



TERRESTRIAL ARTIODACTYL REMAINS FROM THE WHALE HORIZON AT GROß PAMPAU (ANCIENT NORTH SEA BASIN, NORTH GERMANY; SERRAVALLIAN-TORTONIAN BOUNDARY, MIDDLE-LATE MIOCENE)

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Abstract: The mica-clay fossil site Groß Pampau is famous for its later Miocene marine mammal record, which represents the fauna of the then-southern North Sea Basin. Since the 1980s, fossils have been collected and later systematically excavated. For a long time, only marine taxa were identified. In 2017, two nicely preserved remains of terrestrial artiodactyls were discovered as the so far only terrestrial input and northernmost European terrestrial mammal record of the pre-Quaternary Cenozoic. Here, we figure, describe, and compare morphology and dimensions of both specimens. We identified them as fragment of a hemimandible with two lower molars and a distal phalanx of a cervid, but were unable to assign them to a genus or species, due to limited contemporaneous comparative material.

Key words: Neogene, Schleswig-Holstein, Cervidae, mandible, lower molars, phalanx

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Introduction

Groß Pampau is a renowned Miocene marine fossil site, situated approx. 38 km SSW of Lübeck (Schleswig-Holstein, North Germany; Text-fig. 1), and famous for its marine mammal record, collected there since the 1980s (Höpfner 2014). Fossil Cetacea, comprising Mysticeti, Physterioidea, Delphinoidea, and Ziphiioidea, with articulated and partially articulated postcranial and cranial skeletons, as well as single bone remains (e.g., Behrmann 1995, Hampe 1999, 2006, Höpfner 2014, Kazár and Hampe 2014, Montañez-Rivera and Hampe 2020, Hampe and Fahlke 2022) were recovered from a horizon of a fully marine mica-clay, deposited around the Serravallian-Tortonian boundary (Middle-Late Miocene boundary, regional upper Langenfeldian substage), east of the large North German Cenozoic troughs (Hinsch 1975, 1979). It is the largest pre-Quaternary outcrop above sea level in Schleswig-Holstein (Hinsch 1990, Spiegler 2002).

The total thickness of the exposed mica-clay at the Groß Pampau site is about 17 m, covering the regional middle Langenfeldium substage (and probably the upper part of the lower Langenfeldium) to upper Langenfeldium (upper Middle Miocene to lower Upper Miocene), as documented by cored sections drilled by the Geological Survey of Schleswig-Holstein, and underlying Pleistocene gravel (Spiegler and Gürs 1996). The deposition of fine-grained marine sediments, which were predominant during the late Middle Miocene (Serravallian) and early Late Miocene (Tortonian) in the eastern North Sea Basin, is considered a result of increased basin subsidence (Hinsch 1986, Rasmussen 2004a, b). Recently, Carobene et al. (2023) studied palaeoenvironmental proxies of the uppermost 6 m-thick early Tortonian (upper Langenfeldian) strata of the mica-clay deposits. Based on the small grain size, clay mineral composition/geochemistry, the relatively monotonous silty facies and invertebrate fauna, they



Text-fig. 1. Approximate Middle Miocene palaeocoastline map of Western and Central Europe (based on Blackey 2020) with Groß Pampau located in eastwards-extending embayment of North Sea at that time.

concluded on a warm-temperate, mesotrophic, low-energy habitat, mostly below storm wave base, at a water depth of several tens of metres and a pronounced surface-to-bottom water temperature gradient.

Though the site and enclosed fossils have been studied for decades, no evidence of terrestrial influx has been found so far. Hence, the recent discovery of terrestrial mammal remains, a mandible fragment with two molars and a distal phalanx of a cervid at Groß Pampau is a sensation – first, because of the clearly fully marine provenance of the mica-clay deposits, and second, because they form the first tie point between marine and terrestrial vertebrate fauna around the Serravallian-Tortonian boundary, corresponding to the Middle-Late Miocene boundary, at the Central European North Sea shore.

The fossil specimens presented here were found during the field campaign in 2017 from a slag pile which originated from strata 3 to 4 m above the uppermost strata of the middle Langenfeldian substage (Lüneburgian) (A. Malchow, pers. comm., May 2024) by members of the authorized excavation team: a cervid distal phalanx by Andreas Malchow in July and a cervid hemimandible fragment with two teeth by Martin Kupsch in October, both kept at the Museum für Natur und Umwelt in Lübeck, Germany. Within the upper Langenfeldian, the strata ca. 1.5 m to 4.5 m above the middle/upper Langenfeldian substage boundary correlate with the *Bolboforma fragori/subfragoris* Zone, according to Spiegler and Gürs (1996: tabs 2–4), and include the horizon with the cetacean fossils. The *Bolboforma fragori/subfragoris* Zone defines an age between 11.8 and 10.6 Ma (Spiegler and Gürs 1996, Gürs and Spiegler 1999), and covers the Serravallian-Tortonian boundary, which was

dated chronostratigraphically to 11.6 Ma (Hilgen et al. 2003, 2012, Raffi et al. 2020). Hence, the terrestrial artiodactyl remains most likely originate from the horizon that has yielded the cetacean fossils.

The records of the macromammal fauna around the Serravallian-Tortonian boundary and later Neogene in Central Europe (see, e.g., Bruijn et al. 1992, Bernor et al. 2004, Eronen and Rössner 2007, Harzhauser 2009, Böhme et al. 2012, Franzen et al. 2013, Kirscher et al. 2016) are consistent with evidence from other regions in Europe. The latter reflects a major ecological turnover in the context of a dramatic and global reduction of meridional temperature gradients after the Miocene Climatic Optimum and Middle Miocene Climatic Transition (Herbert et al. 2016).

In terms of cervids, the Langhian (early Middle Miocene) diversity of up to five contemporaneous species (depending on the author), mostly stem group (Procervulinae, Dicrocerinae) members, declined to the latest stem cervid, *Heteroprox larteti* (FILHOL, 1891) (Procervulinae), and gained a new crown group species, *Euprox furcatus* (HENSEL, 1927) (Cervinae), during the late Serravallian (late Middle Miocene) (Gentry et al. 1999, Eronen and Rössner 2007, Böhme et al. 2012, Aiglstorfer et al. 2014). The latest *E. furcatus* antler (dichotomous geometry with burr below) is recorded from the very early Tortonian site of Atzelsdorf in Austria (Hillenbrand et al. 2009: pl. 3, fig. 3, there *Euprox* sp.) as the perhaps only cervid of the assemblage. Later Tortonian cervid records comprise Late Miocene members of Cervinae and Capreolinae only (Azanza et al. 2013 and references therein).

Material and methods

The very restricted terrestrial artiodactyl material from the Groß Pampau site poses a challenge for taxonomic assignment. In order to assess the characters of the recorded cervid teeth, we consulted available similarly-aged Central European cervid teeth of *Euprox furcatus* from Gratkorn (Austria, MN 8, late Serravallian or Sarmatian, late Middle Miocene; Aiglstorfer et al. 2014), *Euprox* aff. *furcatus* and Muntiacinae indet. from Hammerschmiede HAM 5 (Germany, early Tortonian, very early Late Miocene; Kirscher et al. 2016, there *Euprox furcatus*), *Euprox furcatus* from Atzelsdorf (Austria, MN 9, early Tortonian or early Pannonian, early Late Miocene; Hillenbrand et al. 2009, there *Euprox* sp., one lower first or second molar only), *Lucentia* aff. *pierensis* from Rudabánya (Hungary, MN 9, early Tortonian, early Late Miocene; Gentry 2004), Muntiacinae gen. and sp. indet., cf. *Cervavitus mimus*, and *Procapreolus* sp. from Dorn-Dürkheim (Germany, MN 11, late Tortonian, late Late Miocene; Azanza et al. 2013). Due to the restricted material and data, we performed non-statistical, plain comparative analyses, considering morphological features as well as metrics (Text-fig. 2). For the distal phalanx, a lack of sufficient reliably taxonomically assignable material for more detailed comparison precluded a similarly designed comparative investigation. Moreover, differently sized front and hind distal phalanges in Cervidae as well as the superficially abraded condition of the Groß Pampau specimen complicated the investigation. However, besides standard osteology works (Schmid 1972, Nickel

et al. 1986), reliably assignable, but so far undescribed distal phalanges from Sandelzhausen (Rössner 2010) and Hambach 6C (Mörs et al. 2000) were most helpful in identifying relevant taxonomical features.

Tooth crown element terminology follows Rössner (1995) and Bärmann and Rössner (2011). Accordingly, “external postprotocristid” has been used to describe what has been named “*Palaeomeryx*-fold” or “pli protoconal” in previous studies. Osteological terminology follows Nickel et al. (1986). Measurements of teeth and the phalanx were taken according to Rössner (1995) and von den Driesch (1982), respectively. Comparative measurements were basically taken from literature, partly by GER personally (see Tab. 1).

Systematic palaeontology

Class Mammalia LINNAEUS, 1758
Subclass Eutheria HUXLEY, 1880
Superorder Laurasiatheria WADDELL,
OKADA et HASEGAWA, 1999
Order Artiodactyla OWEN, 1848
Suborder Ruminantia SCOPOLI, 1777
Infraorder Pecora LINNAEUS, 1758
Family Cervidae GOLDFUSS, 1820

Cervidae incertae sedis

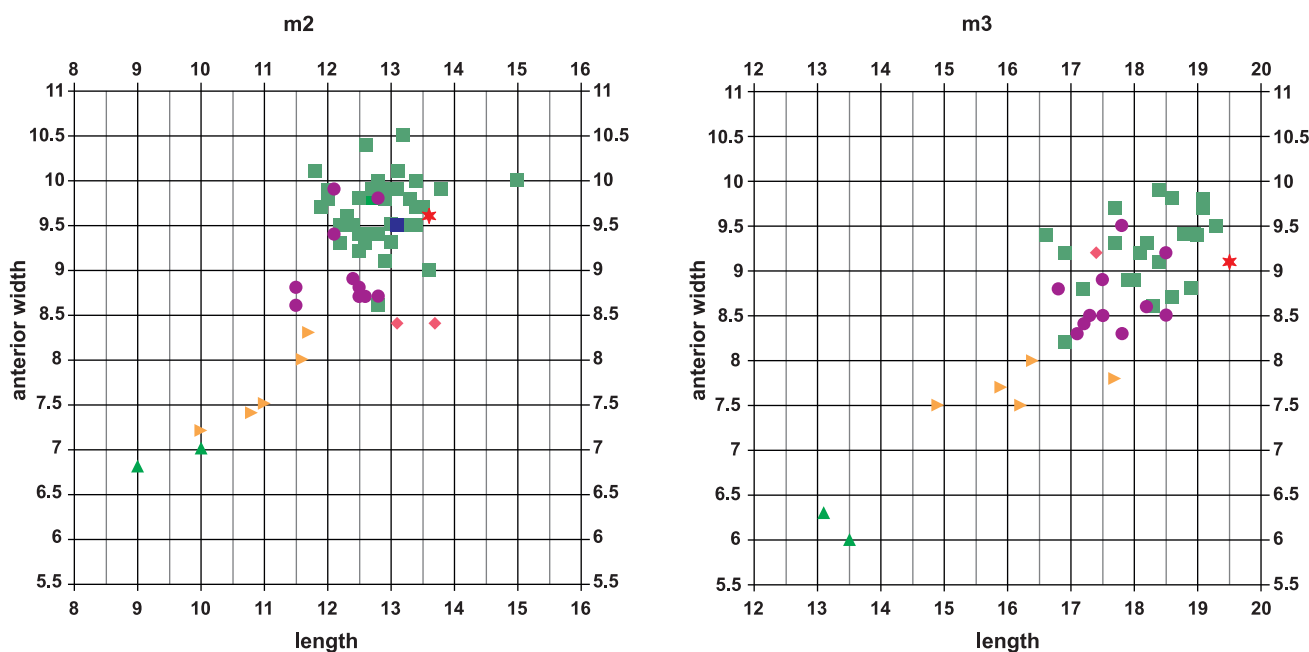
Text-figs 3, 4

Referred material. MNUL.Pal.100.492, fragment of left hemimandible with m2 and m3 (Text-fig. 3a–c); MNUL.Pal.100.491, distal phalanx (Text-fig. 4a–e).

Description and comparison. The hemimandible fragment holds brachyselenodont molars, a second (m2) and a third (m3), in situ, identifiable by the

back fossa at the posterior end of the m3. Both teeth are slightly worn and the posthypoconulidcristid at m3 as well as the root portion below are damaged along the tooth height posteriorly. According to the curvature of the basis of the posterior wall of the third lobe, presumably no more than 0.5 mm is missing, if any at all. The m2 measures 13.6 mm in length, 9.6 mm in anterior width, 9.8 mm in posterior width, and 9.3 mm in preserved height. The m3 is 19.5 mm in preserved length, 9.1 mm in anterior width, 9.0 mm in posterior width, and 9.8 mm in preserved height. Fracture edges of the mandible bone are slightly rolled.

The teeth exhibit v-shaped protoconid- and hypoconid-complexes, encompassing acute angles. Metaconid- and entoconid-complexes are not aligned, but in parallel, showing clear styliform lingual and labial conid ribs, lingually flattened. Their longitudinal axes are in parallel with the longitudinal axes of the teeth. The metastylid is firm and isolated, mesostylid and entostylid are tiny. Lingually, bases of mesostylid and metaconid rib split ca. 3 mm above the crown base, bases of metastylid and metaconid rib split ca. 4 mm above the crown base, and bases of entostylid and entoconid rib split at ca. 4–5 mm above the crown base. Lingual cristids are slightly curved, labial ones are straight. The preprotocristid joins the premetacristid at the anteriolingual extremity of the tooth. A weak external postprotocristid curves from the apex of the protoconid to the base of the internal postprotocristid at the centre of the tooth. Cingulids are lacking. Ectostylids are styliform, reaching between one half and one third of the crown height. The one in m2 is a bit larger than the one in m3. The prehypocristid fuses to the postprotocristid somewhat labially of its lingual end. The postprotocristid, postmetacristid, and preentoconid meet centrolingually. The postmetacristid and preentocristid are unfused, which is obvious in the lingual view. In m2,



Text-fig. 2. Two-variable scatter plots display size variation of lower molars of different cervid species occurring around Serravallian-Tortonian boundary (Middle Miocene-Late Miocene) (in mm). Red stars: MNUL.Pal.100.492; lilac circles: *Euprox furcatus* from Gratkorn; yellow triangles: *Euprox* aff. *furcatus* and Muntiacinae indet. from Hammerschiede; blue square: *Euprox furcatus* from Atzelsdorf; pink rhombs: *Lucentia* aff. *pierensis* from Rudabánya; green triangles: cf. *Cervavitus mimus* from Dorn-Dürkheim; green squares: Muntiacinae gen. and sp. indet. and *Procapreolus* sp. from Dorn-Dürkheim.

Table 1. Cervid tooth dimensions of Groß Pampau and comparative material around Serravallian-Tortonian boundary. Anterior width of *Lucentia* aff. *piemensis* from Rudabánya estimated from width given in Gentry (2004) according to proportions in other contemporaneous cervids.

source	species	locality	catalogue number	tooth	side	length (mm)	anterior width (mm)	symbol in Text-fig. 2
personal		Groß Pampau	MNUL.Pal.100.492	m3	sin	19.5	9.1	red star
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1199	m3	dex	18.9	9.4	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD4794	m3	sin	16.9	9.2	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1222	m3	sin	18.0	8.9	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1225	m3	dex	19.1	9.7	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD4749	m3	dex	18.6	8.7	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD4307	m3	dex	17.2	8.8	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD4528	m3	sin	16.6	9.4	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD3913	m3	sin	17.7	9.7	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1209	m3	dex	17.3		green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1196	m3	dex	18.2	9.3	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1195	m3	dex	19.0	9.4	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1199	m3	dex	18.9	8.8	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1213	m3	sin	18.6	9.8	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1216	m3	dex	18.4	9.1	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1217	m3	dex	18.4	9.9	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1219	m3	sin	17.9	8.9	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1197	m3	sin	18.3	8.6	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1222	m3	sin	18.0	8.9	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1225	m3	dex	19.1	9.8	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1224	m3	dex	18.1	9.2	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD4684	m3	sin	19.3	9.5	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD4794	m3	sin	16.9	8.2	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD4749	m3	dex	18.6	8.7	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD4307	m3	dex	17.2	8.8	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD3913	m3	sin	17.7	9.3	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD4041	m3	dex	18.8	9.4	green square
Azanza et al. 2013	cervid small	Dorn-Dürkheim	DD489	m3	sin	13.5	6.0	green triangle
Azanza et al. 2013	cervid small	Dorn-Dürkheim	DD4512	m3	sin	13.1	6.3	green triangle
Gentry 2004	<i>Lucentia</i> aff. <i>piemensis</i>	Rudabánya	1990/104+113	m3	dex	17.4	9.2	pink rhomb
personal	<i>Euprox</i> aff. <i>furcatus</i>	Hammerschmiede	GPIT/MA/13554	m3	sin	16.4	8.0	yellow triangle
personal	<i>Euprox</i> aff. <i>furcatus</i>	Hammerschmiede	GPIT/MA/10185	m3	dex	14.9	7.5	yellow triangle
personal	<i>Euprox</i> aff. <i>furcatus</i>	Hammerschmiede	GPIT/MA/13556	m3	sin	16.2	7.5	yellow triangle
personal	<i>Euprox</i> aff. <i>furcatus</i>	Hammerschmiede	SNSB-BSPG 2020 XCIV 448	m3	dex	17.7	7.8	yellow triangle
personal	<i>Euprox</i> aff. <i>furcatus</i>	Hammerschmiede	GPIT/MA/13555	m3	dex	15.9	7.7	yellow triangle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	GPIT/MA/2739	m3		17.2	8.4	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	GPIT/MA/2736	m3		17.5	8.5	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	GPIT/MA/2380	m3		17.8	9.5	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	GPIT/MA/2755	m3		18.5	9.2	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	UMJGP 204711	m3		18.5	8.5	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	GPIT/MA/2733	m3		18.2	8.6	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	UMJGP 204713	m3		17.1	8.3	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	UMJGP 204686	m3		16.8	8.8	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	GPIT/MA/2399	m3		17.8	9.5	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	GPIT/MA/2393	m3		17.8	8.3	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	UMJGP 203737	m3		17.5	8.9	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	UMJGP 203737	m3		17.3	8.5	lilac circle

Table 1. continued

source	species	locality	catalogue number	tooth	side	length (mm)	anterior width (mm)	symbol in Text-fig. 2
personal		Groß Pampau	MNUL.Pal.100.492	m2	sin	13.6	9.6	red star
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1199	m2	dex	12.7	9.4	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD4458	m2	sin	15.0	10.0	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1198	m2	sin	12.6	10.4	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1220	m2	sin	12.5	9.2	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1186	m2	sin	12.2	9.3	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1187	m2	dex	13.2	10.5	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1189	m2	dex	12.2	9.5	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1171	m2	dex	12.5	9.4	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1173	m2	dex	12.7	9.8	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1176	m2	dex	12.5	9.8	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1177	m2	dex	13.2	9.5	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1164	m2	sin	12.7	9.9	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1149	m2	sin	13.3	9.8	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1135	m2	sin	12.4	9.5	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1136	m2	dex	13.3	9.8	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1139	m2	dex	12.9	9.9	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1142	m2	sin	13.0	9.3	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1143	m2	dex	12.9	9.8	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1143	m2	sin	11.8	10.1	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1157	m2	sin	13.5	9.7	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1168	m2	dex	12.0	9.8	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1180	m2	dex	13.4	9.5	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1194	m2	sin	13.1	9.9	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1212	m2	sin	13.1	10.1	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1227	m2	dex	13.4	10.0	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1231	m2	sin	12.3	9.6	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1230	m2	dex	13.5	9.7	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD4340	m2	sin	12.8	8.6	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD4071	m2	dex	13.4	9.7	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD4068	m2	dex	12.9	9.1	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1196	m2	dex	12.6	9.3	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1210	m2	sin	13.6	9.0	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1195	m2	dex	12.8	10.0	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD1199	m2	dex	12.8	9.4	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD3840	m2	dex	12.3	9.6	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD4645	m2	dex	12.7	9.4	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD4728	m2	dex	11.9	9.7	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD4772	m2	sin	13.0	9.5	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD4385	m2	sin	12.0	9.9	green square
Azanza et al. 2013	cervid large	Dorn-Dürkheim	DD4496	m2	sin	13.8	9.9	green square
Azanza et al. 2013	cervid small	Dorn-Dürkheim	DD3909	m2	sin	10.0	7.0	green triangle
Azanza et al. 2013	cervid small	Dorn-Dürkheim	DD547	m2	dex	9.6	7.3	green triangle
Azanza et al. 2013	cervid small	Dorn-Dürkheim	DD546	m2	dex	9.0	6.8	green triangle
Gentry 2004	<i>Lucentia</i> aff. <i>pierensis</i>	Rudabánya	1990/221	m2	sin	13.7	8.4	pink rhomb
Gentry 2004	<i>Lucentia</i> aff. <i>pierensis</i>	Rudabánya	1976/V12084	m2	dex	13.1	8.4	pink rhomb
Hillenbrand et al. 2009	<i>Euprox</i> sp.	Atzelsdorf	2008z0052/0001	M1/2	sin	13.1	9.5	blue square
personal	<i>Euprox</i> aff. <i>furcatus</i>	Hammerschmiede	GPIT/MA/13554	m2	sin	11.0	7.5	yellow triangle
personal	<i>Euprox</i> aff. <i>furcatus</i>	Hammerschmiede	GPIT/MA/10185	m2	dex	11.6	8.0	yellow triangle

Table 1. continued

source	species	locality	catalogue number	tooth	side	length (mm)	anterior width (mm)	symbol in Text-fig. 2
personal	<i>Euprox</i> aff. <i>furcatus</i>	Hammerschmiede	GPIT/MA/13556	m2	sin	10.0	7.2	yellow triangle
personal	<i>Euprox</i> aff. <i>furcatus</i>	Hammerschmiede	SNSB-BSPG 2020 XCIV 448	m2	dex	11.7	8.3	yellow triangle
personal	<i>Euprox</i> aff. <i>furcatus</i>	Hammerschmiede	GPIT/MA/13555	m2	dex	10.8	7.4	yellow triangle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	GPIT/MA/2739	m2		11.5	8.6	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	GPIT/MA/2736	m2		12.5	8.7	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	GPIT/MA/2750	m2		12.1	9.9	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	UMJGP 204711	m2		12.8	8.7	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	GPIT/MA/2733	m2		12.5	8.8	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	UMJGP 204686	m2		12.1	9.4	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	GPIT/MA/2399	m2		12.8	9.8	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	GPIT/MA/2393	m2		12.6	8.7	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	UMJGP 210691	m2		11.5	8.8	lilac circle
Aiglstorfer et al. 2014	<i>Euprox furcatus</i>	Gratkorn	UMJGP 203737	m2		12.4	8.9	lilac circle

the postentocristid / entostylid and posthypocristid do not meet at the posterolingual extremity, but leave a very slender opening of the posterior fossa to lingual. The m3 has a small entoconulid-complex fused to the lingual end of the posthypocristid through the preentoconulidcristid. The postentocristid neither contacts the entoconulid nor the posthypocristid, but leaves a very slender opening to the lingual, like in m2. The hypoconulid-complex is labially arranged roughly in parallel with protoconid- and hypoconid-complex, and has a prehypoconulidcristid that fuses to the posthypocristid labially of the entoconulid. The hypoconulid has a prominent column lingually and labially from tip to base. The posthypoconulidcristid is broken off posterolingually and missing. However, the complete entoconulid-complex and remaining basis of the third lobus indicate no connection between postentoconulidcristid and posthypoconulidcristid above the crown basis, hence the third m3-lobus was not closed lingually.

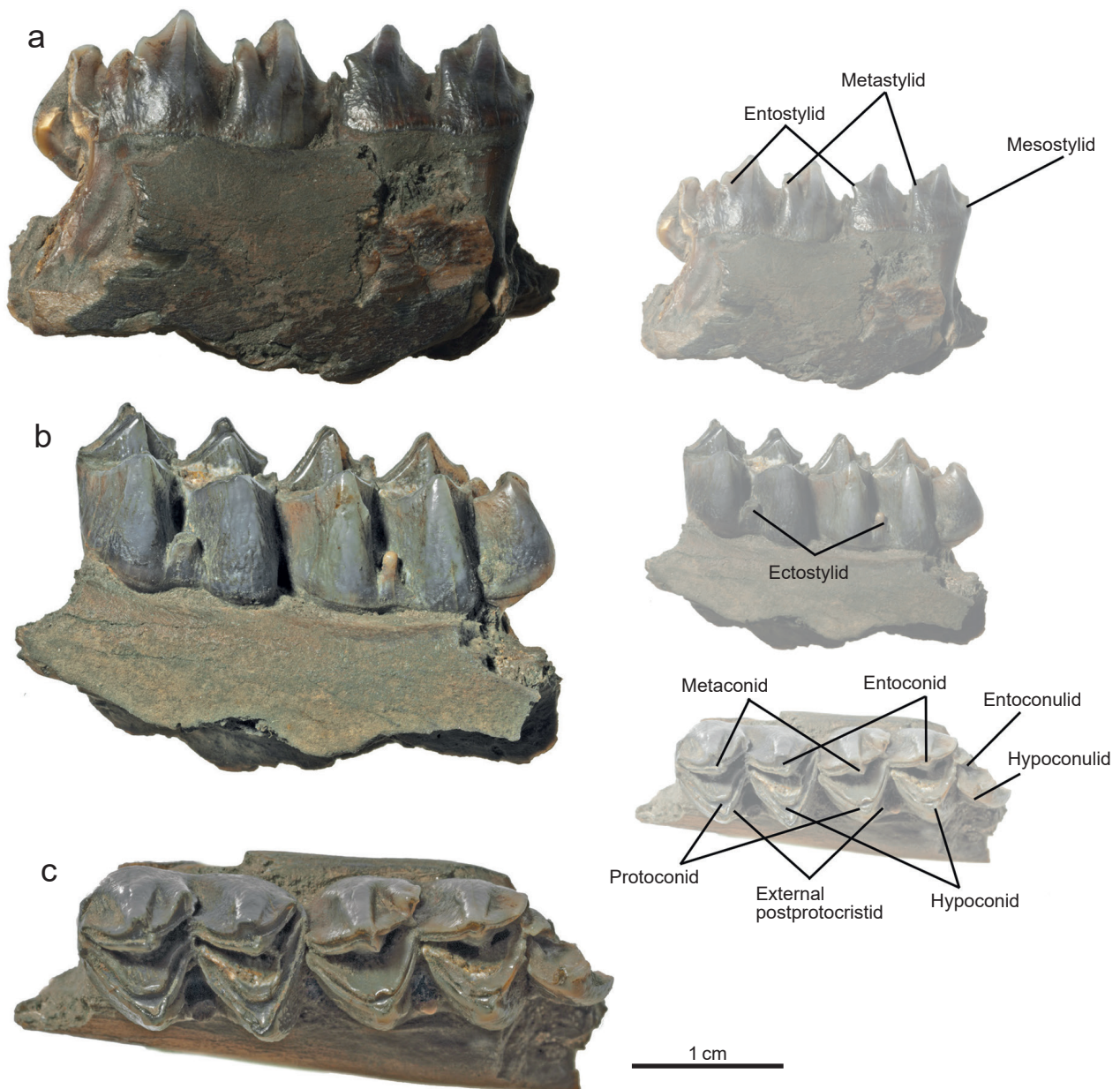
Among the described features, the following combination undoubtedly indicates Cervidae: brachyselenodonty; external postprotocristid; ribs and stylids, which fuse at their bases at different, but medium height levels in the lingual wall of the tooth crown; unfused postmetacristid and preentocristid as well as postentocristid and preentoconulidcristid; and lacking external postmetacristid.

In comparison (Text-fig. 2, Tab. 1), the dimensions of m2 of MNUL.Pal.100.492 ($l = 13.6$ mm, $aw = 9.6$ mm) fall within the variation range of the larger cervids, Muntiacinae gen. and sp. indet. and *Procapreolus* sp., of Dorn-Dürkheim ($l = 11.8$ – 15.0 mm, $aw = 8.6$ – 10.5 mm). It lies within the anterior width variation range of *E. furcatus* from Gratkorn (8.6 – 9.9 mm), but is slightly longer than that (11.5 – 12.8 mm). It overlaps in length with *Lucentia* aff. *pierensis* from Rudabánya (13.1 – 13.7 mm), but is slightly wider than that (8.4 mm). It is larger than the m1/m2 of the cervid from Atzelsdorf ($l = 13.1$ mm, $aw = 9.5$ mm), and clearly larger than m2 of *E. aff. furcatus*/Muntiacinae indet. from Hammerschmiede ($l = 10.0$ – 11.7 , $aw = 7.2$ – 8.3 mm) and those of the smaller cervid, cf. *Cervavitus mimus*, from Dorn-Dürkheim ($l = 9.0$ – 10.0 mm, $aw = 6.8$ – 7.3 mm).

The m3 of MNUL.Pal.100.492 ($l = \sim 20.0$ mm, $aw = 9.1$ mm) lies within the anterior width variation range of the larger cervids, Muntiacinae gen. and sp. indet. and *Procapreolus* sp., from Dorn Dürkheim (8.2 – 9.9 mm), and closest among the comparative species to its largest length (16.6 – 19.3 mm). It falls within anterior width ranges of *E. furcatus* from Gratkorn and *Lucentia* aff. *pierensis* from Rudabánya (9.2 mm), but its length is larger (Gratkorn 16.8 – 18.5 mm, Rudabánya 17.4 mm). It is clearly larger than m3 of *E. aff. furcatus* and Muntiacinae indet. from Hammerschmiede ($l = 14.9$ – 17.7 mm, $aw = 7.5$ – 8.0 mm) and those of the smaller cervid, cf. *Cervavitus mimus*, from Dorn Dürkheim ($l = 13.1$ – 13.5 mm, $aw = 6.0$ – 6.3 mm).

Morphologically, the teeth of MNUL.Pal.100.492 coincide with those of *E. furcatus* from Gratkorn (Aiglstorfer et al. 2014), with the exception of the lacking cingulids, the unsplit posthypocristid, the posterolingually open back fossa, and the lingually arranged hypoconulid.

The teeth of MNUL.Pal.100.492 are higher crowned than *Euprox* aff. *furcatus* / Muntiacinae indet. from Hammerschmiede, as the height of split points of the lingual stylids indicates. On the latter bases of mesostylid and metaconid rib split ca. 2 mm above crown base, bases of metastylid and metaconid rib split ca. 3 mm above crown base, and bases of entostylid and entoconid rib split at ca. 3–4 mm above crown base (compared to 3 mm, 4 mm, and 4–5 mm respectively in MNUL.Pal.100.492, see above). In contrast to the Hammerschmiede material, the Groß Pampau teeth include an open back fossa, no cingulids, and a fusion of posthypocristid to the preentoconulid. In contrast to the Atzelsdorf cervid molar (Hillenbrand et al. 2009: pl. 3, fig. 3), they lack cingulids and have a weaker external postprotocristid. They correspond, especially in the lingually open back fossa, to *Lucentia* aff. *pierensis* from Rudabánya (Gentry 2004: text-fig. 9), with the exception of lacking cingulids. They differ from the larger cervid dentition of Dorn-Dürkheim (Muntiacinae gen. and sp. indet. / *Procapreolus* sp., Azanza et al. 2013) by lacking cingulids, a smaller entoconulid-complex, and a posterolingually open back fossa.

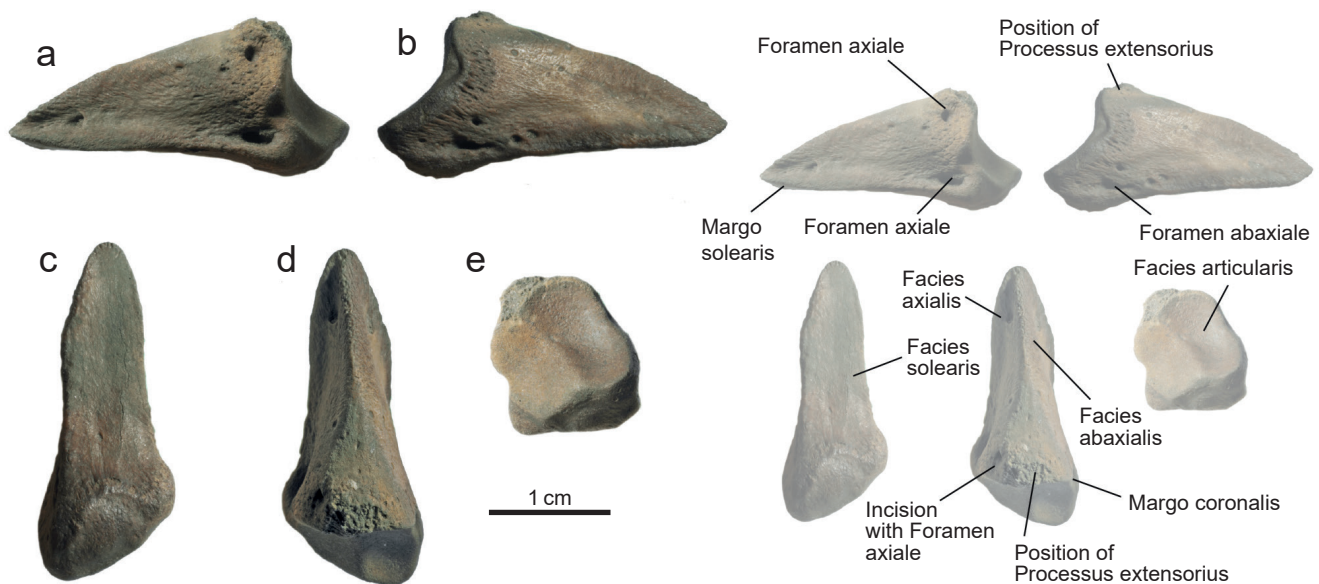


Text-fig. 3. Cervidae incertae sedis, MNUL.Pal.100.492, fragment of left hemimandible with m2 and m3. On the left – a: lingual view; b: labial view; c: occlusal view. On the right – same views with labeled terminology of tooth crown elements.

Accordingly, the size of the teeth of MNUL.Pal.100.492 may fall within the variation range of *E. furcatus* of Gratkorn, *Euprox furcatus* of Atzelsdorf. *L. aff. pierensis* of Rudabánya, and Muntiacinae gen. and sp. indet. / *Procapreolus* sp. of Dorn-Dürkheim for the m2 and the width of m3. As the original length of the m3 most likely was ca. 20.0 mm, it has a clearly larger length than all comparative species, and therefore is specific among the considered Central European Serravallian-Tortonian cervids. The morphology appears to be most similar to *L. aff. pierensis* of Rudabánya. As it is impossible to clearly assign the hemimandible fragment for the time being, we remain with Cervidae incertae sedis.

The distal phalanx, MNUL.Pal.100.491, is slightly rolled and has a distinct triangular outline in abaxial, axial, proximal or distal view, which is diagnostic of a distal phalanx of many members of Ruminantia or Suoidea. It measures 28.7 mm in maximum length, 11.4 mm in maximum width, 14.9 mm in maximum height, 24.1 mm in dorsal length, 7.0 mm in

medium width, and 7.0 mm in length of the facies articularis, so dorsal and palmar/plantar length of the bone are clearly longer than its height. It is distinctly smaller than distal phalanges of Palaeomerycidae. The dorsal profile is straight, in contrast to many bovids, where the dorsal profile is slightly to strongly convex (Köhler 1993: 26f). The parietal surface is slightly convex abaxially (facies abaxialis), and flat to slightly concave axially (facies axialis). The sole surface is flat, meeting with the parietal surface in the prominent sole edge (margo solearis) axially and abaxially. The longitudinal axis of the bone is axially inclined, with an angle of about 60° between sole and axis, which is typical to pecorans, larger than in suids and tragulids (Schmid 1972: pl. XXXII), and slightly concave axially/convex abaxially, which is also visible in the shape of the sole. The axial and abaxial parietal surfaces meet dorsally in a sharp ridge. Proximodorsally, the ridge diminishes and the parietal surface flattens, whereas at the most dorsoproximal axial region, the abrasion area



Text-fig. 4. Cervidae incertae sedis, MNUL.Pal.100.491, distal phalanx. On the left – a: axial view; b: abaxial view; c: palmar/plantar view; d: dorsal view; e: proximal view. On the right – same views with labeled anatomical terminology.

of an originally present processus extensorius is located. The latter is typical for Pecora, but not for Tragulidae and Suidae. Proximopalmarly/-plantarly on the facies abaxialis, the sulcus parietalis ends with the foramen abaxiale. Proximally on the facies axialis, foramina axiale are located right above the margo solearis and close to the dorsal edge. The latter is placed in an incision of the dorsoproximal margin of the facies axialis. Heintz (1970) described the dorsal foramen axiale as a character of Cervidae, as long as it is not accompanied by a dorsal foramen abaxiale, what is typical for Bovidae. In Suidae, only the foramen axiale above the margo solearis is present (Nickel et al. 1986). Additional smaller taxonomically non-indicative foramina of the vascular system are present on MNUL.Pal.100.491, distally on the facies axialis, right above the margo solearis, and on the facies abaxialis, proximally above the sulcus parietalis. The proximal facies articularis is axially inclined, following the general geometry of the bone, and articulated with the caput of the medium phalanx during lifetime. Accordingly, it is in general concave, but divided into an axial and an abaxial half by an axially inclined central dorsopalmar/-plantar ridge. Both articular facets have the same width. Its delimiting edge, the margo coronalis, clearly projects beyond the parietal and sole surfaces. The abaxial edge is longer than the axial edge, due to the overall inclination. Yet, it is incomplete because of the loss of the processus extensorius, which in complete specimens of pecorans, proximally holds the dorsalmost portion of the abaxial half of the facies articularis (Heintz 1970, Köhler 1993). Hence, we must assume that the abaxial articular facet originally was clearly higher than it is presently. This is in contrast to suids and tragulids, which do not have a processus extensorius, but a subhorseshoe or trapezoidal shape, proportionally less slender (Schmid 1972: pl. XXXII, van der Made 2010: fig. 27 A5, Morales et al. 2012: fig. 80). Further, pecorans are usually indicated by a step-like dorsal outline of the facies articularis caused by the above-mentioned incision of the

dorsoproximal margin of the facies axialis, in which the dorsal foramen axiale is located (Heintz 1970, Schmid 1972: pl. XXXII, Köhler 1993). Proximopalmarly/-plantarly the facies articularis is placed on the thickened area (tuberculum flexorium) proximally to the sole, more proximally extended abaxially. The entirety of the morphological features indicates a distal phalanx of a cervid.

Discussion

In palaeomammalogy, taxonomic diagnoses are predominantly based on odontological material, and only second-tier to osteological material, due to the more species-specific morphological characters of teeth and the better record of completely preserved specimens.

However, this is not the case for cervid species, which are commonly established based on antler holotypes, as those are more specific than their relatively uniform cervid dentition. Yet, rarely, antlers are recorded still attached to a cranium with full dentition. Accordingly, a reliable association of teeth to antlers is dependent on clear size distribution among the ruminant species of a fossil site. This does not apply for the Groß Pampau hemimandible fragment. Moreover, premolars are generally more species-specific among ruminants than molars, especially the lower fourth premolar (e.g., Janis and Lister 1985). Thus, the Central European cervid species records around the Serravallian-Tortonian boundary are an important hint for its taxonomic identification, yet comparisons did not lead to a reliable assignment more specific than Cervidae incertae sedis. It must be noted that dentition data of *Euprox dicranoceros* (KAUP, 1893) and *Amphiprox anocerus* (KAUP, 1833) from Eppelsheim (Germany, MN 9, early Tortonian, early Late Miocene) (Böhme et al. 2012) are critical. They are biochronologically positioned between the older Hammerschmiede as well as Atzelsdorf assemblages and the younger Rudabánya assemblage (Bernor et al. 2004, Böhme et al. 2012, Daxner-Höck et al. 2016, Kirscher et al. 2016).

But descriptions are not available in the literature yet, and we could not visit the respective collections due to restricted time.

The study of the distal phalanx is further challenged by the fact that the reliable taxonomic association of disarticulated bones is dependent on the sample size and taxonomic composition at a fossil site. Furthermore, phalanges are not the preferred osteological elements to be described, and so are rarely found in the scientific literature. Accordingly, the distal phalanx of Groß Pampau can be a record of any of the represented cervid species around the Serravallian-Tortonian boundary (*Heteroprox larteti*, Muntiacinae indet., *Euprox furcatus*, *Euprox dicranoceros*, *Amphiprox anocerus*, *Lucentia* aff. *piereensis*, *Cervavitulius mimus*, and *Procapreolus* sp. (Gentry et al. 1999, Gentry 2004, Eronen and Rössner 2007, Hillenbrand et al. 2009, Böhme et al. 2012, Azanza et al. 2013, Aiglstorfer et al. 2014, Kirscher et al. 2016) or any other genus or species we do not yet know about. It may or may not have belonged to the same individual as the Groß Pampau cervid hemimandible fragment.

How the remains of one or two cervid individuals ended up at the mica-clay depositional site of whale carcasses at Groß Pampau in the sublittoral zone of a neritic environment with a minimum of 40 to 60 m water depth (Moths 1989, 1994, Carobene et al. 2023) is still an enigma. The breakage edges of the mandible and the phalanx are slightly rolled, which points to embedding after a short distance transport. This agrees with the lack of transport traces on the teeth, as enamel is much more resistant than bone tissue. However, the marine mammal remains of the whale horizon are sometimes partially articulated, and hence deposited in a different way. Fragmentation of the terrestrial mammal remains must have happened on land, possibly at the shore, prior to transport into the North Sea Basin, yet terrestrial influx is unknown so far from the Groß Pampau site.

Artiodactyls are generally excellent swimmers. Reindeer, for example, are observed often crossing not only large rivers but even wide estuaries (Heck 1979), and moose are seen swimming in water bodies trying to escape attacking wolves (Jordan et al. 2010). As extant cervids are known to feed at the shore on aquatic vegetation in order to enrich their food with minerals and proteins (Faber et al. 1988, Ditchkoff and Mayer 2009, Ceacero et al. 2010, 2014, Gómez et al. 2012) and can get in life-threatening situations (for example, in 1987, a young male red deer was rescued from the mudflats (Wadden Sea) of the North Sea off Büsum by a SAR cruiser; Borkenhagen 2011), it is possible they did in the Late Miocene too, and were regularly in the tidal area. The tidal area could have become a place of death for the individual/s to which the Groß Pampau specimens belonged, possibly during a storm or when hunted by odontocetes. However, no bite marks are preserved and the cause of death remains unknown.

Conclusions

A cervid mandible fragment with molars and a cervid distal phalanx from the previously purely marine-assessed Groß Pampau fossil site indicate certain terrestrial input. These terrestrial mammal records are the northern-most known of the pre-Quaternary Cenozoic, and provide the first tie point in the area of the southern North Sea Basin between

synchronous marine and terrestrial vertebrate fauna at the Serravallian-Tortonian boundary. We expect more terrestrial fossils to be unearthed at Groß Pampau in the future.

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