the paracone relative to the cervical plane is like the situation in *Masrimeryx*, but it differs from the layout observed in *Jaggermeryx* Pickford et Gawad, 2024, *Brachyodus* and *Aegyptomeryx* Pickford et Gawad, 2024. For these reasons, we consider that the Eggenburg/Wolkenspiegel tooth probably belongs to a species of *Masrimeryx*, and in terms of dimensions it is compatible with the type species, *Masrimeryx palustris*.

The identification of the Eggenburg/Wolkenspiegel tooth as *Masrimeryx palustris* suggests that during the Eggenburgian Stage, there could have been a biogeographic link to the Moghara Basin, northern Egypt. The succession of strata at Moghara spans much the same period as the Eggenburgian (Pickford and Gawad 2024). The Bozovici, Romania, specimen which is morphologically similar, underlines such as biogeographic scenario.



Text-fig. 23. Cast of IPUW 2629, left mandible with p/4–m/3 of *Br. pontigneensis* from Eggenburg, housed in the Krahuletz Museum. a: buccal view, b: stereo occlusal views, c: lingual view, d: lateral view of the original fossil prior to damage that removed the ascending ramus and the anterior and posterior parts of the jaw as well as the p/2 and p/3 (image modified from Depéret 1895).

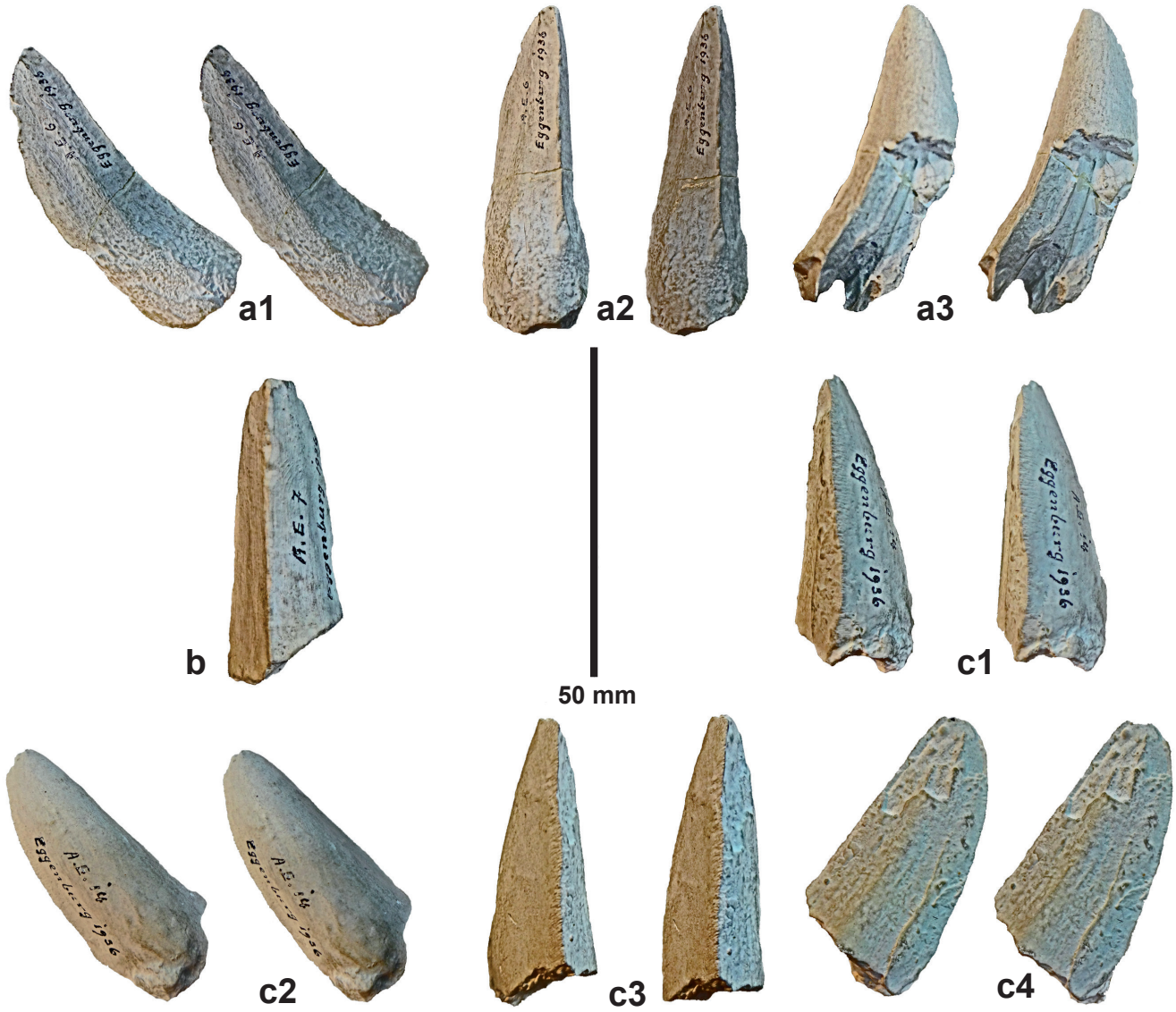
Illustrated catalogue

Some of the published anthracothere fossils from Austria were not illustrated, and some that were, have been damaged since being figured, including the relatively complete mandible described by Depéret (1895) (Text-fig. 23). Because of difficulties experienced by diverse authors in determining the correct meristic position of the tusk-like teeth of these mammals, we herein illustrate all the fossil dento-gnathic specimens from Austria that were accessible (Text-figs 24–32). Casts of some of the fossils are also illustrated, because morphological features are often more clearly observed on white casts than on the dark original fossils. Radicular views are included where they yield information about meristic position, the case with the M3/s which have a distally projecting radicular extension fused to the metacone root, a structure that supports the metastyle. M1/s and M2/s do not have a corresponding structure.

Metric analysis of Early Miocene large anthracotheres

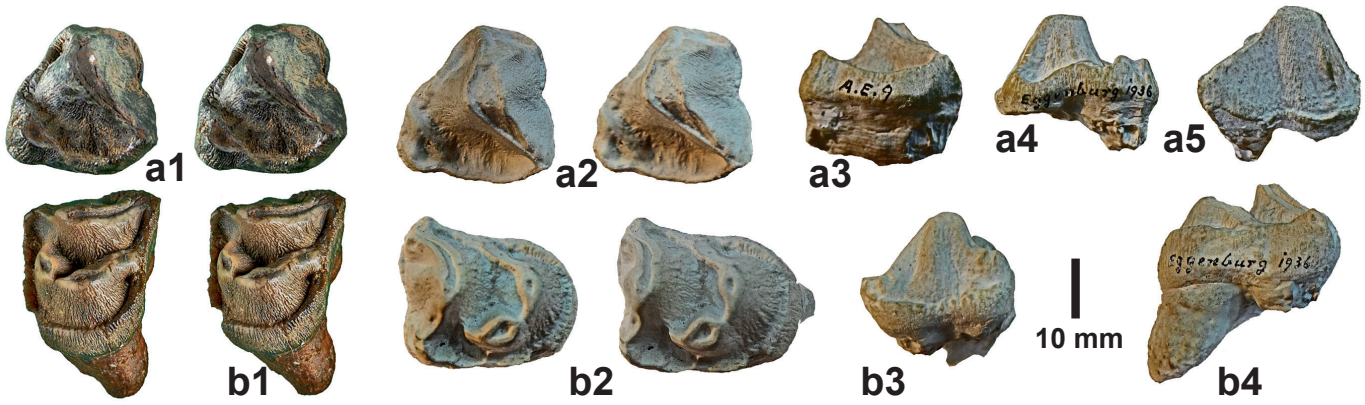
The metric data indicates that most of the anthracothere fossils from the Eggenburgian region belong to *Brachyodus pontigneensis* and *Brachyodus onoideus*. There is, however, one tooth (the mesial loph of an M3/ from Eggenburg/ Wolkenspiegel) that is much larger than specimens attributed to these two species. Its bucco-lingual breadth is 49 mm and, as such, it is the broadest known upper molar of an anthracothere from the Early Miocene of Europe. It is herein attributed to *Masrimeryx palustris*, a species defined at Moghara, Egypt (Pickford and Gawad 2024) but that also occurs in Romania (Grigorescu 1985).

The following bivariate analyses (Text-figs 33–41) support the attribution of most of the Eggenburg anthracothere teeth to *Brachyodus pontigneensis* and *Brachyodus onoideus*, only one specimen from Eggenburg/Wolkenspiegel plotting

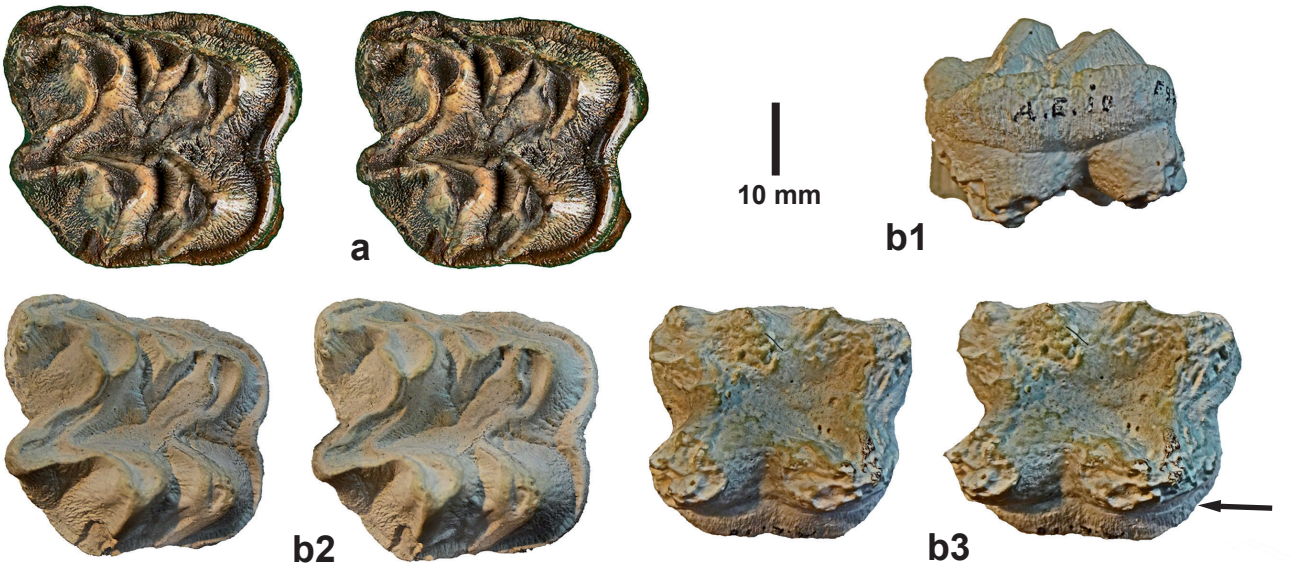


Text-fig. 24. Casts of lower second incisors of *Brachyodus* from the Early Miocene of Austria housed in the Naturhistorisches Museum, Basel. a: NHMB AE 6, right i/2 of *Br. pontigneensis*, a1 – stereo lingual view, a2 – stereo distal view, a3 – stereo labial view. b: NHMB AE 7, left i/2 of *Br. pontigneensis* from Eggenburg, distal view. c: NHMB AE 14, left i/2 of *Br. onoideus* from Sigmundsherberg, c1– stereo mesial view, c2 – stereo labial view, c3 – stereo distal view, c4 – stereo lingual view.

Text-fig. 25. Stereo images of HO 2681, lower second incisors (partly reconstructed) of *Br. pontigneensis* from Sonndorf. a: right i/2, a1 – lingual view, a2 – distal view, a3 – mesial view, a4 – labial view. b: left i/2, b1 – labial view, b2 – distal view, b3 – mesial view, b4 – lingual view.

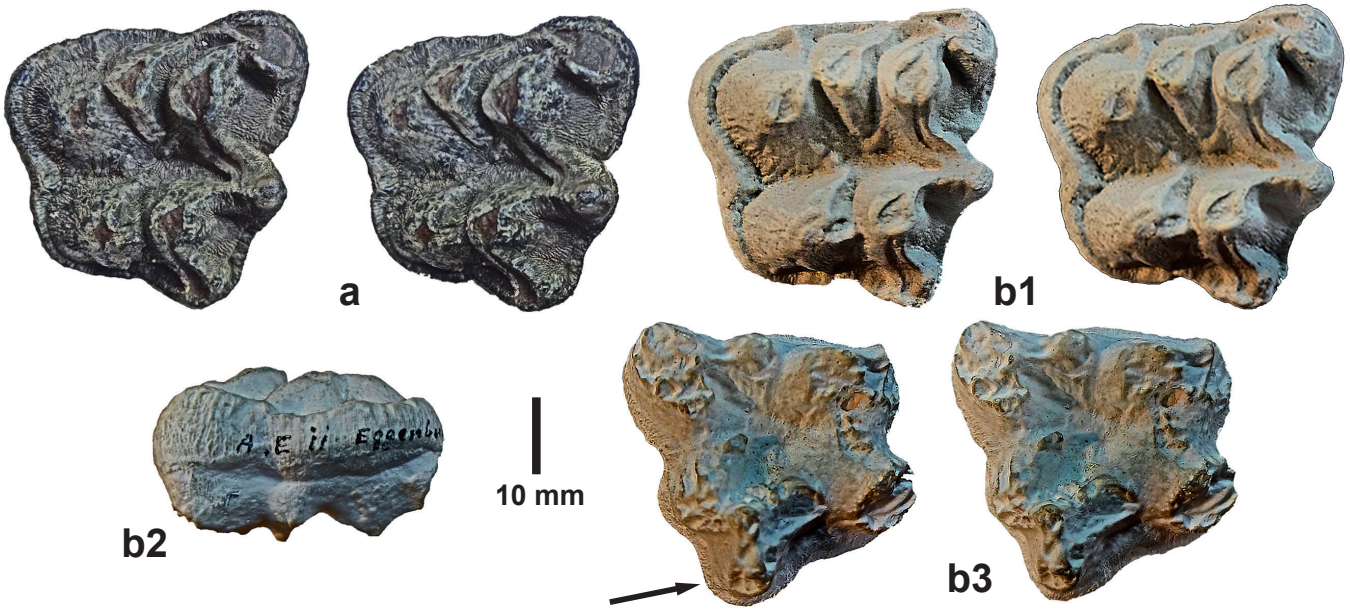


Text-fig. 26. Upper premolars of *Brachyodus* from Austria. a: left P3/ of *Br. onoideus* from Eggenburg, a1 – KM F/1361, stereo occlusal view, a2 – NHMB AE 9, stereo occlusal view of cast, a3 – distal view, a4 – mesial view, a5 – buccal view. b: KM F/1362, right P4/ of *Br. pontigneensis* from Gauderndorf, b1 – stereo occlusal view, b2 – NHMB AE 8, stereo occlusal view of cast, b3 – buccal view, b4 – mesial view.

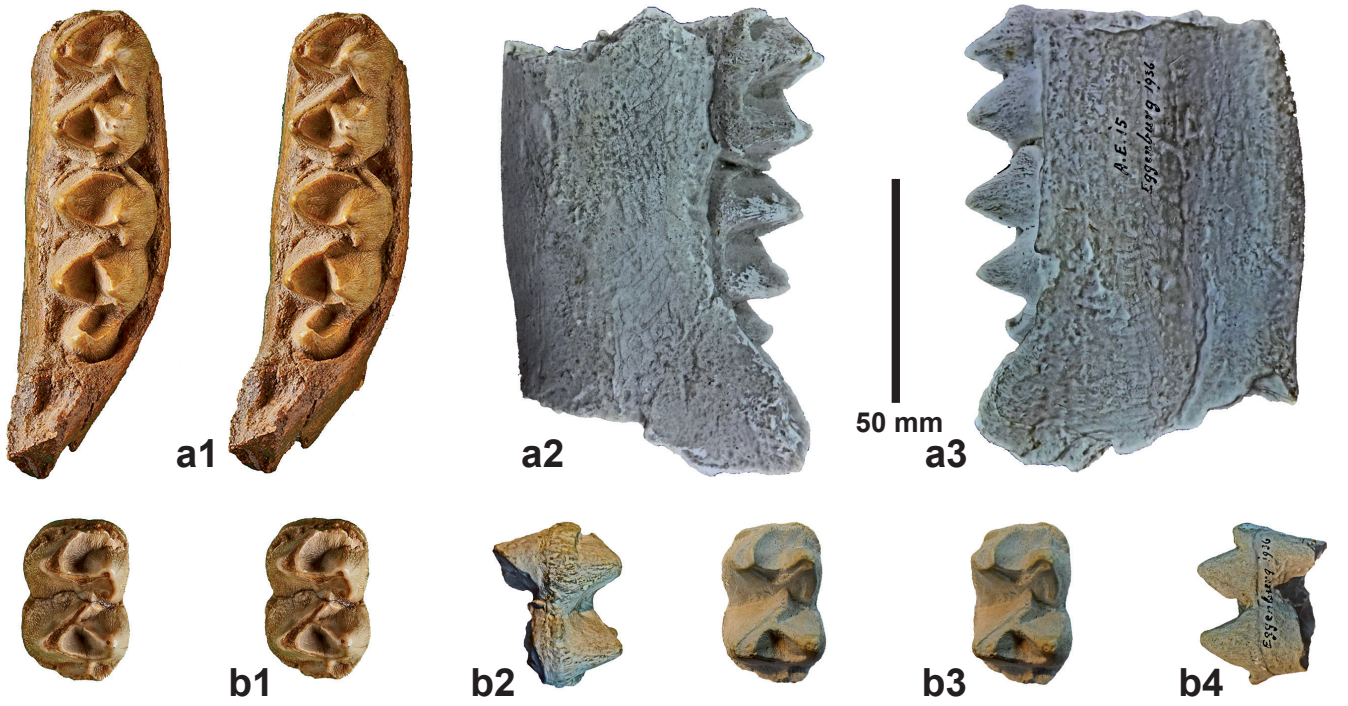


Text-fig. 27. Right M2/ of *Br. pontigneensis* from Eggenburg. a: KM F/1364, stereo occlusal view. b: NHMB AE 10 cast, b1 – distal view, b2 – stereo occlusal view, b3 – stereo radicular view (arrow shows the root that supports the metacone).

Text-fig. 28. Left M2/ of *Br. onoideus* from Roggendorf. a: KM 3710 c, stereo occlusal view. b: NHMB AE 16, cast curated at the Naturhistorisches Museum, Basel, b1 – stereo occlusal view, b2 – mesial view.

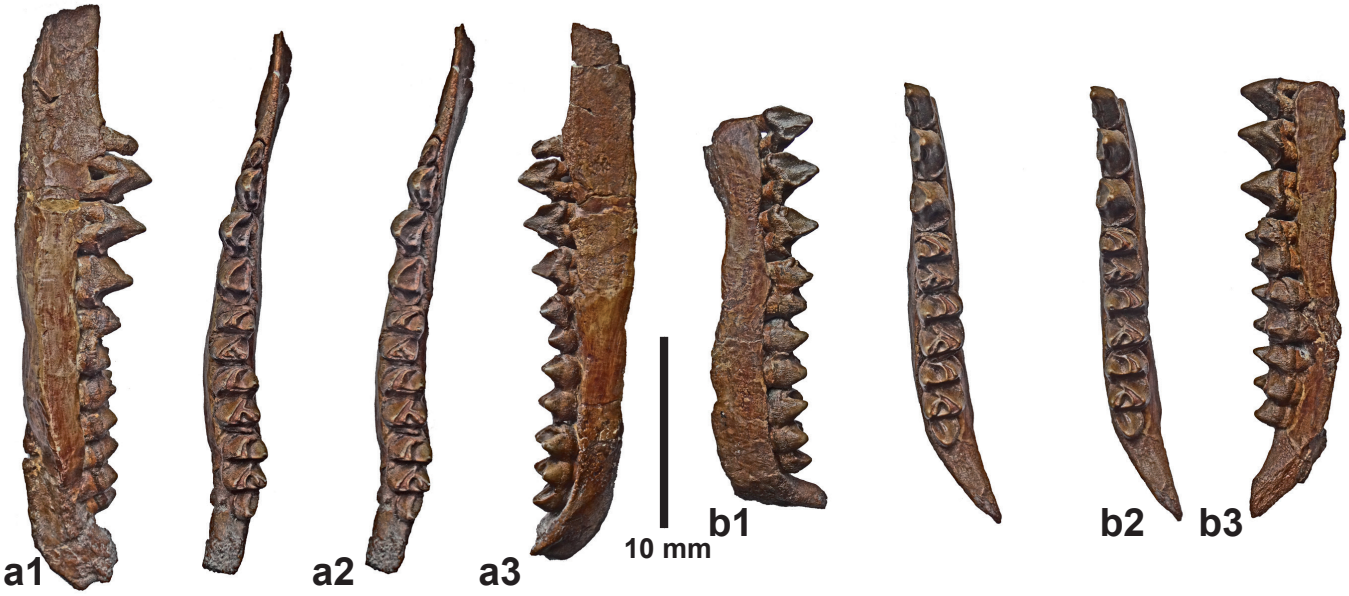


Text-fig. 29. Left M3/ of *Brachyodus onoideus* from Gauderndorf. a: KM 3710 a, stereo occlusal view. b: NHMB AE 11, cast curated at the Naturhistorisches Museum, Basel, b1 – stereo occlusal view, b2 – mesial view, b3 – stereo radicular view (arrow shows the distal root extension that supports the metastyle).



Text-fig. 30. a: KM F/3703 (G 584), left mandible of *Br. pontigneensis* from Reinprechtspölla, a1 – stereo occlusal view, a2 – NHMB AE 15, cast in lateral view, a3 – NHMB AE 15, cast in medial view. b: KM F/1365 (G I-13), isolated left m/2 of *Br. onoideus* from Reinprechtspölla, b1 – stereo occlusal view, b2 – NHMB AE 12, cast in buccal view, b3 – stereo occlusal view, b4 – lingual view.

Text-fig. 31. KM F/3710c (G I-6), distal half of a left m/2 of *Br. onoideus* from Reinprechtspölla. a: lingual view, b: stereo occlusal view, c: stereo distal view, d: buccal view.



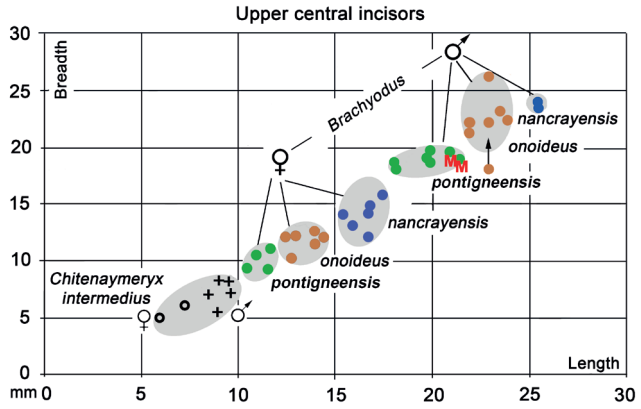
Text-fig. 32. HO 26061, left and right mandibles of *Br. pontigneensis* from Sonndorf curated at the Horn Museum. a: left mandible with p/1–m/3, a1 – buccal view, a2 – stereo occlusal view, a3 – lingual view. b: right mandible with p/2–m/3, b1 – lingual view, b2 – stereo occlusal view, b3 – buccal view.

outside the ranges of metric variation of these two species. None of the Austrian fossils plot within the range of metric variation of *Chitenaymeryx intermedius*.

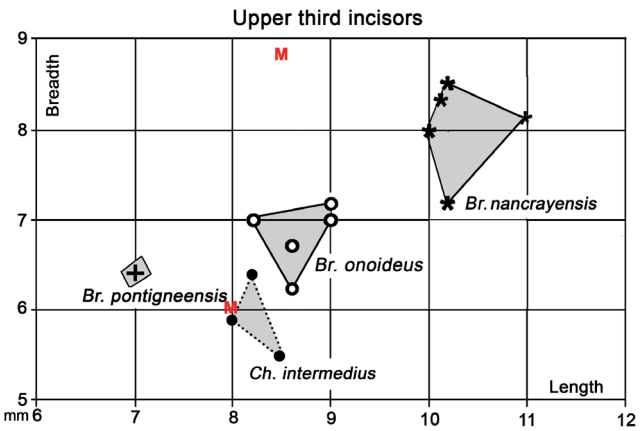
Discussion and conclusions

Previous researchers attributed the Early Miocene anthracotheres from Austria to the species *Brachyodus onoideus* (Depéret 1895, Melentis 1965, Daxner-Hoeck 1971). In France, where the type species was described (Gervais 1859) the material attributed to it has a great range of metric variation, to such an extent that Dineur and Ginsburg (1986) were unable to decide whether some of the specimens belonged to the larger of the two taxa recognised at the time of their study (*Brachyodus onoideus*), or to the smaller species, at the time known as *Brachyodus intermedius* Mayet, 1908. In their bivariate (length/breadth) plots of the m/3, several specimens were left unassigned in the space between the clouds representing *Brachyodus intermedius* and *Brachyodus onoideus* (see Pickford 2024).

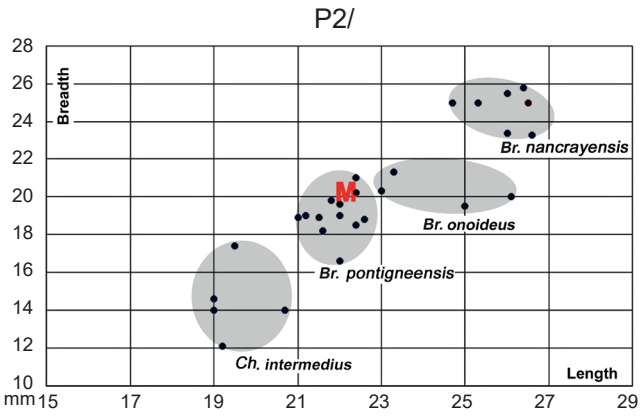
Pickford (2025) studied nearly two thousand anthracothere teeth from the French Faluns and the Sables de l'Orléanais, and concluded that there were three species of *Brachyodus* in the collections, as well as a distinct genus to which the small species *Brachyodus intermedius* belongs (Pickford 2024). The latter genus was named *Chitenaymeryx* Pickford, 2025, after the toponym of the locality of the type species *Chitenaymeryx intermedius*. The intermediate-sized French fossils that were left unassigned



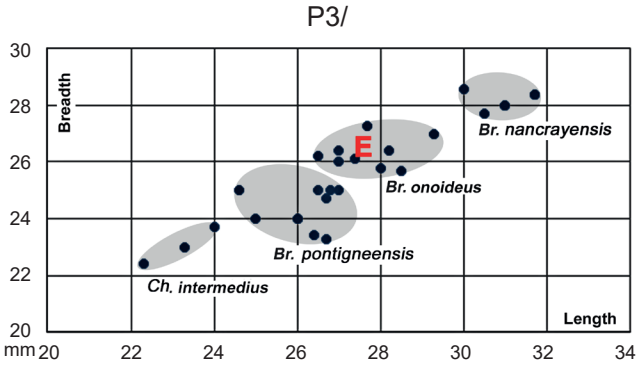
Text-fig. 33. Bivariate (length/breath) plots of upper central incisors of anthracotheres from the French Faluns and the Sables de l'Orléanais (grey ovals; data from Pickford 2025) and Austrian Early Miocene Paratethys deposits (red capital letters). M – Maigen.



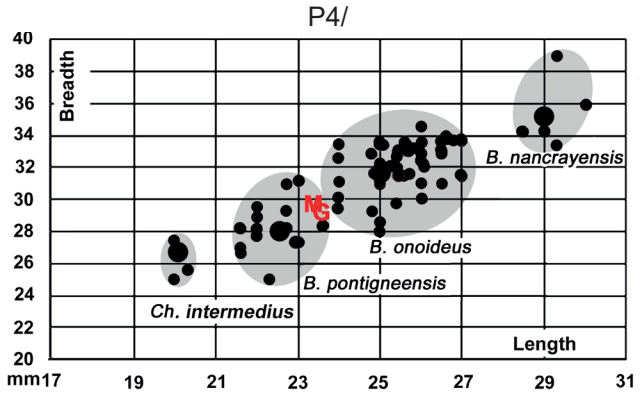
Text-fig. 34. Bivariate (length/breadth) plots of upper third incisors of anthracotheres from the French Faluns and Sables de l'Orléanais (grey polygons; data from Pickford 2024, 2025), and from Maigen, Austria (red M).



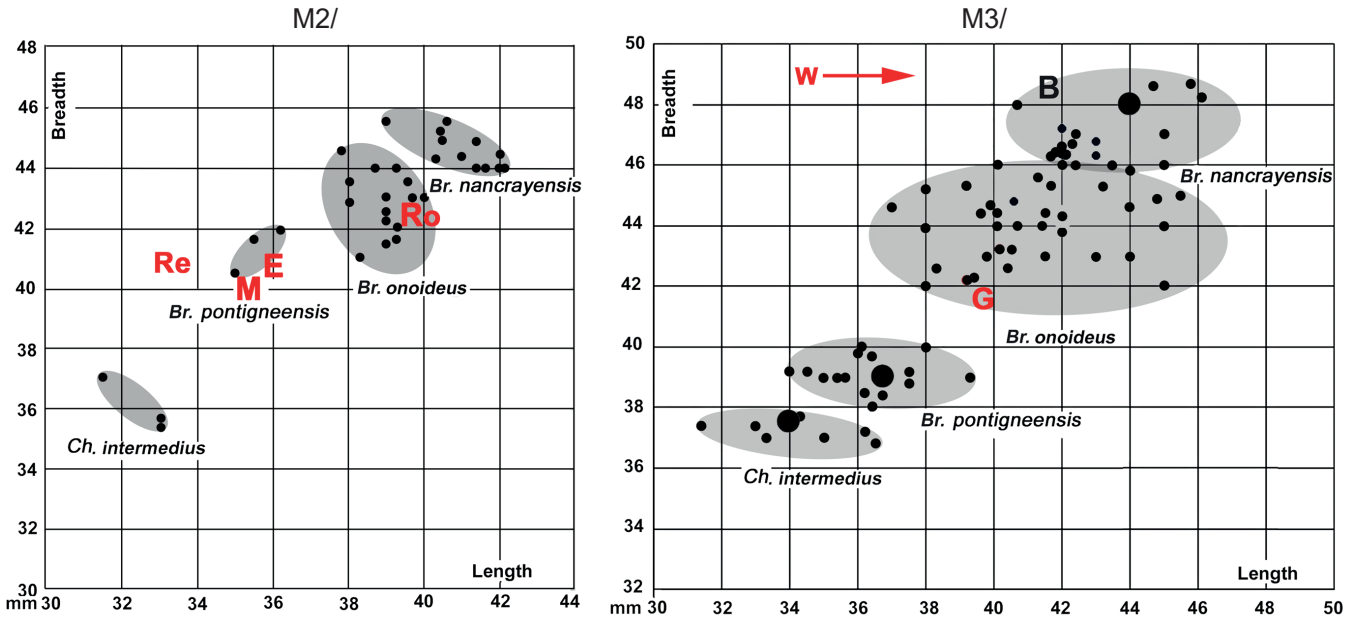
Text-fig. 35. Bivariate (length/breadth) plots of upper second premolars of anthracotheres from the French Faluns and Sables de l'Orléanais (grey ovals; data from Pickford 2024, 2025), with a specimen from Maigen, Austria (red M).



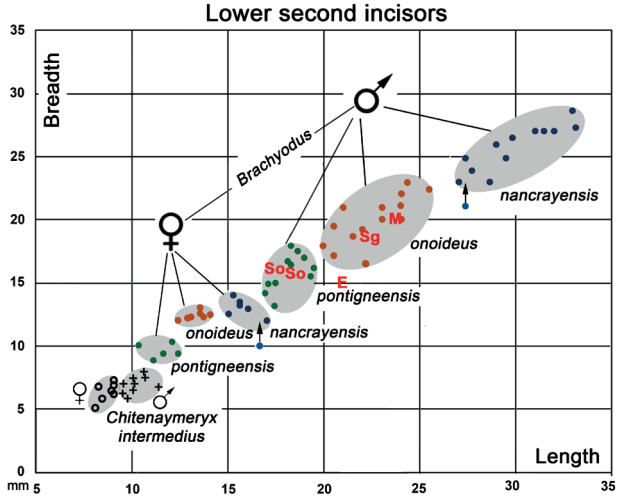
Text-fig. 36. Bivariate (length/breadth) plots of upper third premolars of anthracotheres from the French Faluns and Sables de l'Orléanais (grey ovals; data from Pickford 2024, 2025), with a specimen from Eggenburg, Austria (red E).



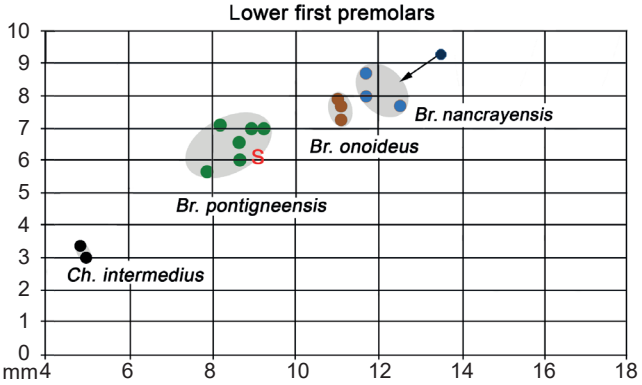
Text-fig. 37. Bivariate (length/breath) plots of upper fourth premolars of anthracotheres from the French Faluns and the Sables de l'Orléanais (grey ovals; data from Pickford 2024, 2025) and Austrian Early Miocene Paratethys deposits (red capital letters). G – Gauderndorf, M – Maigen.



Text-fig. 38. Bivariate (length/breath) plots of upper second and third molars of anthracotheres from the French Faluns and the Sables de l'Orléanais (grey ovals; data from Pickford 2024, 2025) and Austrian Early Miocene Paratethys deposits (red capital letters; E – Eggenburg, G – Gauderndorf, M – Maigen, Re – Reinprechtspölla, Ro – Roggendorf, W – Wolkenspiegel). The specimen with the red arrow is the broken tooth from Eggenburg/Wolkenspiegel. B – Bozovici, Romania.



Text-fig. 39. Bivariate (length/breath) plots of lower second incisors of anthracotheres from the French Faluns and the Sables de l'Orléanais (grey ovals; data from Pickford 2025) and Austrian Early Miocene Paratethys deposits (red capital letters). E – Eggenburg, M – Maigen, Sg – Sigmundsherberg, So – Sonndorf.

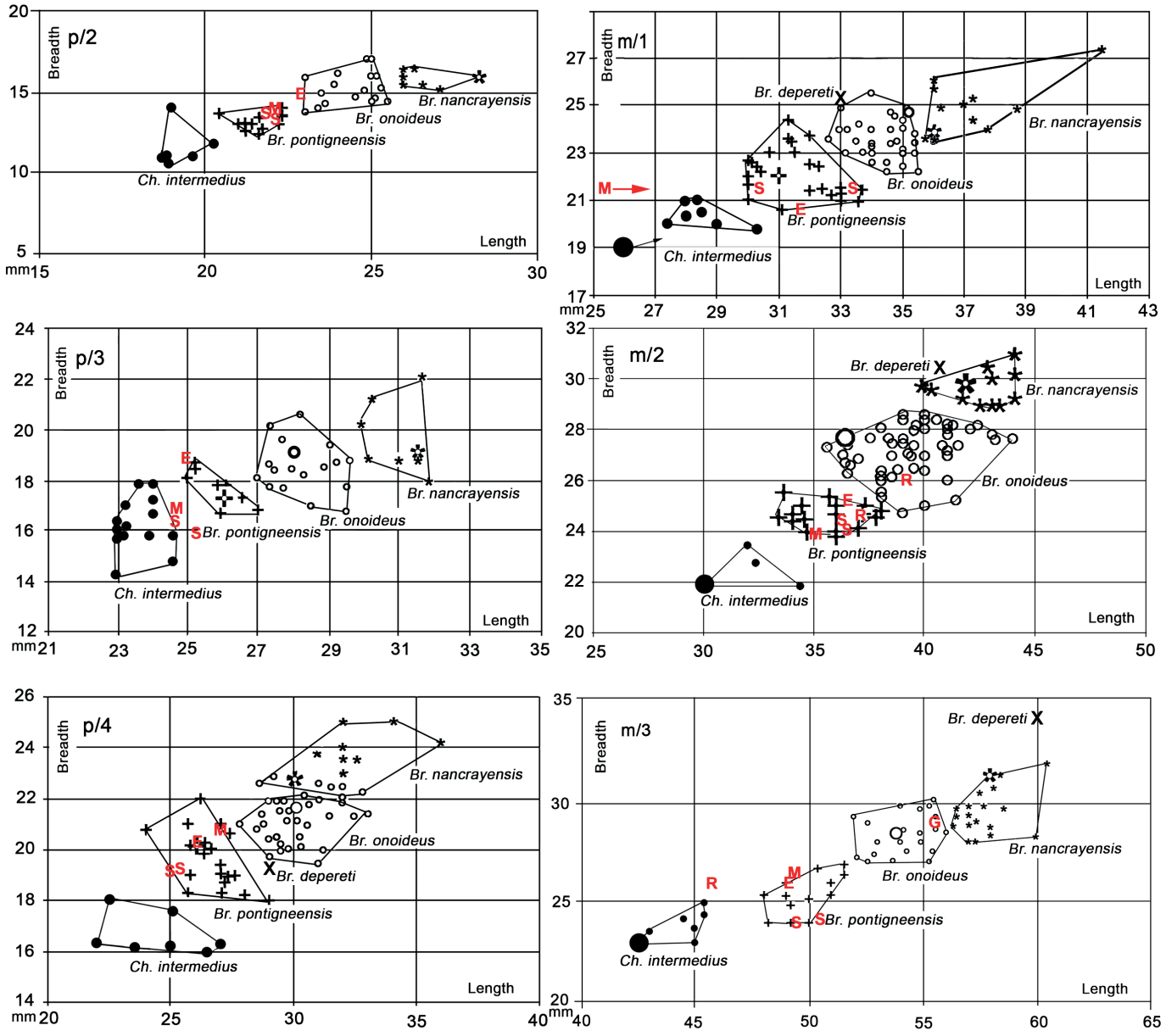


Text-fig. 40. Bivariate (length/breath) plots of lower first premolars of anthracotheres from the French Faluns and the Sables de l'Orléanais (grey ovals; data from Pickford 2025) with a specimen from Sonndorf, Austria (red S).

by Dineur and Ginsburg (1986) were attributed to a new species, *Brachyodus pontigneensis*, by Pickford (2025) and the largest fossils from the French deposits were attributed to a new species, *Brachyodus nancrayensis*, named after the type locality, Nancray, Loire Valley.

All three species of *Brachyodus* in Europe, and the Egyptian species *Brachyodus depereti* are sexually dimorphic, in that the upper central incisors and lower second incisors are tusk-like; large in males and smaller in females. In contrast, *Chitenaymeryx* has small upper and lower incisors, as well as a suite of other features that distinguish it from *Brachyodus*, including the fact that the mandibular symphysis is unfused in juveniles as well as in adults, unlike the fully fused symphysis of *Brachyodus*, even those of juveniles.

The outcome of the present study, is that the Austrian anthracotheres from the Early Miocene deposits in the surroundings of Eggenburg are attributed to three species, the commonest being *Brachyodus pontigneensis*, currently known by 41 teeth from five localities, *Brachyodus onoideus* being represented at six localities but by fewer specimens (nine teeth), and one specimen that accords in dimensions with the large species *Masrimeryx palustris*. The last tooth also agrees in dimensions with *Brachyodus depereti* from Moghara, Egypt (Pickford and Gawad 2024). Up to now, no specimens of the smallest of the French Early Miocene anthracotheres, *Chitenaymeryx intermedius* (previously classified as *Brachyodus intermedius*) have been recognised in Austria.

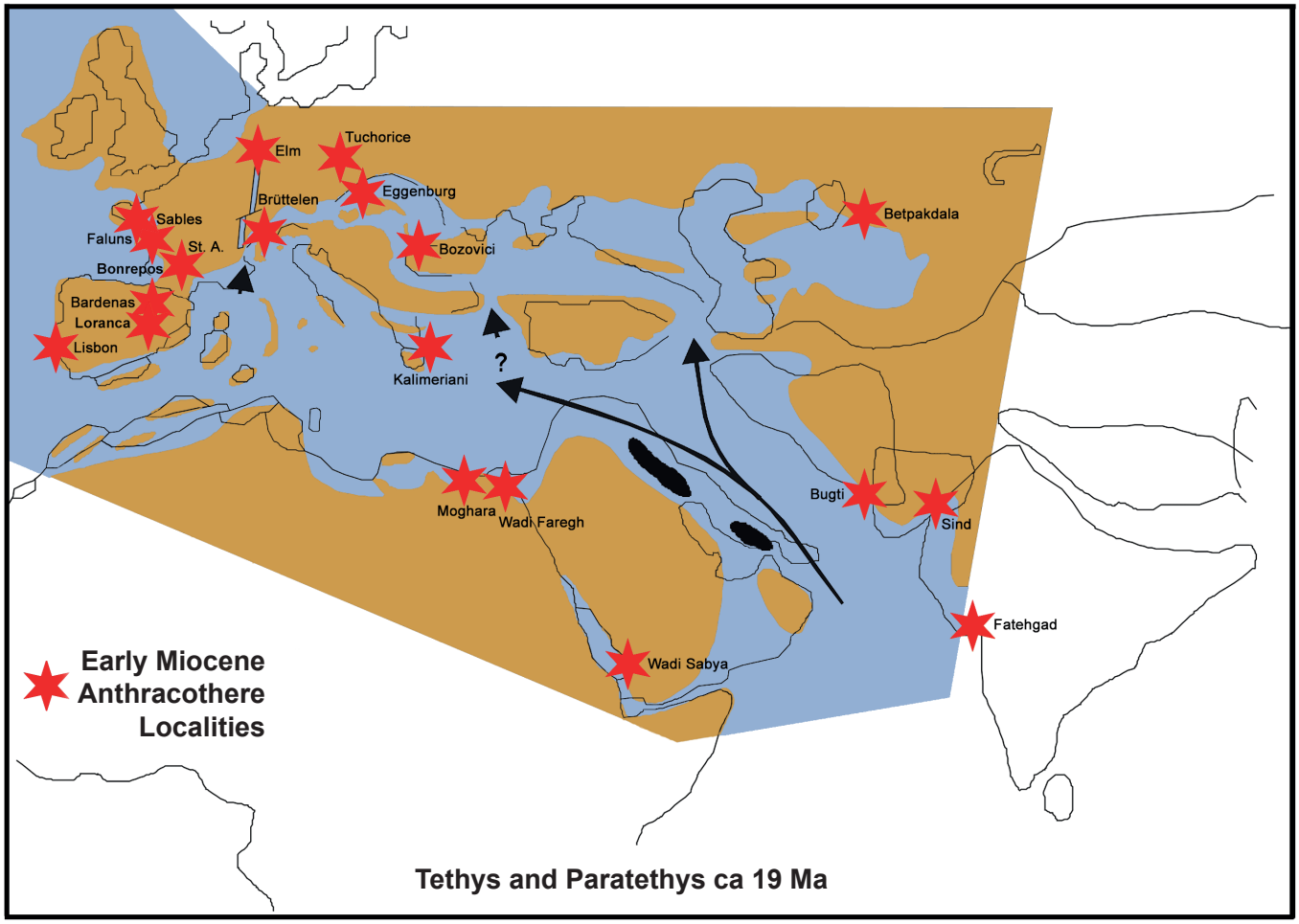


Text-fig. 41. Bivariate (length/breadth) plots of lower cheek teeth of anthracotheres from the French Faluns and the Sables de l'Orléanais (black symbols; data from Pickford 2025) and Austrian Early Miocene Paratethys deposits (red capital letters). E – Eggenburg, G – Gauderndorf, M – Maigen, R – Reinprechtspölla, S – Sonndorf. The specimen with an arrow is the incomplete m/1 from Maigen. The m/3 from Reinprechtspölla has a particularly small hypoconulid, which explains its relatively short mesio-distal diameter.

In biostratigraphic terms, the Austrian Early Miocene (Eggenburgian) anthracotheres indicate correlation to the late Aquitanian-early Burdigalian, corresponding to the period ca. 18.2–21.4 Ma (Piller et al. 2007). In this context, it is pertinent to note that the anthracothere fossils from Tuchořice (the Czech Republic) belong to the same two species that are common in the Eggenburgian deposits; *Brachyodus pontigneensis* (right p/4, right m/3) and *Brachyodus onoideus* (left P4/). Tuchořice was considered to be close in age to Maigen by Fejfar et al. (2003) who correlated it to MN 3 (?its upper part). The upper third molar from Bozovici, Romania, described by Grigorescu (1985) is as broad as the damaged specimen from Eggenburg/Wolkenspiegel that is herein attributed to *Masrimeryx palustris*. The deposits at Bozovici were correlated to the Eggenburgian by Grigorescu (1985) and Codrea et al. (2023).

In terms of palaeobiogeography (Text-fig. 42), the links between the Austrian (Eggenburgian) and French (Faluns, Sables de l'Orléanais) anthracothere localities are evident, at least two species being common to the two regions (*Br. pontigneensis*, *Br. onoideus*). One specimen from Eggenburg/Wolkenspiegel attributed to *Masrimeryx palustris*, suggests that there could have been a biogeographic link to the Romanian locality of Bozovici and the Egyptian locality of Moghara. There does not appear to be any close biogeographic relationship between the Austrian anthracotheres and those from the rich contemporaneous faunas from the Bugti and Sind regions of Pakistan (Pickford 1987).

Up to now, no remains of *Chitenaymeryx intermedius* have been recorded from the Central or Eastern Paratethys,



Text-fig. 42. Distribution of large-bodied anthracotheres (*Brachyodus*, *Masrimeryx*) in the western Tethys and Paratethys regions during the Early Miocene (Burdigalian/Eggenburgian) (St. A. – St Antoine-de-Ficalba, Bonrepos – Bonrepos-sur-Ausonelle). Base map modified from Rögl (1998, 1999).

nor from the Tethyan realm, although the species may have been present in the Baikal region (Vislobokova 1994), a record that requires confirmation. Dineur and Ginsburg (1986) concluded that *Brachyodus intermedius* was confined to the basal part of MN 3, while *Brachyodus onoideus* occurred in the upper part of MN 3 (without proboscideans) and MN 4 (with proboscideans). This distribution implies a replacement of one species by the other, either due to evolution (e.g., *Br. intermedius* was ancestral to *Br. onoideus* as thought by Dineur 1982) or to extinction of one followed by the immigration of a species that had evolved elsewhere. The attribution of *Br. intermedius* to the genus *Chitenaymeryx* by Pickford (2025) indicates that the former of the two hypotheses is unlikely to be valid. Furthermore, the new analyses of the French fossils suggest that *Chitenaymeryx intermedius* may well have been a contemporary of *Brachyodus pontigneensis*, which would upset the biostratigraphic inferences of Dineur and Ginsburg (1986). Further research is required.

The origin of the genus *Brachyodus* also requires to be resolved. Was it derived from a lineage such as *Elomeryx cluai* (Depéret, 1906) as implied by the initial attribution of this species to the genus *Brachyodus* by Depéret (1906) or could its ancestor have been an African lineage such as *Bothriogenys* Schmidt, 1913, as suggested by Lihoreau and Ducrocq (2007: fig. 7.5) admittedly with a question mark?

Although it is suitably positioned in geological time and palaeogeography to have given rise to *Brachyodus*, the medium-sized anthracothere *Anthracotherium frehi* Spillmann, 1974, from the Oligocene coastal deposits at Linz, Upper Austria (Spillmann 1974), is unlikely to have been its ancestor. In its upper molar morphology, the latter species differs markedly from *Brachyodus*, especially in the pinched in postparacrista and premetacrista, with a detached mesostyle, a combination that recalls closely the morphology observed in *Heptacodon* Marsh, 1894a, from North America (Marsh 1894a).

The earliest record of the genus *Brachyodus* in Europe is from Loranca, Spain (MN 2) (Morales and Soria 1984) but the only specimen from this locality is a fragment of upper molar that might represent a different genus such as *Chitenaymeryx*. Being a hydrophilic large mammal, it is possible that *Masrimeryx* dispersed across the Tethys some time before the proboscideans managed to do so (MN 4).

There could be a link between *Brachyodus* sensu stricto and the African genus *Rusingameryx*, which possessed fully fused mandibular symphyses and enlarged i/2s and I1/s. The mandibular symphysis of the subspecies

Brachyodus aequatorialis nacholaensis from Nachola, Kenya, resembles a specimen from France, MSNO 746, an edentulous mandibular symphysis of *Brachyodus onoideus* from Chilleurs aux-Bois (Pickford 2025: fig. 44). In particular it lacks the alveolus of the lower canine, a tooth that is present in the mandible of *Rusingameryx aequatorialis* from Napak XIX, Uganda (Pickford 2022). In this context, all that can be said about the Austrian species of *Brachyodus*, is that they probably immigrated into the region from elsewhere at the beginning of the Eggenburgian Regional Stage, about 20.4 million years ago, and then went extinct locally before the onset of the Ottnangian Regional Stage, ca. 18.2 Ma.

Concerning the debate about the origin of Hippopotamidae (Lihoreau et al. 2015), the Austrian fossils attributed to *Brachyodus pontigneensis* and *Brachyodus onoideus*, especially the tusk-like I1/ and i/2, distance the genus from Hippopotamidae, in which the tusk-like teeth are canines. Furthermore, the I1/ and i/2 from Maigen are tall teeth with enlarged roots and well-formed crowns covered in enamel. The corresponding incisors of hippopotamids are hypselorhizic, meaning that the enamel cap is reduced or absent, and the bulk of the teeth is comprised of the ever-growing root. For these reasons among others, the hypothesis of a close phylogenetic link between anthracotheres and hippopotamids is considered to be untenable.

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