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Geobios 35 (2002) 489–514

GEOBIOS

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A partial skeleton of *Prodeinotherium bavaricum* (Proboscidea, Mammalia) from the Middle Miocene of Unterzolling (Upper Freshwater Molasse, Germany)

Un squelette partiel de *Prodeinotherium bavaricum* (Proboscidea, Mammalia) du Miocène moyen de Unterzolling (Molasse d'eau douce supérieure, Allemagne)

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Received 5 November 2001; accepted 28 January 2002

Abstract

Here, a partial skeleton of *Prodeinotherium bavaricum* from Unterzolling (Southern Germany) is documented. The following elements are preserved and described for the first time: cervical vertebrae 1–2 and 5–7, the first thoracic vertebra, one lumbar vertebra, trapezium, metacarpals 1–5, tibia, calcaneus, endo- and mesocuneiform, cuboid, the fourth metatarsal, and some phalanges. Comparisons with the skeletons of *P. bavaricum* from Franzensbad (Czech Republic) and *Deinotherium giganteum* from Eserovo (Bulgaria) show osteological differences that are described and discussed.

Résumé

Un squelette partiel de *Prodeinotherium bavaricum* de Unterzolling (Allemagne Sud) est étudié. Les spécimens suivants sont décrits pour la première fois : les vertèbres cervicales 1–2 et 5–7, première vertèbre thoracique, une vertèbre lombaire, trapéze, métacarpiens 1–5, tibia, calcanéum, ento- et mésocunéiforme, cuboïde, métatarsien 4, et quelques phalanges. Une comparaison avec les squelettes de *Prodeinotherium bavaricum* de Franzensbad (Tchéquie) et *Deinotherium giganteum* de Eserovo (Bulgarie) montre des différences ostéologiques qui sont discutées.

Keywords: Deinotheres; *Prodeinotherium bavaricum*; Skeleton; Middle Miocene; Upper Freshwater Molasse

Mots clés: Deinothères; *Prodeinotherium bavaricum*; Squelette; Miocène moyen; Molasse d'eau douce

1. Introduction

The partial skeleton described herein was found in 1977 in a gravel pit of the company Kronthaler, about 1 km north of the town of Unterzolling (Bavaria, Germany, topographic map 7536 Freising Nord, r: 44 83 150, h: 53 69 100, circa 450 m NN). Unterzolling is located about 40 km north-northeast of Munich and about 4 km north of the city Freising near the river Glon (Fig. 1). The skeletal remains belonging to one *Prodeinotherium bavaricum* individual were discovered by the owner of the gravel pit, Mr. Schneider, and were excavated by Professor K. Heissig and preparator E. Schmieja (Bayerische Staatssammlung für Paläontologie und Geologie München). The remains are housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (Coll. No. BSP 1977 I 229).

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PII: S0016-6995(02)00042-6

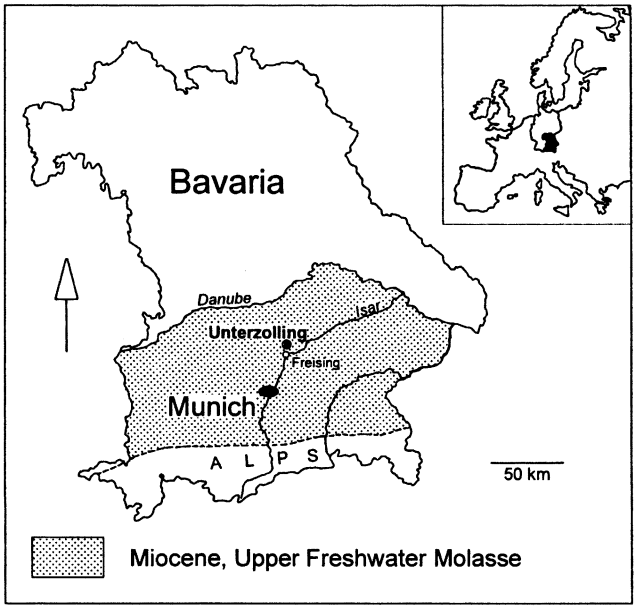

Fig. 1. Geographic position of the locality of Unterzolling.
Fig. 1. Position géographique de la localité de Unterzolling.

This work is the first detailed documentation of the postcranial elements of a European *Prodeinotherium*. Apart from the descriptions by Éhik (1930), Bergounioux and Crouzel (1962a), and Huttunen (in press c), no further postcranial descriptions of European *Prodeinotherium* elements are available. Additionally, the postcranial skeleton of the genus *Deinotherium* is poorly documented in Europe. The most relevant works on the *Deinotherium* skeleton are Stefanescu (1894), Stromer (1938), Tobien (1962), Bergounioux and Crouzel (1962a, b), and Harris (1973). For the determination of constant characters, comparisons were made between the Unterzolling skeleton and other associated deinotheriid material from Europe.

2. Geology and stratigraphy of the locality of Unterzolling

The limnofluviatile deposits in Unterzolling belong to the Miocene Upper Freshwater Molasse (Fig. 1). Based on proboscidean fossil remains, Dehm (1955) divided the Upper Freshwater Molasse into three series. The basal "Tortonian" ("Ältere Serie") is defined by the lack of *Prodeinotherium* and presence of *Gomphotherium angustidens*, whereas in the Early and Middle Sarmatian ("Mittlere Serie"), both *P. bavaricum* and *G. angustidens* coexist. The Late Sarmatian and Early Pannonian ("Jüngere Serie") is dominated by gomphotheres of different individual sizes and the large taxon *D.* aff. *giganteum* (Dehm, 1955, 82ff). The gravel pit Kronthaler in Unterzolling contains mostly sediments of the "Mittlere Serie" (basal "Brockhorizont" overlain by the "Hauptschotter" and "hängende Feldspatsande"), with the uppermost coarse gravel belonging to the basal "Jüngere Serie" (Heissig, 1989, p. 245). The vertebrate fauna of Unterzolling 1a, dominated by micromammals, was discovered and studied by Heissig (1989). (Unterzolling 1b was a small lens of marl.) Most of the large mammal remains, and most likely also the *Prodeinotherium* remains of this study, originate from sandy layers about 15–23 m above the "Brockhorizont" at the base of the pit and belong to the "Mittlere Serie". Based on the micromammal content of the locality, Heissig (1989, p. 254) referred the fauna of Unterzolling 1a to Mammalian Neogene Unit MN6 (Astaracian, Middle Miocene).

3. Methods

The measurements given in the tables for each element are based on the method of Göhlich (1998) and, for the mandible, on the method of Huttunen (in press c). In the comparisons, the *Prodeinotherium* material from Franzensbad, Czech Republic (inventory number NHMW2000-z0047/0001, exhibition hall of the Naturhistorisches Museum in Vienna, Austria), the *Deinotherium* material from Eserovo, Bulgaria (exhibition hall of the Paleontological Museum of the Sofia University, Bulgaria), and a few isolated *Prodeinotherium* specimens at the Muséum National d'Histoire Naturelle, Paris, are discussed, along with the most relevant results of previous postcranial descriptions by Tobien (1962), Harris (1973, 1978), and Huttunen (in press c).

3.1. Abbreviations

BSP	Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich
dext.	dexter (right)
Mc	metacarpalia
MN	Mammalian Neogene Zone
Mt	metatarsalia
m1–3	lower molars
NHMW	Naturhistorisches Museum in Wien
p2–3	lower premolars
Sin.	sinister (left)
**n*	estimated measurement because of abrasion or breakage
–	the structure is not present

4. Systematics

Order Proboscidea ILLIGER, 1811
Family Deinotheriidae BONAPARTE, 1845
Genus ***Prodeinotherium*** ÉHIK, 1930

Diagnosis (Éhik, 1930, p. 14): "In p3 the entoconid lies inside the cingulum and is not in connection with it. Posterior mental foramen falls between the p3 and p4; the anterior limb is mesatipod [broad] opposed to the dolichopod [long] limb of *D. giganteum*."

Diagnosis (Harris, 1973, p. 293): "Small deinotheres. Dental formula for the family; M2–3 with well-defined postmetaloph ornamentation. Skull rostrum turned down parallel to the mandibular symphysis; rostral trough and

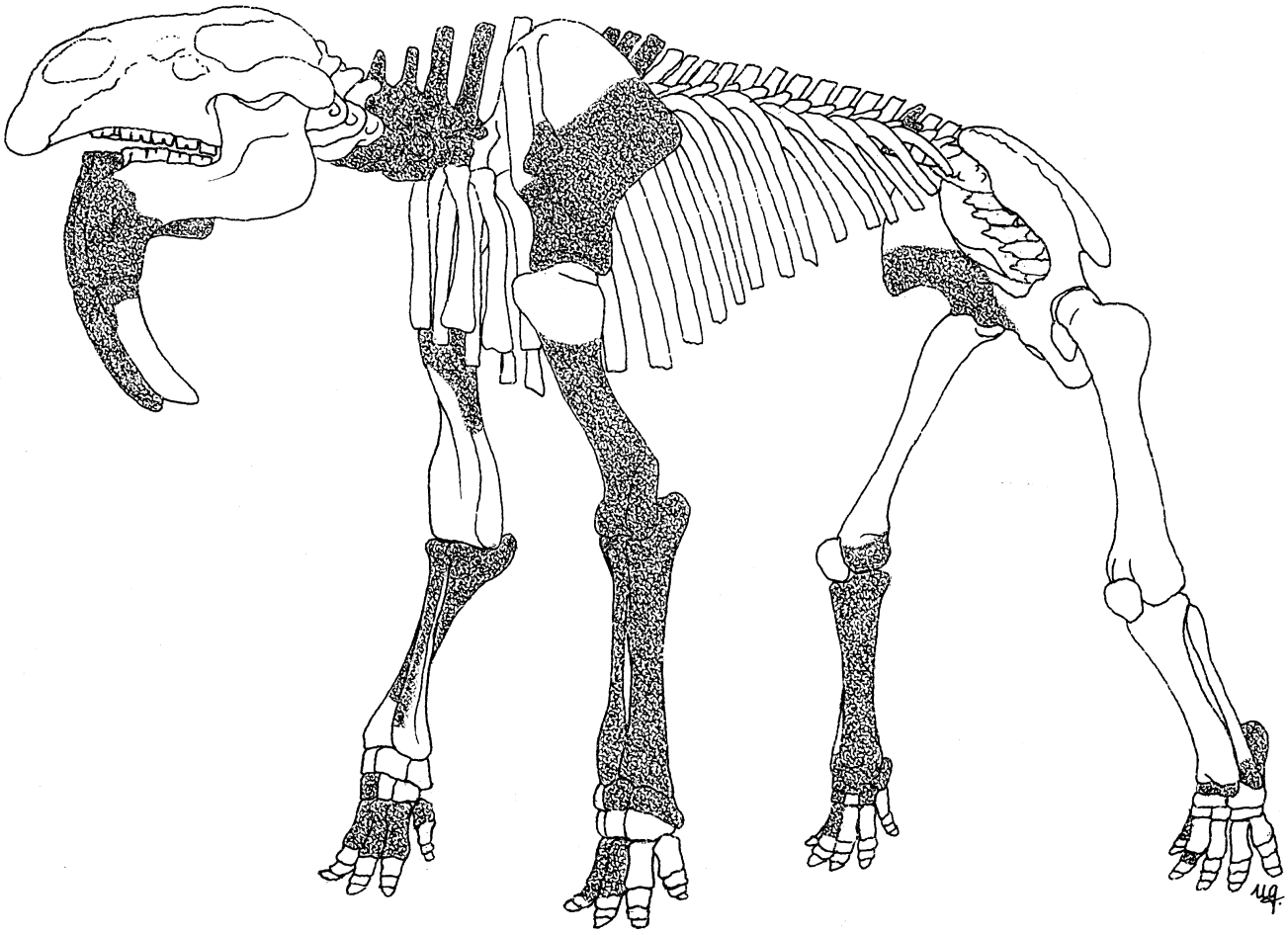

Fig. 2. The *Prodeinotherium bavaricum* skeleton from Unterzolling. Preserved elements coloured grey.
Fig. 2. Le squelette de *Prodeinotherium bavaricum* de Unterzolling. En coloré gris : les éléments préservés.

external nares narrow; preorbital swelling close to orbit; external nares anteriorly positioned and nasal bones with anterior median projection; skull roof relatively longer and wider than in *Deinotherium*; occiput more vertically inclined; occipital condyles positioned more ventrally than in *Deinotherium* and level with the Frankfurt plane; paroccipital processes short. Postcranial skeleton graviportally adapted; scapula with well-defined spine and stout acromion and metacromion; tarsals and carpals narrow but not dolichopodous."

Type species *Deinotherium bavaricum* VON MEYER, 1831 (first description 1833).

Other recognized species *Prodeinotherium pentapotamiae* (FALCONER and LYDEKKER, 1876, pp. 54–57, Asia), *Prodeinotherium hobleyi* (ANDREWS, 1911, pp. 943–945, Africa)

Species *Prodeinotherium bavaricum* (Fig. 2)

Diagnosis: "*D. bavaricum* is one fourth smaller than *D. giganteum*" (Von Meyer, 1833, p. 511, translated from German).

Synonymy

1832 *Dinotherium Cuvieri*—Kaup, p. 14–16.

1836 *Dinotherium secundarium*—Lartet, p. 218.

1930 *Prodinotherium hungaricum*—Éhik, p. 14, pl. 1–4.

Type specimen: Lower p3 dext., specimen number BSP AS I 220, a lectotype designated by Gräf (1957).

Type locality: ?Georgensgmünd, Bavaria, Germany, MN6 (Göhlich, 1999, p. 166).

Geographic distribution: Austria (Mottl, 1969; Huttunen, in press a), Bulgaria (Bakalov and Nikolov, 1962), Czech Republic (Huttunen, in press c), France (Antoine et al., 1997), Georgia (NOW database), Germany (Gräf, 1957), Hungary (Gasparik, 1993), Portugal (Antunes, 1989), Serbia (Laskarev, 1944), Spain (Bergounioux and Crouzel, 1962a, b), Switzerland (Weinsheimer, 1883).

Stratigraphic distribution: From Early to Middle Miocene, Mammalian Neogene Zones MN4 (several European localities) to MN9 (only Dinotheriensande, Germany).

Description

Mandible (Fig. 3(1); Tables 1–3)

Table 1
Measurements (mm) of the mandible of *Prodeinotherium bavaricum* from Unterzolling
Tableau 1
Mensurations (mm) de la mandibule de *Prodeinotherium bavaricum* de Unterzolling

	Unterzolling (dext.)	Franzensbad (dext.)
Length from angulus to posterior incisor alveolus	680	518
Height from angulus to caput mandibulae plane	330	310
Depth between caput mandibulae and processus coronoideus	280	230
Length of the symphysis from p3 alveolus to incisor alveolus	350	280
Length of the toothrow	310	310
Height of the corpus mandibulae at m2, m3	120, 115	110, 120
Width of the corpus mandibulae at p4, m1, m2, m3	109, 100, 113, 119	95, 105, 110, 120
Anteroposterior length of the symphysis	185	185
Width of the symphysis at incisor alveolus	209	165
Width of the symphysis at p3 alveolus	185	123

The mandible fragment consists of a complete hemimandible dext. with p3–m3 and the lower incisor and symphysis sin. with a broken incisor alveolus and an incisor fragment. In lateral view, the mandible has all the usual deinotheriid mandible characters: straight corpus mandibulae with distally flexed symphysis and tusks, and caudally, a nearly straight angulus. The two mental foramina are at the level of p4 and anterior to p3. The anterior foramen is much larger than the posterior one. The toothrow ends at the anterior edge of the ramus mandibulae. The caput mandibulae is medially extended (width: 121 mm). It surpasses the processus coronoideus greatly in height. Between them, the ramus mandibulae has a deep, concave muscle attachment. The surface of the angulus is also concave.

The medial side of the ramus mandibulae is divided into two concavities, one ventral and another dorsal to the foramen mandibulae. The foramen mandibulae is situated in the middle of the ramus mandibulae. The angulus and the processus coronoideus are rough. Observed on the anterior corpus mandibulae is a rounded concavity for the musculus digastricus attachment (after Harris, 1975).

In anterior view, a deep sulcus (width: 80 mm) runs along the entire length of the symphysis. The sulcus is bounded by sharp ridges.

The incisor dext. is complete. In lateral view, the tooth is strongly curved caudally. It is oval in transverse section. The anteroposterior diameter exceeds the transverse diameter. The medial side of the tooth is slightly flattened. The apex of the tusk has an elongated, smooth medial wear facet (circa 100 mm long). Only the proximal one-third of the incisor sin. is preserved. The broken symphysis shows that the incisor extends proximally up to the level of p3.

The toothrow is complete (p3–m3 toothrow length: 310 mm) (Fig. 3(1d)). The p3–m1 are heavily worn with exposed dentine, while the m2–m3 have only well-developed wear facets.

Morphology of p3: The tooth is triangular in occlusal outline. Two anterior conids, and proto- and metaconid are present. Although they are well worn, two separate conids may be identified because of a vertical depression on the anterior wall. The depression ends anteriorly at a well-pronounced elevation at the level of the cingulum. The protoconid is connected to the hypoconid by a well-worn ectolophid that is low in the middle. The posterior conids, and hypo- and entoconids are interconnected by a worn transverse hypolophid. There is a cingulum present on the labial and posterior walls.

Table 2
Measurements (mm) of the lower tusk dext. of *Prodeinotherium bavaricum* from Unterzolling
Tableau 2
Mensurations (mm) de la défense inférieure dext. de *Prodeinotherium bavaricum* de Unterzolling

Incisor dext.	Length	Maximum curved length	Proximal diameter (max./min.)	Diameter at the midpoint of the tooth (max./min.)
	285	395	97/81	85/72

Table 3
Measurements (mm) of the lower premolars and molars dext. of *Prodeinotherium bavaricum* from Unterzolling
Tableau 3
Mensurations (mm) des prémolaires et molaires inférieures dext. de *Prodeinotherium bavaricum* de Unterzolling

Tooth	Length	Anterior width (p4–m3 metalophid)	Posterior width (hypolophid)	Tritolophid width
p3	44	30	36	–
p4	55	45	47	–
m1	67	45	47	47
m2	64	56	58	–
m3	68	58	50	–

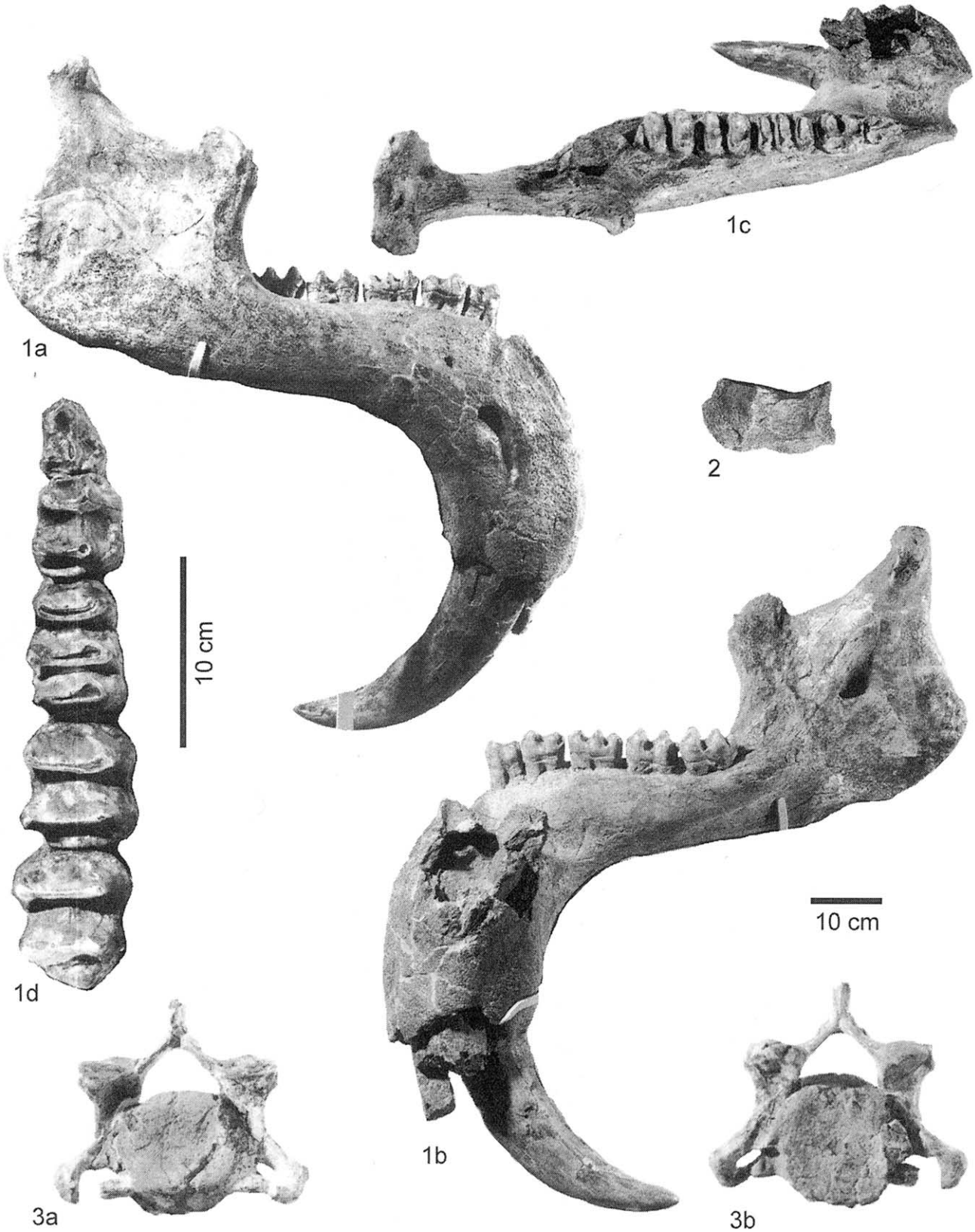

Fig. 3. **1–3.** *Prodeinotherium bavaricum* from Unterzolling (BSP 1977 I 229) (1:8). **1**. Mandible dext.: **a**, lateral view; **b**, medial view; **c**, dorsal view; **d**, toothrow dext., occlusal view (1:3). **2**. Atlas, caudal view. **3**. Cervical vertebra no. 5: **a**, cranial view; **b**, caudal view.
Fig. 3. **1–3.** *Prodeinotherium bavaricum* de Unterzolling (BSP 1977 I 229) (1:8). **1**. Mandibule dext. : **a**, vue latérale ; **b**, vue médiale ; **c**, vue dorsale ; **d**, série dentaire dext., vue occlusale (1:3). **2**. Atlas, vue caudale. **3**. Vertèbre cervicale no. 5 : **a**, vue craniale ; **b**, vue caudale.

Table 4
Tooth size (mm) comparisons of *P. bavaricum* and *D. giganteum* from European localities from MN5 to MN10. Comparative material: measurements MN5–MN10 from Huttunen (2000); MN5—Pontlevoy, France; MN6—Sansan, France; MN7/8—La Grive, France (descriptions in Depéret, 1887); MN9—Dinotheriensande, several localities, Germany (descriptions in Gräf, 1957); MN10—Montredon, France (descriptions in Tobien, 1988). Abbreviations: OR = observed range, X = mean (number in parentheses indicates the sample size), L = length, W = width, W1/2/3 = width of the first/second/third lophid

Tableau 4
Comparaison de la taille (mm) des dents de *P. bavaricum* et *D. giganteum* pour les localités Européennes de MN5 à MN10. Matériel comparatif: mensurations MN5–MN10 de Huttunen (2000) ; MN5—Pontlevoy, France ; MN6—Sansan, France ; MN7/8—La Grive, France (descriptions Depéret, 1887) ; MN9—Dinotheriensande (nombreuses localités), Allemagne (descriptions Gräf, 1957) ; MN10—Montredon, France (descriptions Tobien, 1988) ; Abréviations: OR = extrêmes, X = moyenne (le nombre entre paranthèses indique la taille de l'échantillon), L = longueur, W = largeur, W1/2/3 = largeur du premier/deuxième/troisième lophide

Tooth			*P. bavaricum*					*D. giganteum*	
			MN5	Unterzolling (MN6)	MN6	MN7/8	MN9	MN9	MN10
p3	L	X	41 (8)	44	57	44	46	63	65 (8)
		OR	35–49				38–50 (22)	55–72 (17)	58–74
	W	X	31 (8)	36	54	37	35	50	52 (8)
		OR	20–37				30–39 (22)	48–56 (17)	49–58
p4	L	X	51 (9)	55		64	58	68	74 (7)
		OR	46–61				49–64 (6)	52–76 (17)	68–79
	W1	X	40 (9)	45		44	45	68	57 (8)
		OR	35–44				41–48 (6)	52–76 (17)	49–59
	W2	X	42 (8)	47		49	46	55	60 (6)
		OR	38–48				40–49 (6)	46–64 (17)	56–64
m1	L	X	63 (6)	67		86	68	86	92 (2)
		OR	56–70					81–91 (12)	90–94
	W1	X	41 (6)	45		54	51	58	63 (3)
		OR	37–43					62–65 (12)	58–69
	W2	X	43 (6)	47		56 (2)	49	60	64 (6)
		OR	39–48			55–57		56–65 (12)	60–69
	W3	X	39 (6)	47		52 (2)	45	54	60 (5)
		OR	34–46			50–53		50–62 (12)	58–64
m2	L	X	65 (12)	64	78			78 (17)	80 (3)
		OR	56–74					64–104	78–81
	W1	X	53 (13)	56	69			68 (16)	72 (3)
		OR	48–62					54–87	69–75
	W2	X	53 (12)	58	63			68 (16)	65 (3)
		OR	46–60					49–75	63–68
m3	L	X	66 (11)	68	90 (2)	78		83 (19)	78 (3)
		OR	61–76		82–97			67–104	84–90
	W1	X	53 (10)	58	70 (2)	61		68 (19)	78 (3)
		OR	48–61		68–71			50–87	73–82
	W2	X	49 (10)	50	64 (2)	57		62 (19)	75 (3)
		OR	44–51		59–69			49–75	72–79

Morphology of p4: The tooth is bilophodont and is slightly narrower anteriorly than posteriorly. The transverse lophids are of equal width. The lateral conids have straight, anteriorly extending protocristids that end in the anterior cingulum and on the posterior wall of the protoconid. The low protocristid connecting the hypoconid and protoconid is worn, which suggests that it was a functional ectolophid. A cingulum is present on the anterior, labial, and posterior walls. In the lingual valley, there is a small remnant of the cingulum.

Morphology of m1: The tooth has three transverse lophids of nearly equal width. The protocristids are not as well developed as in p4. A cingulum is present on the anterior, labial, and posterior walls. The labial edge of the anterior cingulum has a distinct wear facet.

Morphology of m2: The tooth is nearly quadratic in occlusal outline and has two transverse lophids of equal width. A cingulum is present on the anterior, labial, and posterior walls. The metalophid has two protocristids that both extend medially and end on the anterior cingulum. Such protocristids are less pronounced on the hypolophid.

Morphology of m3: The tooth narrows posteriorly. The hypolophid is narrower than the metalophid, and the posterior cingulum is posteriorly extended to a small, triangular talonid. The talonid is laterally skewed and has a small, incipient cuspid.

Comparisons (Table 4): All deinotheriid mandibles share the same basic morphology, and it may be assumed that the main differences are in the size of the mandible and teeth. The *Prodeinotherium* mandible from Unterzolling is, in general, larger than the *Prodeinotherium* from Franzensbad (see measurements above), although the teeth and corpus mandibulae are of similar size. This may be an indication of sexual dimorphism, but the size difference may also be due to age variation. The tooth wear shows that the Unterzolling mandible is an older individual than the Franzensbad

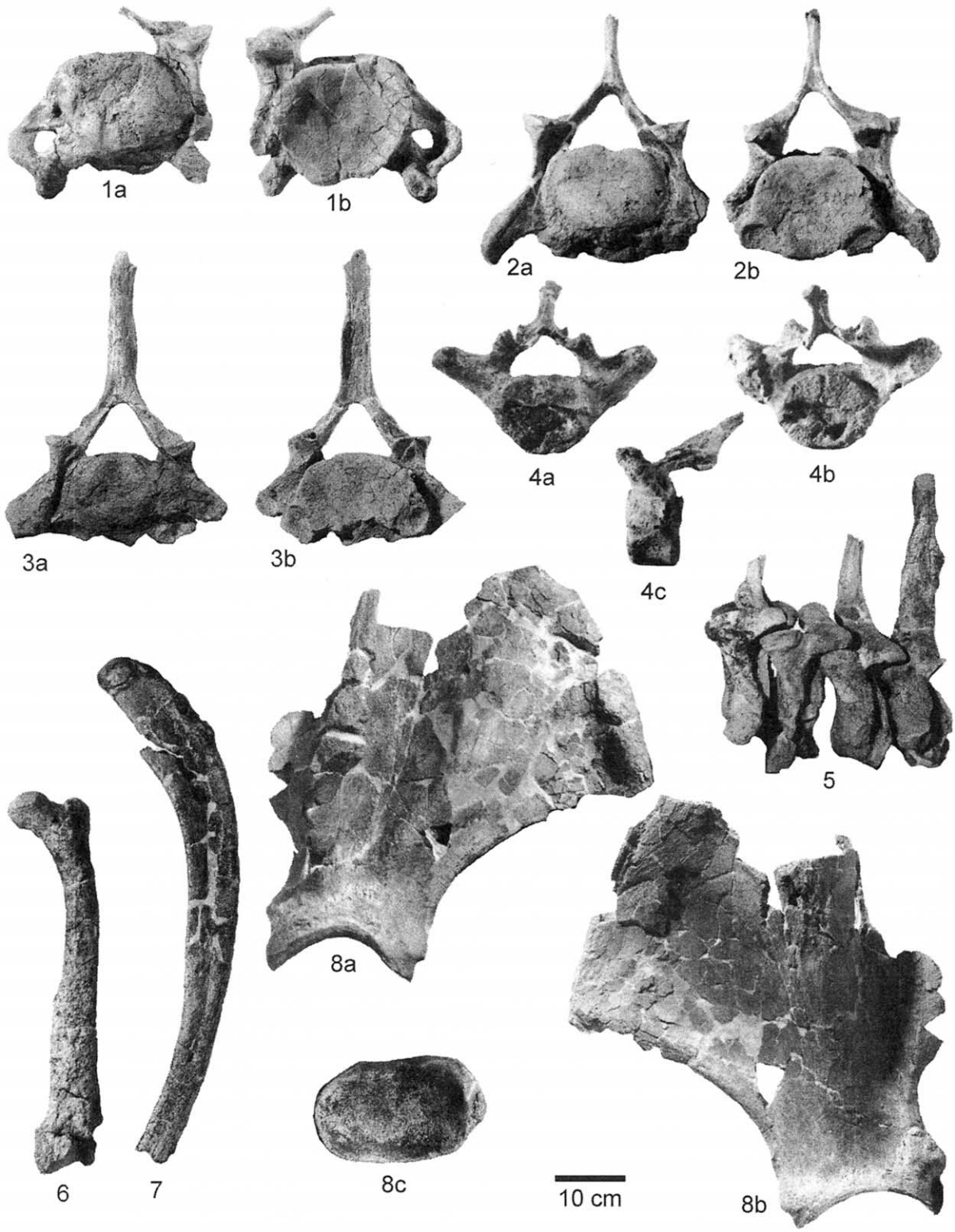

Fig. 4. **1–8.** *Prodeinotherium bavaricum* from Unterzolling (BSP 1977 I 229) (1:8). **1**. Cervical vertebra no. 6: **a**, cranial view; **b**, caudal view. **2**. Cervical vertebra no. 7: **a**, cranial view; **b**, caudal view. **3**. Thoracic vertebra no. 1: **a**, cranial view; **b**, caudal view. **4**. Lumbar vertebra: **a**, cranial view; **b**, caudal view; **c**, lateral view. **5**. Cervical vertebrae no. 5–7 and thoracic vertebra no. 1, lateral view. **6**. Rib 1, cranial view. **7**. Rib 2, cranial view. **8**. Scapula sin.: **a**, lateral view; **b**, medial view; **c**, distal view.

Fig. 4. **1–8.** *Prodeinotherium bavaricum* de Unterzolling (BSP 1977 I 229) (1:8). **1**. Vertèbre cervicale no. 6 : **a**, vue craniale ; **b**, vue caudale. **2**. Vertèbre cervicale no. 7: **a**, vue craniale ; **b**, vue caudale. **3**. Vertèbre thoracique no. 1 : **a**, vue craniale ; **b**, vue caudale. **4**. Vertèbre lombaire : **a**, vue craniale ; **b**, vue caudale ; **c**, vue latérale. **5**. Vertèbres cervicales no. 5–7 et vertèbre thoracique no. 1, vue latérale. **6**. Côte 1, vue craniale. **7**. Côte 2, vue craniale. **8**. Omoplate sin. : **a**, vue latérale ; **b**, vue médiale ; **c**, vue distale.

mandible. The Unterzolling specimen also has a deep muscle attachment on the dorsal ramus mandibulae, which is not present in the Franzensbad mandible.

The tooth size of the Unterzolling specimen is similar to the tooth size ranges of *P. bavaricum* from MN5–MN9 localities of Europe. The Unterzolling teeth are clearly smaller than the *D. giganteum* teeth from Montredon (MN10). As indicated in Table 4, deinotheriid tooth size increases continuously from MN5 to MN10 in Europe. However, identification of *P. bavaricum* teeth based on size is not always straightforward. The measurements from Sansan (supposed *P. bavaricum*) are very large. In addition, the Dinotheriensande localities contain both *Prodeinotherium* and *Deinotherium* material. The estimated size limits for each tooth position was based on relatively small sample sizes, and therefore, the variation within an MN Zone was not analysed. For tooth positions m2 and m3 from Dinotheriensande, no generic size limit could be estimated (detailed comparisons in Huttunen, in press b).

In general, the morphologies of p4–m3 are similar within both the *P. bavaricum* and *D. giganteum* finds. The latest comparative study of Huttunen (in press b) indicates that only the lower p3 morphology can be used for species identification. The p3 morphology of the Unterzolling specimen is typical for *P. bavaricum* present in Europe from the Early to Middle Miocene (from MN5 to MN9). The morphology is also similar to that of the *P. bavaricum* lectotype: not only are the anterior conids separated, but also the posterior conids are connected by a hypolophid. The specimen differs, however, in the hypolophid morphology from the *P. hungaricum* p3 described by Éhik (1930, pl. 1, Figs. 4, 5, 7). *P. hungaricum* p3 has an incomplete transverse ridge between the posterior conids. At the Dinotheriensande localities, the p3 morphology from Unterzolling is typical for the small sized teeth.

Atlas (Fig. 3(2))

The atlas fragment is a part of the arcus ventralis containing the fovea dentis and a remnant of the fovea articularis cranialis sin. The maximum width of the fragment is 170 mm, and length of the arcus ventralis 79 mm. The length of the fovea dentis is 51 mm and width 48 mm. Distal to the fovea dentis, there is a well-pronounced tuberositas ventralis.

Axis

Only the dens that articulates with the fovea dentis of the atlas is preserved. The fragment is a pointed, conoidal structure. The length of the fragment is 81 mm, with a maximum diameter of 66 mm. The articulating facet is convex and rounded in outline, although the facet is not completely preserved.

Cervical vertebrae (*vertebrae cervicales*) (Figs. 3(3) and 4(1, 2, 5); Table 5)

Cervical vertebra no. 5 (Fig. 3(3)): The processus spinosus and circa 20 mm of the processus transversi dext. are broken off. The corpus is craniocaudally compressed. The extremitas caudalis extends more distally than the extremitas cranialis. The arcus vertebrae are delicate. They form a triangular foramen vertebrale and point slightly in caudal direction. The processus articulares craniales and caudales are flat and inclined slightly medially. The edges of the processus transversi are rounded and end above the distal edge of the corpus. The foramina transversaria are long–oval (maximum diameter: 40 mm).

Cervical vertebra no. 6 (Fig. 4(1)): Preserved are the central corpus, processus articulares craniales and caudales sin., and the processus transversus dext. The processus articulares craniales and caudales are slightly inclined in the medial direction. The processus transversus has a round–oval (maximum diameter: 38 mm) foramen transversarium. On the distal edge, there exists a tuberculum ventrale pointing distocaudally. It extends over the distal margin of the corpus. The extremitas caudalis extends more distally than the extremitas cranialis.

Cervical vertebra no. 7 (Fig. 4(2)): The processus spinosus and the processus transversus dext. are broken off. The processus articulares craniales are flat and medially inclined. The processus articularis cranialis dext. is flat. The processus articularis cranialis sin. is extended and bent distally on the cranial edge. The arcus vertebrae are stronger, and the foramen vertebrae is higher than in the previous vertebrae positions. Oval foveae costales caudales are situated at the distal corpus (their maximum width is 53 mm). The surfaces of the processus caudales are nearly flat and medially inclined. The processus transversus and the corpus end distally at the same level. The extremitas caudalis extends more distally than the extremitas cranialis.

Thoracic vertebrae (*vertebrae thoracicae*) (Fig. 4(3); Table 6)

The first thoracic vertebra is completely preserved. The surface of the extremitas cranialis is badly distorted, and the processus transversus sin. is broken off. The extremitas cranialis bears laterodistally two oval and concave foveae costales craniales. The processus transversus dext. is at the level of the distal corpus; its distal edge is occupied by a straight, rounded facet. The processus articulares craniales are smaller than on the cervical vertebrae. They are slightly convex and medially inclined. The foramen vertebrale is triangular, with a vertically pointing processus spinosus. The extremitas caudalis is concave and ends distally in two foveae costales caudales. The processus articulares caudales are flat and strongly inclined in a cranial direction. The processus spinosus is strongly concave on the caudal side. In caudal view, it has a strong, oval canal nutritum on the arcus vertebrae sin.

Three fragments of thoracic vertebrae are available. Two fragments that are of similar size may originate from the caudalmost part of the thoracic spinal column, as their spinae point strongly in a caudal direction (circa 45° to the horizontal). The fragments are characterized by a strong and long processus spinosus that is craniocaudally flattened. There are processus articulares craniales and caudales at the base of the arcus vertebrae. They are nearly vertically

Fig. 5. **1–4.** *Prodeinotherium bavaricum* from Unterzolling (BSP 1977 I 229) (1:8). **1**. Humerus dext., proximal half, cranial view. **2**. Humerus sin., distal 2/3: **a**, caudal view; **b**, medial view; **c**, lateral view, **d**, distal view. **3**. Ulna dext.: **a**, lateral view; **b**, dorsal view; **c**, medial view; **d**, proximal view. **4**. Radius sin.: **a**, medial view; **b**, dorsal view; **c**, lateral view; **d**, proximal view; **e**, distal view.

Fig. 5. **1–4.** *Prodeinotherium bavaricum* de Unterzolling (BSP 1977 I 229) (1:8). **1**. Humérus dext., partie proximale (1/2 de l'os), vue craniale. **2**. Humérus sin., partie distale (2/3 de l'os) : **a**, vue caudale ; **b**, vue médiale ; **c**, vue latérale ; **d**, vue distale. **3**. Cubitus dext.: **a**, vue latérale ; **b**, vue dorsale ; **c**, vue médiale ; **d**, vue proximale. **4**. Radius sin. : **a**, vue médiale ; **b**, vue dorsale ; **c**, vue latérale ; **d**, vue proximale ; **e**, vue distale.

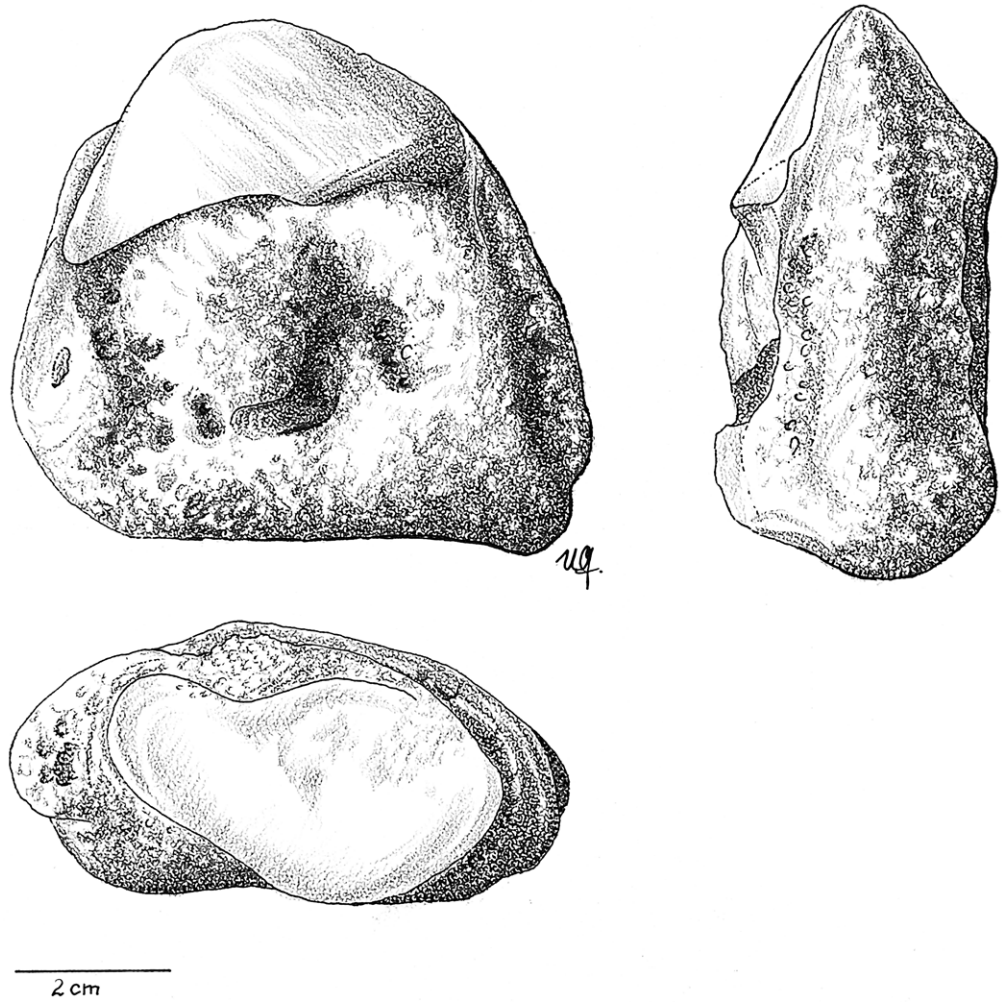

Fig. 6. Trapezium of *Prodeinotherium bavaricum* from Unterzolling: **a**, lateral aspect; **b**, dorsal aspect; **c**, distal aspect.
Fig. 6. Trapèze de *Prodeinotherium bavaricum* de Unterzolling : **a**, vue latérale ; **b**, vue dorsale ; **c**, vue distale.

aligned. The third specimen is a large processus spinosus fragment, the position of which cannot be identified. It is different in that its transverse section is proximally triangular rather than flattened.

Lumbar vertebra (*vertebra lumbalis*) (Fig. 4(4); Table 7)

The lumbar vertebra lacks only the proximal end of the processus spinosus and some caudal and cranial surface of the corpus. The processus costarii are at the level of the foramen vertebrale, and the processus spinosus points strongly caudally. The surface of the extremitas cranialis is flat. Both the processus articulares craniales and processus costarii extend further cranially than the extremitas cranialis. Processus articulares craniales have oval and medially inclined facets, with their longest axis facing craniocaudally. The foramen vertebrale is wider than higher. The processus articulares caudales are at the top of the arcus vertebrae and are oriented laterally. They are situated further caudally than the extremitas caudalis. The facets are oval and flat. The processus spinosus is triangular in transverse section, though slightly concave caudally.

Costae (Fig. 4(6, 7); Table 8)

Because of the fragmentary preservation of the costal remains, the exact position of the specimens cannot be verified. There are six costal fragments, four of them without distal and proximal ends.

Rib 1 (Fig. 4(6)): The fragment bears a complete caput and collum and an articulating facet at the level distal to collum. Distal to the collum, the corpus continues distally in a nearly straight line. In cranial view, a circular facies articularis (maximum diameter: 41 mm) is visible. The corpus continues distally and widens and flattens out. On the caudal side, there is a small depression in the area between the collum and the tuberculum costae. A facet is located on the cranial side at this level. There is also a small tuberculum present. The caput diameter (measured mediolaterally) is 63 mm, the caput–tuberculum costae distance is 116 mm, and the collum width is 42 mm.

Rib 2 (Fig. 4(7)): The bone has a complete caput, no collum, a tuberculum costae, and a craniocaudally flattened corpus. The part from the tuberculum to the middle part of

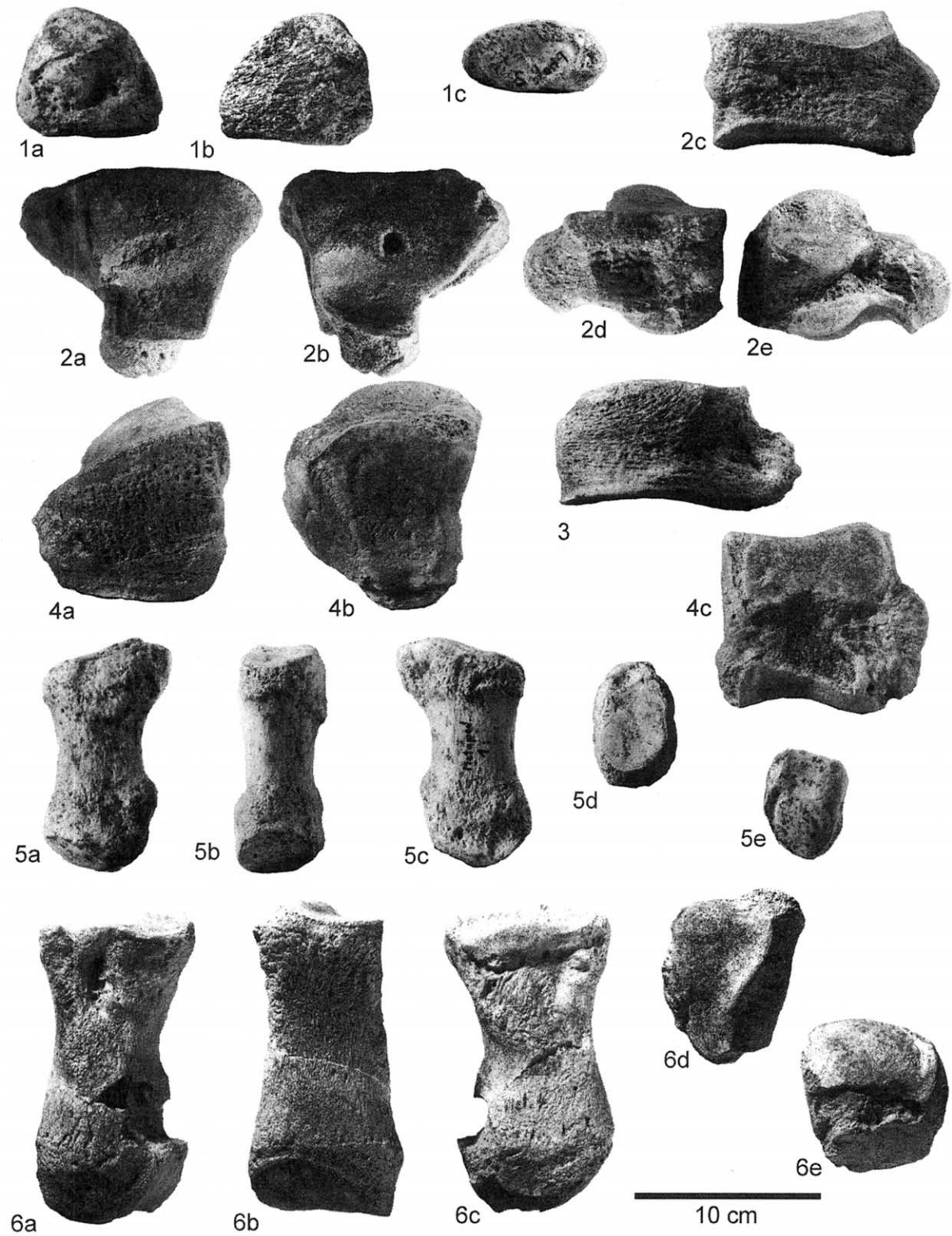

Fig. 7. **1–6.** *Prodeinotherium bavaricum* from Unterzolling (BSP 1977 I 229) (1:3). **1**. Trapezium dext.: **a**, lateral view; **b**, medial view; **c**, distal view. **2**. Lunar sin.: **a**, proximal view; **b**, distal view; **c**, dorsal view; **d**, lateral view; **e**, medial view. **3**. Cuneiform sin., dorsal view. **4**. Unciform dext.: **a**, dorsal view; **b**, distal view; **c**, medial view. **5**. Mc1 dext.: **a**, medial view; **b**, dorsal view; **c**, lateral view; **d**, proximal view; **e**, distal view. **6**. Mc2 dext.: **a**, medial view; **b**, dorsal view; **c**, lateral view; **d**, proximal view; **e**, distal view.

Fig. 7. **1–6.** *Prodeinotherium bavaricum* de Unterzolling (BSP 1977 I 229) (1:3). **1**. Trapèze dext. : **a**, vue latérale ; **b**, vue médiale ; **c**, vue distale. **2**. Lunaire sin. : **a**, vue proximale ; **b**, vue distale ; **c**, vue dorsale ; **d**, vue latérale ; **e**, vue médiale. **3**. Cunéiforme sin., vue dorsal. **4**. Unciforme dext. : **a**, vue dorsale ; **b**, vue distale ; **c**, vue médiale. **5**. Mc1 dext. : **a**, vue médiale ; **b**, vue dorsale ; **c**, vue latérale ; **d**, vue proximale ; **e**, vue distale. **6**. Mc2 dext. : **a**, vue médiale ; **b**, vue dorsale ; **c**, vue latérale ; **d**, vue proximale ; **e**, vue distale.

Table 5
Measurements (mm) of the cervical vertebrae 5–7 of *Prodeinotherium bavaricum* from Unterzolling
Tableau 5
Mensurations (mm) des vertébres cervicales 5–7 de *Prodeinotherium bavaricum* de Unterzolling

	Cervical vertebra no. 5	Cervical vertebra no. 6	Cervical vertebra no. 7
Length of corpus, central	74	64	74
Maximum length at processus articulares	135	126	72
Width at processus articulares craniales	224	*284	227
Width at processus articulares caudales	252	*234	204
Width at processus transversi	333	*314	*352
Height of the extremitas cranialis	157	132	121
Width of the extremitas cranialis	*178	167	163
Height of the extremitas caudalis	135	150	144
Width of the extremitas caudalis	*163	183	171
Minimum width of the vertebra	217	*284	204
Height (fragment)	280	251	352
Length (fragment) of the processus spinosus	67	–	119
Width of the foramen vertebrale	95	–	102
Height of the foramen vertebrale	54	–	87
Width at the foveae costales caudales	–	–	204

the corpus has a dorsal sulcus costae cranially and caudally. The fragment is uniformly curved from the caput to the distal end.

Scapula (Fig. 4(8); Table 9)

The proximal one-third with the angulus cranialis of the scapula sin. is broken off. The maximum height of the fragment is 626 mm, and the maximum length is 530 mm. The spina scapulae is complete only at its base; the acromion and metacromion are not preserved. The scapula is divided by the spina scapulae into circa one-fourth of fossa supraspinata and three-fourth of fossa infraspinata. The fossa infraspinata is concave next to the spina and then convex in a caudal direction. The margo caudalis is concave until the angulus caudalis. The cavitas glenoidalis is oval in outline and concave. In lateral view, the tuberculum supraglenoidale extends distally below the cavitas glenoidalis. There are two tuberosities both on the cranial and caudal sides of the cavity. The medial facies is strongly convex at the level of the spina. Circa the cranial one-third of the facies is flat, while the caudal side is concave.

The scapula dext. is preserved in full length, but the fossa supraspinata, spina scapulae, and angulus caudalis are broken off. The straight margo dorsalis is nearly complete. The scapula dext. allows an estimation of the shape of the proximal part of the bone. The fossa supraspinata is concave proximally.

Comparisons: The *Prodeinotherium* scapulae from Unterzolling are slightly larger at the cavitas glenoidalis than in the fragmentary Franzensbad scapula, while their shapes are very similar.

Harris (1973, 1978, p. 319) has identified a generic difference between *Prodeinotherium* and *Deinotherium* in the form of the meta- and acromion. In addition, Huttunen (in press c) has observed that in the *Deinotherium scapula* from Eserovo (Bulgaria), the spina scapulae seems to be without any acromion and metacromion. This morphologi-

Table 6
Measurements (mm) of the thoracic vertebrae of *Prodeinotherium bavaricum* from Unterzolling
Tableau 6
Mensurations (mm) de la première vertébre thoracique de *Prodeinotherium bavaricum* de Unterzolling

	Thoracic vertebra no. 1	Fragment 1	Fragment 2	Fragment 3
Length of corpus, central	*80	–	–	–
Maximum length at processus articulares	96	–	–	–
Width at processus articulares craniales	179	–	–	–
Width at processus articulares caudales	213	–	–	–
Width at processus transversi	316	–	–	–
Height of the extremitas cranialis	124	–	–	–
Width of the extremitas cranialis	175	–	–	–
Height of the extremitas caudalis	*112	–	–	–
Width of the extremitas caudalis	*150	–	–	–
Minimum width of the vertebra	204	–	–	–
Height	430	486	497	266
Length of the processus spinosus	205	339	322	–
Width of the foramen vertebrale	104	88	*68	–
Height of the foramen vertebrale	67	*83	*66	–
Width at the foveae costales caudales	213	–	–	–
Width at the fovea costales craniales	207	–	–	–

Table 7
Measurements (mm) of the lumbar vertebra of *Prodeinotherium bavaricum* from Unterzolling
Tableau 7
Mensurations (mm) des vertèbres lombaires de *Prodeinotherium bavaricum* de Unterzolling

Length of corpus, central	82
Maximum length from processus articulares craniales to processus articulares caudales	146
Width at processus articulares craniales	131
Width at processus articulares caudales	70
Width at processus costarii (maximum width)	297
Width of the extremitas cranialis	109
Height of the extremitas cranialis	137
Width of the extremitas caudalis	123
Height of the extremitas caudalis	*101
Width of the foramen vertebrale	91
Height of the foramen vertebrale	54
Height	231
Height of the processus spinosus	*109
Angle between processus spinosus and horizontal plane	40°

Table 8
Measurements (mm) of the costae of *Prodeinotherium bavaricum* from Unterzolling
Tableau 8
Mensurations (mm) des côtes de *Prodeinotherium bavaricum* de Unterzolling

	Fragment 1	Fragment 2
Maximum length fragment	531	695
Maximum width	102	100
Minimum width	42	53

Table 9
Measurements (mm) of the scapulae of *Prodeinotherium bavaricum* from Unterzolling
Tableau 9
Mensurations (mm) des omoplates de *Prodeinotherium bavaricum* de Unterzolling

	Sin.	Dext.	Franzensbad
Maximum height at spina scapulae	–	791	*688
Maximum width of the cavitas glenoidalis	134	134	*105
Maximum length of the cavitas glenoidalis	202	199	*165

cal difference in *Deinotherium* in relation to *Prodeinotherium* has been interpreted by Harris (1973, p. 342) as a cursorial modification.

Humerus (Fig. 5(1, 2); Table 10)

The distal two-thirds of the humerus sin. is preserved (Fig. 5(2)). The diaphysis is strongly broadened at the tuberositas deltoidea and at the epicondylus lateralis. The minimum width is approximately in the middle of the shaft. The shaft at the level of the epicondyles is wider than the distal condyle. The tuberositas deltoidea is laterally extended as far as the epicondylus lateralis. The strong crista humeri flattens out distally. The crista epicondylus lateralis continues proximocaudally and flattens out. The epicondylus lateralis is twice as high as the medial one. The distal trochlea is divided by a shallow groove. The condylus medialis is somewhat wider than the lateral one. The caudal fossa radialis is deep and wide.

The humerus dext. is a proximal half of the bone (Fig. 5(1)). The maximum length of the fragment is 692 mm and width is 256 mm. It is deformed both in mediolateral and craniocaudal directions. The proximal caput humeri is almost preserved, while the tuberculum majus, the base of which lies higher than the caput, is broken off. The caput and tuberculum majus are separated by a craniocaudally running depression. In the middle of the cranial side, there is a strong, elongated bulge with distinct concavities on both sides. On the medial surface, there is considerable prominence present, but this could also be due to deformation.

Comparisons: The Unterzolling specimen has somewhat similar proportions to the Franzensbad specimen. Distal to the epicondylus lateralis, the Unterzolling specimen has a much stronger lateral prominence than the Franzensbad humerus. The Franzensbad specimen has a medial extension on the medial epicondyle, which is lacking in the Unterzolling specimen.

Harris (1973, 1978, p. 319) listed the form of the lateral epicondyle as the most important generic character. In *Prodeinotherium*, it tapers proximally, while in *Deinotherium* it does not. This character can be proved in the *Deinotherium* from Eserovo. Further differences are a slightly deeper sulcus musculus brachialis and a wider tuberositas deltoidea in *Prodeinotherium* than in *Deinotherium* (Huttunen, in press c).

Ulna (Fig. 5(3); Table 11)

The ulna sin. is complete, and circa two-thirds of the ulna dext. is preserved.

The tuber olecrani is moderately extended medially. There is a depression on its medial side.

The processus coronoideus medialis is round and approximately twice as large as the half circle-shaped lateral one. The processus anconaeus is relatively short and at a

Table 10
Measurements (mm) of the humerus sin. of *Prodeinotherium bavaricum* from Unterzolling
Tableau 10
Mensurations (mm) de l'humérus de *Prodeinotherium bavaricum* de Unterzolling

	Sin.	Franzensbad
Maximum length	Length of fragment: 699	*790
Minimum width of the diaphysis	132	104
Minimum perimeter of the diaphysis	420	130
Distal width	281	175
Distal depth	168	100
Width of the trochlea	208	–

Table 11
Measurements (mm) of the ulnae of *Prodeinotherium bavaricum* from Unterzolling and Franzensbad
Tableau 11
Mensurations (mm) des cubitus de *Prodeinotherium bavaricum* de Unterzolling et Franzensbad

	Sin.	Dext.	Franzensbad
Maximum length	Fragment:635	*805	*800
Proximal width at processus coronoideus	–	199	130
Proximal depth	–	272	–
Length of the incisura trochlearis	–	115	–
Width at the tuber olecrani	*113	124	–
Minimum depth from processus anconaeus to volar edge of the ulna	212	204	150
Minimum width of the diaphysis	–	97	110
Minimum depth of the diaphysis	–	105	89
Minimum perimeter of the diaphysis	–	330	–
Distal width at caput ulnae	–	*152	–

slightly lower level than the tuber olecrani. Dorsomedially on the processus coronoideus lateralis, a 47 mm wide radial facet (circumferentia articularis radii) is observed. Distal to the facet, there is a strong horizontal groove for a tuberosity on the proximal radius. The processus coronoideus lateralis has no articulating facet to the radius. The cross section of the shaft is triangular, with a flat dorsal surface. The proximal facies cranialis is strongly concave within the incisura radialis ulnae. The margo interosseus begins in the middle of the medial shaft and runs distodorsally until the distal epiphysis. It is the dorsal border of the radius facet on the medial side of the ulna. The distalmost part is badly distorted. The distal facet for cuneiform articulation is broken to a great extent, but the general concavoconvex surface is visible. Medially on the distal epiphysis, a half circle-shaped facet for the radius exists.

Comparisons: The comparisons suggest that the *Prodeinotherium* specimens from Unterzolling and Franzensbad are uniform in morphology, but vary in size. As the observations by Huttunen (in press c) show, the incisura radialis and the incisura trochlearis on the *Prodeinotherium* ulna are deeper than in *Deinotherium* from Eserovo. An additional character of the *Deinotherium* ulna from Eserovo is that the distal third of the bone is mediolaterally flattened compared to the proximal part.

Radius (Fig. 5(4); Table 12)

The radius sin. is complete, with only the distal end damaged. The radius dext. is a fragment containing the proximal end and the lateral side of the shaft.

The radius shaft is both bent convex mediodorsally and twisted proximodistally. The shape of the caput radii is triangular. The proximal facet is convex along a dorsovolar axis. The lateral side is concave and occupies circa two-thirds of the surface, while the medial one-third slopes laterally. There is a laterovolar half circle-shaped facet (circumferentia articularis), but no lateromedial facet, for volar articulation with the ulna. Medially, the proximal end has a prominent vertical bulge. The proximal end of the corpus has a triangular transversal section. Distally, it becomes mediolaterally flattened. At the level where the radius shaft is in contact with the ulna, the transversal section becomes strong. The crista interossea runs proximodistally along the volar side of the bone. In the distal third of the element, it splits up into two cristae to form a triangular incisura ulnaris radii. On the dorsal side, a crista runs laterally from proximal to distal. The distal facies articularis carpea is piriform. Its surface is both concave dorsally and convex volarly. Its convex part turns up in a volar direction.

A remarkable physical injury is present on the medial side of the distal end, where two deep and rounded holes are

Table 12
Measurements (mm) of the radii of *Prodeinotherium bavaricum* from Unterzolling
Tableau 12
Mensurations (mm) des radius de *Prodeinotherium bavaricum* de Unterzolling

	Sin.	Dext.	Franzensbad
Maximum length	726	Fragment: 627	695
Physiological length of the radius	694	–	–
Proximal width at caput radii	108	*96	89
Proximal depth at caput radii	80	*76	70
Width of the fovea capitis radii	94	*82	–
Depth of the fovea capitis radii	65	66	–
Minimum width of the diaphysis	56	–	–
Minimum depth of the diaphysis	78	–	–
Minimum perimeter of the diaphysis	200	–	–
Distal width	*105	–	230
Distal depth	156	–	–
Width of the facies articularis carpea	*99	–	–

Table 13
Measurements (mm) of the lunar sin. of *Prodeinotherium bavaricum* from Unterzolling
Tableau 13
Mensurations (mm) du lunaire sin. de *Prodeinotherium bavaricum* de Unterzolling

Maximum height	79
Maximum depth	117
Maximum width	130
Width of the facies articularis proximalis for radius	101
Depth of the facies articularis proximalis for radius	97
Height of the proximal facies articularis lateralis	52
Depth of the proximal facies articularis lateralis	63
Height of the distal facies articularis lateralis	18
Depth of the distal facies articularis lateralis	74
Height of the proximal facies articularis medialis	21
Depth of the proximal facies articularis medialis	67
Height of the distal facies articularis medialis	18
Depth of the distal facies articularis medialis	41
Width of the facies articularis distalis	111
Depth of the facies articularis distalis	92

present (distance between the holes: 20 mm, diameter: 10 mm, depth: 10–15 mm). These holes and the other damages on the surface of the distal end suggest that they may be biting traces caused by a carnivore (or a crocodile). It is not possible to conclude whether the injury occurred before or after the death of the animal.

Comparisons: The Franzensbad radius has a much larger distal epiphysis than the Unterzolling specimen. The Franzensbad radius is from a young individual. It is not clear if the large size of the distal end is due to individual variation, pathological reasons, or specific diagnostic characters. The *Deinotherium* radius from Eserovo shows that there is no distinct triangular–round neck distal to the caput radii as in *Prodeinotherium*, but the entire radius is nearly straight and mediolaterally flattened. The radius from Eserovo seems to be less curved mediodorsally, and its distal end seems to be wider in relation to the distal ulna (Huttunen, in press c).

Lunar (*os carpi intermedium*) (Fig. 7(2); Table 13)

The lunar sin. is complete. Its shape is triangular. The proximal facet is convex along a mediolateral axis on its dorsal half and concave on its volar half. In dorsal view, the proximal facet is flat medially and elevated in a lateral direction. Lateral to the proximal facet, there exists a triangular and concave proximolateral facet for the radius. The distal facet is triangular and convex dorsally and strongly concave volarly. The lateral side has one distal facet for cuneiform articulation. The medial side has two facets of unequal length, where the proximal facet is longer than the distal one. The proximal facet has an equal width in a dorsovolar direction. The distal facet is high in the dorsal end and flattens out before the volar tuberosity. Like the distal radius described above, the lunar also shows some biting traces. The most distinct trace is a round hole (about 10 mm in diameter and depth) in the middle of the distal facet. There is also another possible biting trace on the lateral edge of the distal facet. The laterodorsal edge of the distal facet, the middle of the proximal facies, and the mediodorsal edge of the facies articularis lateralis bear shallow biting traces, probably caused by small rodents.

Table 14
Measurements (mm) of the trapezium dext. of *Prodeinotherium bavaricum* from Unterzolling
Tableau 14
Mensurations (mm) du trapèze dext. de *Prodeinotherium bavaricum* de Unterzolling

Maximum height	72
Maximum width	81
Depth of the medioproximal facet for trapezoideum	61
Height of the medioproximal facet for trapezoideum	37
Width of the distal facet for Mc1	33
Depth of the distal facet for Mc1	61

Cuneiform (*os carpi ulnare*) (Fig. 7(3))

The cuneiform sin. is a fragment of the dorsal and laterodorsal side. The lateral process is broken off. The maximum width of the fragment is 129 mm. The height of the fragment is 65 mm. The proximal facet (dorsal edge) is medially convex and laterally concave. The distal facet is concave. It continues laterally and forms a facies articularis lateralis for articulation with the proximolateral Mc5. On the dorsolateral edge, medial to the lateral process, there is a distinct depression present. Both on the proximal and distal surface, there are parallel traces that have been caused by small rodent's incisors.

Trapezium (*os carpi primum*) (Figs. 6 and 7(1); Table 14)

The trapezium dext. is rounded triangular in medial view. It is mediolaterally flattened. On the proximal edge of the medial side, there is a triangular, slightly convex, and oblique facet for articulation with the trapezoideum. The volar margin of the facet bends volarly for articulation with the scaphoid (maximum width: about 6 mm, maximum height: about 25 mm). The dorsodistal margin of the facet bends vertically for articulation with the Mc2 (maximum depth: about 20 mm, maximum height: 13 mm). The distal articulating facet is flat and elongated piriform. On the lateral side exist a deep depression and a tuberosity in the middle of the element.

Unciform (*os carpi quartum*) (Fig. 7(4); Table 15)

The unciform dext. is complete and triangular in outline. The bone flattens out laterally. The medial side is flat, while the other sides are rounded. The proximal facet is triangular and concave. It slopes laterally where it articulates with the lateral process of the cuneiform. The distal side has one triangular concave facet for Mc4. The Mc3 facet is elongated, concave, and situated along the distal edge of the medial side. The Mc5 facet is situated on the lateral side of the distal facet, and it is slightly convex. The size of the distal facets is in decreasing order Mc4 > Mc5 > Mc3. On the volar side, there is a large tuberositas present. Medially, there is one proximal, elongated facet for the magnum, and it occupies the proximal half of the medial side. There are small parallel rodent biting traces in the middle of the proximal facet and between the distal Mc4 and Mc5 facets.

Table 15
Measurements (mm) of the unciform of *Prodeinotherium bavaricum* from Unterzolling
Tableau 15
Mensurations (mm) de l'unciforme de *Prodeinotherium bavaricum* de Unterzolling

	Dext.	Franzensbad
Maximum height	97	80
Dorsal height	91	–
Maximum width	100	98
Maximum depth	113	111
Diagonal depth	107	–
Width of the facies articularis proximalis	91	121
Depth of the facies articularis proximalis	90	–
Height of the facies articularis medialis	43	–
Depth of the facies articularis medialis	78	–
Width of the lateral facies articularis distalis for Mc5	49	58
Depth of the lateral facies articularis distalis for Mc5	72	74
Width of the medial facies articularis distalis for Mc3	30	66
Depth of the medial facies articularis distalis for Mc3	74	–
Width of the facies articularis distalis for Mc4	63	–
Depth of the facies articularis distalis for Mc4	88	–

Table 16
Measurements (mm) of the Mc1 dext. of *Prodeinotherium bavaricum* from Unterzolling
Tableau 16
Mensurations (mm) du Mc1 dext. de *Prodeinotherium bavaricum* de Unterzolling

Maximum length	128
Proximal depth	68
Proximal width	47
Width of the facies articularis proximalis	38
Depth of the facies articularis proximalis	56
Minimum width of the diaphysis	35
Minimum depth of the diaphysis	47
Minimum perimeter of the diaphysis	132
Distal width (of the trochlea)	44
Distal depth (of the trochlea)	64

Comparisons: The Unterzolling specimen is larger than the Franzensbad specimen. Tobien (1962) stated, based on the Höwenegg (Germany) material, that the size of the distal articulation facets in *Deinotherium* is in the decreasing order Mc4 > Mc3 > Mc5. This differs from the *Prodeinotherium* condition described here, where the order is Mc4 > Mc5 > Mc3 and the Mc3 articulation is on the medial side, not on the distal. Harris (1978) considered the Mc5 facet largest for the African *P. hobleyi*, and for *Deinotherium* the Mc4 as largest.

Os metacarpale primum (*Mc1*) (Fig. 7(5); Table 16)

The Mc1 dext. is complete. Mc1 is the shortest metacarpal bone. The dorsal view shows that the element is slender on the corpus, while the distal trochlea and the proximal base are wider. Proximally, there is an oval trapezoid facet that is flat and slopes strongly dorsally. In volar view, the proximal end has an oval protuberance. Distomedially on the shaft, there is a large tuber. The distal trochlea is dorsovolarly convex. It has dorsally and volarly oval facets for the phalanx and a single sesamoid articulation, respectively.

Comparisons: Harris (1973) discussed the manus and pes morphology of *Prodeinotherium* in connection with the description of *P. hobleyi* from Africa. The above documentation of the Mc1 of the European *P. bavaricum* confirms that the first metapodials were functional and not as reduced as the Mc1 and Mt1 in *Deinotherium* (as described by Tobien, 1962).

Os metacarpale secundum (*Mc2*) (Fig. 7(6); Table 17)

Both Mc2 sin. and dext. are nearly complete. It is the second longest of the metacarpal bones. The proximal surface of Mc2 has two facets, the medial one for the trapezoid and the lateral one for the magnum. The proximal medial facet is triangular. It is medially flat and elevated in a lateral direction, where it ends at the edge of the proximal lateral facet. The proximal lateral facet is elongated dorsovolarly and forms a 90° angle to the medial one by sloping

Table 17
Measurements (mm) of the Mc2–Mc3 of *Prodeinotherium bavaricum* from Unterzolling
Tableau 17
Mensurations (mm) des Mc2–3 de *Prodeinotherium bavaricum* de Unterzolling

	Mc2sin.	Mc2dext.	Mc3sin.	Mc3dext.
Maximum length	174	175	190	189
Proximal depth	88	97	74	96
Proximal width	68	71	74	77
Width of the medial facies articularis proximalis	57	55	57	52
Depth of the medial facies articularis proximalis	85	86	92	93
Width of the lateral facies articularis proximalis	30	31	30	23
Depth of the lateral facies articularis proximalis	*74	82	86	80
Length of the facies articularis lateralis	25	16	29	26
Depth of the facies articularis lateralis	*56	68	64	65
Length of the facies articularis medialis	13	13	32	27
Depth of the facies articularis medialis	26	27	75	63
Minimum width of the diaphysis	60	62	57	62
Minimum depth of the diaphysis	62	60	58	58
Minimum perimeter of the diaphysis	201	203	206	205
Distal width	81	82	84	84
Distal depth (of the trochlea)	*84	89	87	87
Width of the trochlea	74	74	71	71

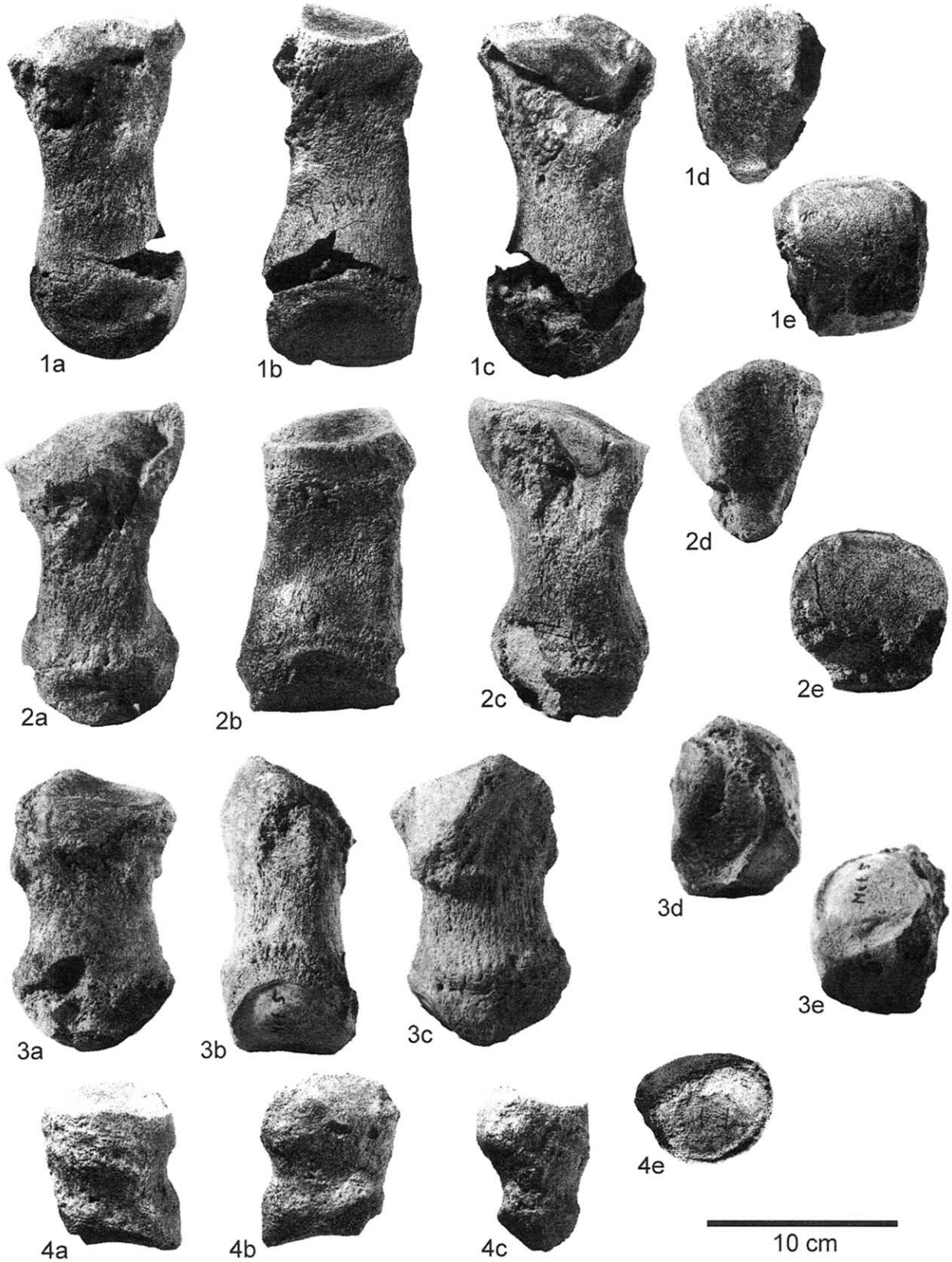

Fig. 8. **1–4**. *Prodeinotherium bavaricum* from Unterzolling (BSP 1977 I 229) (1:3). **1**. Mc3 dext.: **a**, medial view; **b**, dorsal view; **c**, lateral view; **d**, proximal view; **e**, distal view. **2**. Mc4 dext.: **a**, medial view; **b**, dorsal view; **c**, lateral view; **d**, proximal view; **e**, distal view. **3**. Mc5 dext.: **a**, medial view; **b**, dorsal view; **c**, lateral view; **d**, proximal view; **e**, distal view. **4**. Phalanx proximalis ?2 sin.: **a**, dorsal view; **b**, volar view; **c**, lateral view; **d**, proximal view.
Fig. 8. **1–4**. *Prodeinotherium bavaricum* de Unterzolling (BSP 1977 I 229) (1:3). **1**. Mc3 dext.: **a**, vue médiale; **b**, vue dorsale; **c**, vue latérale; **d**, vue proximale; **e**, vue distale. **2**. Mc4 dext.: **a**, vue médiale; **b**, vue dorsale; **c**, vue latérale; **d**, vue proximale; **e**, vue distale. **3**. Mc5 dext.: **a**, vue médiale; **b**, vue dorsale; **c**, vue latérale; **d**, vue proximale; **e**, vue distale. **4**. Phalange proximale ?2 sin.: **a**, vue dorsale; **b**, vue volaire; **c**, vue latérale; **d**, vue proximale.

laterally. On the lateral side, there is a proximal facet for Mc3. It is elongated, while the medial one for os carpi primum is minute (depth: 10 mm). Proximally, on the medial side of the corpus, there is a deep proximodistal tendon groove distovolar to the os carpi primum facet. On the medial side of the distal end, there is a stronger tendon protuberance than on the lateral side. In dorsal view, the phalanx facet of the distal trochlea is asymmetrical and slopes laterally. On the volar side of the trochlea, there are two symmetrical sesamoid facets side by side.

Os metacarpale tertium (*Mc3*) (Fig. 8(1))

The Mc3 sin. and Mc3 dext. are nearly complete. The Mc3 is the largest metacarpal. In dorsal view, the bone widens out distally. In proximal view, the proximal surface shows three facets. The largest facet for magnum articulation is situated in the middle of the surface and is triangular. It is convex in dorsovolar direction and declines medially. The facet is bordered on the lateral side by the second largest facet, the laterally declining and elongated unciform facet. The magnum facet is bordered medially by the smallest, medially declining Mc2 facet. Distal to the unciform facet, on the lateral side of the proximal end, there is a facet for Mc4 that inclines inward. On the lateral side of the proximal end, there is a distinct groove behind the unciform facet and Mc4 facet. The groove splits and runs in distal and dorsal directions. In dorsal view, the trochlea inclines medially. The dorsal phalanx articulation is symmetrical and nearly oval shaped. On the volar side of the trochlea, there are two symmetrical sesamoid facets side by side.

Os metacarpale quartum (*Mc4*) (Fig. 8(2); Table 18)

The Mc4 dext. is almost complete. Only the distal trochlea is damaged volarly. Mc4 is the third longest of the metacarpal bones. In dorsal view, the bone widens slightly distally. There are two facets in proximal view. The larger, lateral facet is triangular and convex in a dorsovolar direction. The dorsal and volar margins are slightly concave. On the proximal medial side, there is a smaller facet for Mc3 articulation. The flat facet is elongated along the medial edge (the volar end of the facet is broken). On the lateral side of the proximal end, there is a small, flat Mc5 facet that has the shape of a half circle. On the trochlea, the facet for the phalanx declines laterally, and its outline is symmetrical.

Table 18
Measurements (mm) of the Mc4 dext. of *Prodeinotherium bavaricum* from Unterzolling
Tableau 18
Mensurations (mm) du Mc4 dext. de *Prodeinotherium bavaricum* de Unterzolling

Maximum length	172
Proximal depth	98
Proximal width	82
Width of the facies articularis proximalis for C4	70
Depth of the medial facies articularis proximalis for C4	94
Length of the facies articularis lateralis for Mc5	34
Depth of the facies articularis lateralis for Mc5	42
Length of the facies articularis medialis for Mc3	45
Depth of the facies articularis medialis for Mc3	48
Minimum width of the diaphysis	72
Minimum depth of the diaphysis	57
Minimum perimeter of the diaphysis	227
Distal width	91
Distal depth (of the trochlea)	86
Width of the trochlea	78

Table 19
Measurements (mm) of the Mc5 dext. of *Prodeinotherium bavaricum* from Unterzolling
Tableau 19
Mensurations (mm) du Mc5 dext. de *Prodeinotherium bavaricum* de Unterzolling

Maximum length	155
Proximal depth	89
Proximal width	68
Width of the facies articularis proximalis	55
Depth of the facies articularis proximalis	72
Width of the lateral facies articularis proximalis	38
Depth of the lateral facies articularis proximalis	55
Length of the facies articularis lateralis for Mc4	28
Depth of the facies articularis lateralis for Mc4	55
Minimum width of the diaphysis	55
Minimum depth of the diaphysis	68
Minimum perimeter of the diaphysis	198
Distal width	70
Distal depth (of the trochlea)	88
Width of the trochlea	65

Os metacarpale quintum (*Mc5*) (Fig. 8(3); Table 19)

The Mc5 is almost complete. It is the second shortest metacarpal bone. It is somewhat mediolaterally compressed. There are large protuberances on the volar and dorsal sides of the proximal end. In proximal view, there are three articulating facets in different planes. The proximal unciform facet is rounded triangular and slightly concave. In dorsal view, it declines strongly in a medial direction, so that the lateral edge of proximal end is much higher than the medial. Lateral to the unciform facet is a cuneiform facet that is triangular, flat, and slopes strongly laterally. The cuneiform facet serves as the facet for the lateral process of the cuneiform. Medial to the unciform facet, there is a small, triangular facet for Mc4 articulation. The distal trochlea has an oval phalanx articulation dorsally and two symmetrical sesamoid facets volarly.

Phalanx proximalis (Fig. 8(4); Table 20)

Table 20
Measurements (mm) of the phalanx proximalis ?2 sin. of *Prodeinotherium bavaricum* from Unterzolling
Tableau 20
Mensurations (mm) de la phalange proximale ?2 sin. de *Prodeinotherium bavaricum* de Unterzolling

Maximum length	92
Proximal width	74
Proximal depth	61
Width of the fovea articularis	65
Depth of the fovea articularis	52
Minimum depth of the diaphysis	44
Distal width	66
Distal depth	44
Width of the facies articularis distalis	64
Depth of the facies articularis distalis	36

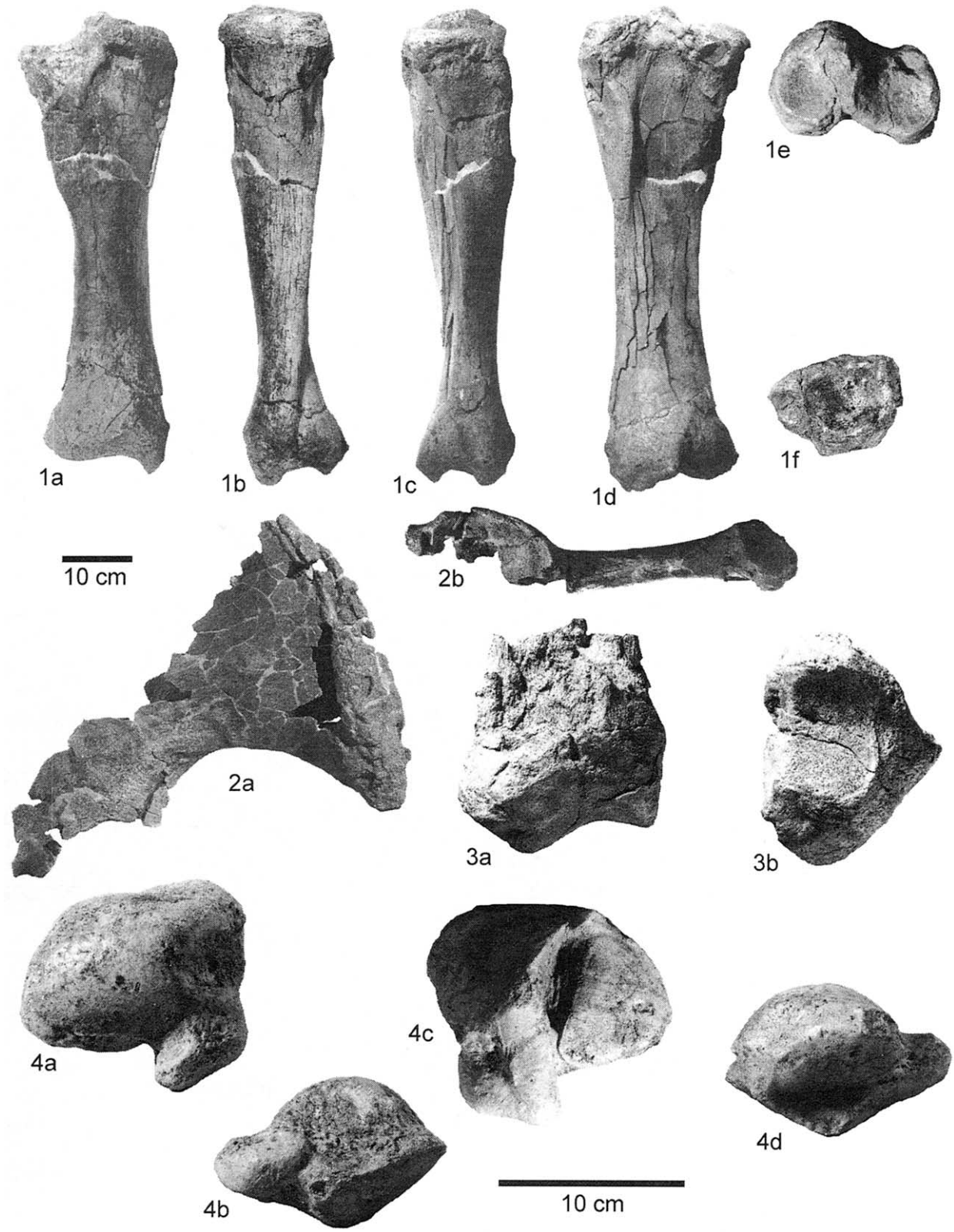

Fig. 9. **1–4.** *Prodeinotherium bavaricum* from Unterzolling (BSP 1977 I 229) (1:8). **1**. Tibia dext.: **a**, dorsal view; **b**, medial view; **c**, lateral view; **d**, plantar view; **e**, proximal view; **f**, distal view. **2**. Pelvis dext.: **a**, dorsal view; **b**, caudal view. **3**. Fibula dext.: **a**, medial view; **b**, distal view. **4**. Astragalus sin. (1:3): **a**, proximal view; **b**, distal view; **c**, medial view; **d**, lateral view.

Fig. 9. **1–4.** *Prodeinotherium bavaricum* de Unterzolling (BSP 1977 I 229) (1:8). **1**. Tibia dext. : **a**, vue dorsale ; **b**, vue médiale ; **c**, vue latérale ; **d**, vue plantaire ; **e**, vue proximale ; **f**, vue distale. **2**. Pelvis dext. : **a**, vue dorsale ; **b**, vue caudale. **3**. Péroné dext. : **a**, vue médiale ; **b**, vue distale. **4**. Astragale sin. (1:3) : **a**, vue proximale ; **b**, vue distale ; **c**, vue médiale ; **d**, vue latérale.

Phalanx proximalis ?2 sin.: The specimen is complete. In dorsal view, the shape is trapezoid. The proximal fovea articularis is oval and slightly concave along a mediolateral axis. On the medial side of the proximal end, there is a strong tendon tuberculum. The distal trochlea is medially inclined. The asymmetric outline and the size of the element suggest that it is belongs either to Mc2 sin., Mc4 dext., or Mc5 dext. However, the fovea articularis is too large for Mc5 dext. Additionally, the articulation with Mc4 dext. did not fit well. The articulation, size, asymmetric shape, and similar preservation suggest that the phalanx most likely belongs to Mc2 sin.

Ossa pelvis (Fig. 9(2))

A fragment of the os ilium dext. with the lateral half of the ala, including tuber coxae and the dorsal half of the corpus and acetabulum, is preserved. The maximum width of the fragment is 580 mm. The estimated width of the acetabulum is about 180 mm. The ala is flat. The distance between the lateral edge of the acetabulum and the tuber coxae is 370 mm. The crista iliaca is thickened. The corpus is flat up to the acetabulum.

Femur

The femur dext. is a fragment of the distal condyles. The medial half is better preserved than the lateral one. The articulating condyles extend farther proximally on the caudal side than on the cranial side of the trochlea. The medial condyle is 1.5 times wider than the lateral one. The maximum width of the fragment is 248 mm; the maximum width of the articulating condyles is 191 mm.

Tibia (Fig. 9(1); Table 21)

The tibia dext. is complete. The proximal and distal ends are larger than the shaft. The medial facies articularis proximalis is larger and higher in relation to the smaller lateral facet. The dorsal side of the lateral facet is abraded. In proximal view, the dorsal notch between the condylus lateralis and medialis is situated somewhat lateral to the eminentia intercondylaris. The tuberositas tibiae is situated dorsolaterally and extends over the proximal third of the shaft. On the plantar side of the condylus lateralis is a fibula facet. It is rounded (diameter: 37 mm) and slightly concave. The plantar side of the corpus is bordered by the lateral and medial margins. The vertical margo lateralis begins lateral to the fibula facet and terminates distally on the plantolateral side. The margo medialis runs proximodistally from the plantar condylus medialis to the distomedial end. Its proximal third is strong and protruding. The plantar side is concave up to the distal third, where it becomes convex. Distally on the plantarmedial side is a 150 mm long sulcus malleolaris that runs parallel to the medial margin. The distal cochlea tibiae is quadrate and concave. Its medial edge is strongly concave, with a vertical inner wall. In medial view, the distal end has a distinct notch for the medioplantar process of the astragalus. Lateral to the astragalus facet exists an elongated fibula facet. It inclines proximally. The plantar side of the distal edge is abraded, so that the border between the astragalus and fibula facets is not clearly preserved.

Table 21
Measurements (mm) of the tibia dext. of *Prodeinotherium bavaricum* from Unterzolling
Tableau 21
Mensurations (mm) du tibia dext. de *Prodeinotherium bavaricum* de Unterzolling

Maximum length	701
Physiological length	680
Medial length	621
Proximal width	240
Proximal depth	157
Width of the medial facies articularis proximalis	119
Depth of the medial facies articularis proximalis	132
Width of the lateral facies articularis proximalis	*93
Depth of the lateral facies articularis proximalis	*96
Width of the facies articulares proximales	236
Minimum width of the diaphysis	*115
Minimum depth of the diaphysis	*79
Minimum perimeter of the diaphysis	330
Distal width	144
Distal depth	190
Width of the cochlea tibiae for astragalus	111
Depth of the cochlea tibiae for astragalus	107
Width of the incisura fibularis for the distal end of the fibula	49
Depth of the incisura fibularis for the distal end of the fibula	54

Fibula (Fig. 9(3))

Both fibula sin. and dext. distal epiphyses fragments are preserved. The larger fibula fragment (dext.) has the maximum height of 138 mm. Its distal depth is 126 mm and distal width is 105 mm. The lateral side has a very strongly pronounced tuberosity. The distal facies (sin. depth 80 and width 78 mm, dext. depth 83 mm and width 68 mm) are divided into two facets, the lateral one for the calcaneus being larger than the medial astragalus facet. The calcaneus facet is rounded rectangular and concave along a mediolateral axis. The astragalus facet is elongated and mediodistally oriented. Medially in the dorsal half and above the astragalus facet, there is an oval convex facet (width 50 mm) for articulation with the tibia.

Calcaneus (*os tarsi fibulare*) (Figs. 10 and 12(1); Table 22)

The calcaneus dext. is a complete specimen with a broken plantar edge. The calcaneus sin. is a fragment of the tuber calcanei and a part of the lateral astragalus facet (length of fragment: 161 mm). The tuber calcanei is, in plantar view, higher than wide. Proximally, there are three facets. The lateral one (A) is a dorsoplantarly convex, rectangular facet for distal fibula articulation. The two astragalus facets are separated by a deep sulcus calcanei. It widens out in a dorsal direction. The larger lateral facet (B) is rounded triangular. The smaller medial facet (B") is on the sustentaculum tali. Its dorsal edge is broken off. On the medial side of the dorsal base of the calcaneus (dorsal to the sustentaculum tali), there is a small rounded navicular facet (C). There is another, very small navicular facet on the proximal side of the dorsal base (C"). The distodorsal side of the bone has a large facies articularis. It is slightly concave, and its outline is piriform. The distoplantar side of the calcaneus bears a large tuberosity.

Table 22
Measurements (mm) of the calcaneus dext. of *Prodeinotherium bavaricum* from Unterzolling
Tableau 22
Mensurations (mm) du calcanéum dext. de *Prodeinotherium bavaricum* de Unterzolling

Maximum height	118
Maximum depth	206
Maximum width	158
Height of the tuber calcanei	106
Width of the tuber calcanei	92
Depth of the facies articularis proximalis for the fibula	76
Width of the facies articularis proximalis for the fibula	56
Depth of the lateral facies articularis talaris	72
Width of the lateral facies articularis talaris	71
Depth of the medial facies articularis talaris	–
Width of the lateral facies articularis talaris	35
Height of the medial facies articularis dorsalis	56
Width of the medial facies articularis dorsalis	89
Height of the lateral facies articularis dorsalis	26
Width of the lateral facies articularis dorsalis	25
Minimum distance between tuber calcanei and facies articularis proximalis for fibula	62

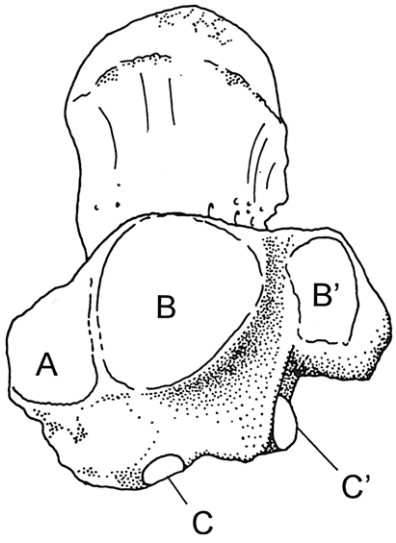

Fig. 10. Calcaneus of *Prodeinotherium bavaricum* from Unterzolling. Proximal aspect. Facet for fibula (A), for astragalus (B + B"), and for navicular (C + C").
Fig. 10. Calcanéum de *Prodeinotherium bavaricum* de Unterzolling. Vue proximale. Facette péronière (A), facette astragalienne (B + B"), facette scaphoïdienne (C + C").

Comparisons: The calcaneus of the Franzensbad skeleton is not available for comparison because it is within the tarsal bones in the mounted skeleton.

Astragalus (*os tarsi tibiale*, *talus*) (Fig. 9(4); Table 23)

Astragalus sin. and dext. are complete. The astragalus dext. is damaged on the plantar side. On the medioplantar angle of the bone, there is a very strong, protruding tuberculum. The proximal trochlea tali for tibia articulation is trapezoidal and strongly convex from dorsal to plantar. In the medioplantar angle, the proximal facet extends above the tuberculum and becomes concave. The plantarmedial tuberculum fits exactly into the plantarmedial notch of the distal end of the tibia. Next to the proximal facet, there is a

Table 23
Measurements (mm) of the astragalus of *Prodeinotherium bavaricum* from Unterzolling
Tableau 23
Mensurations (mm) de l'astragale de *Prodeinotherium bavaricum* de Unterzolling

	Sin.	Dext.
Maximum height	86	84
Maximum width	132	131
Maximum depth	131	134
Width of the facies articularis proximalis	125	129
Medial depth of the facies articularis proximalis including the facet on tuberculum medialis	106	100
Lateral depth of the facies articularis proximalis	93	*99
Width at facies articularis calcanea	107	108
Width of the medial facies articularis calcanea	28	32
Depth of the medial facies articularis calcanea	66	68
Width of the lateral facies articularis calcanea	77	75
Depth of the lateral facies articularis calcanea	68	60
Width of the facies articularis distalis	101	*89
Depth of the facies articularis distalis	73	79
Depth of the facies articularis lateralis for fibula	68	–
Height of the facies articularis lateralis for fibula	31	–

lateral elongated facet for distal fibula articulation. On the distoplantar side are two facies articulares calcaneae, separated by a deep sulcus. The sulcus widens and deepens in a dorsal direction and contains a large vascular foramen. The lateral facies articularis calcanea is large, triangular, and flat, while the medial side is rectangular, elongated, and slightly concave. The medial facet is placed more distally in relation to the lateral facet. The medial facet is connected distally to the navicular facet. The navicular facet is large, convex, and triangular. The astragalus dext. has a depression on the lateral calcaneus facet, a possible fossa synovialis.

Comparisons: Tobien (1962, p. 234) recognized an important deinotheriid feature that is different from the other Proboscidea: in Deinotheriidae, the navicular facet is situated more on the distal side, so that all three distal facets are visible in distal view. Harris (1973, p. 295) stated that the diagnostic features of the *Prodeinotherium* astragalus are the rectangular and convex tibial facet and a prominent plantarmedial process. These features can be confirmed here. The astragalus morphology suggests that the deinotheres had a different tarsus construction, with steeper position of the metatarsals. In comparison to the Franzensbad specimen, the astragalus from Unterzolling has a much stronger plantarmedial process.

Navicular (*os tarsi centrale*) (Figs. 11 and 12(2); Table 24)

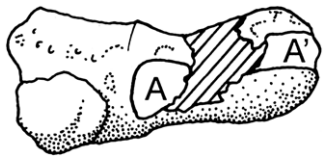

Fig. 11. Navicular dext. of *Prodeinotherium bavaricum* from Unterzolling. Plantar aspect. Facet for calcaneus (A + A").
Fig. 11. Naviculaire dext. de *Prodeinotherium bavaricum* de Unterzolling. Vue plantaire. Facette calcanéenne (A + A").

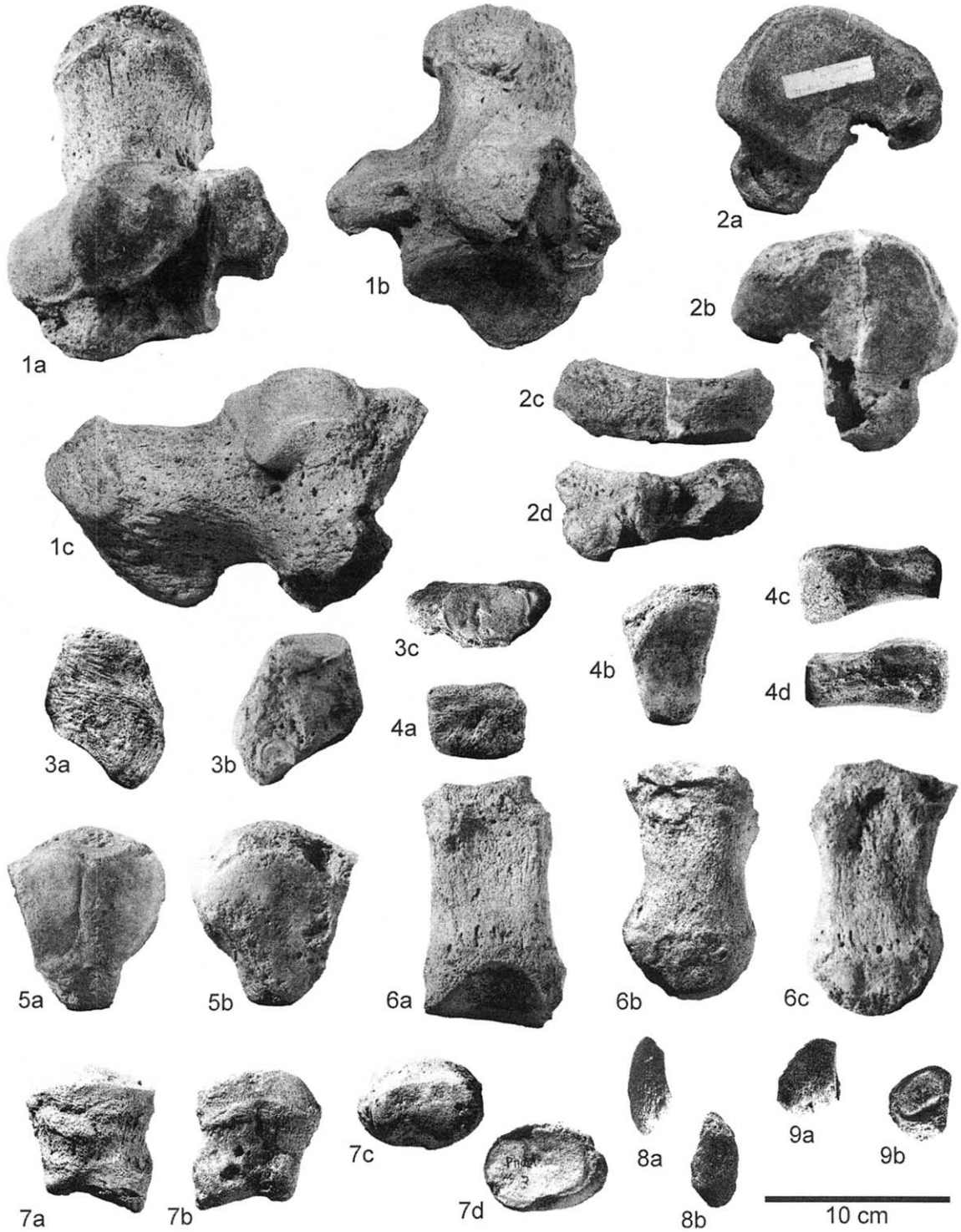

Fig. 12. **1–9.** *Prodeinotherium bavaricum* from Unterzolling (BSP 1977 I 229) (1:3). **1**. Calcaneus dext.: **a**, proximal view; **b**, distal view; **c**, lateral view. **2**. Navicular sin.: **a**, proximal view; **b**, distal view; **c**, dorsal view; **d**, plantar view. **3**. Endocuneiform sin.: **a**, medial view; **b**, lateral view; **c**, distal view. **4**. Mesocuneiform dext.: **a**, dorsal view; **b**, proximal view; **c**, medial view; **d**, lateral view. **5**. Cuboid sin. (medial side broken off): **a**, distal view; **b**, proximal view. **6**. Mt4? dext.: **a**, dorsal view; **b**, medial view; **c**, lateral view. **7**. Phalanx proximalis ?2 sin.: **a**, dorsal view; **b**, plantar view; **c**, distal view; **e**, proximal view. **8**. Sesamoid A: **a**, lateral/medial? view; **b**, dorsal view. **9**. Sesamoid B: **a**, lateral/medial? view, **b**, dorsal view.

Fig. 12. **1–9.** *Prodeinotherium bavaricum* de Unterzolling (BSP 1977 I 229) (1:3). **1**. Calcanéum dext. : **a**, vue proximale ; **b**, vue distale ; **c**, vue latérale. **2**. Naviculaire sin. : **a**, vue proximale ; **b**, vue distale ; **c**, vue dorsale ; **d**, vue plantaire. **3**. Endocunéiforme sin. : **a**, vue médiale ; **b**, vue latérale ; **c**, vue distale. **4**. Mésocunéiforme dext. : **a**, vue dorsale ; **b**, vue proximale ; **c**, vue médiale ; **d**, vue latérale. **5**. Cuboïde sin. : **a**, vue distale ; **b**, vue proximale. **6**. Mt4? dext. : **a**, vue dorsale ; **b**, vue médiale ; **c**, vue latérale. **7**. Phalange proximale ?2 sin. : **a**, vue dorsale ; **b**, vue plantaire ; **c**, vue distale ; **e**, vue proximale. **8**. Sésamoïde A : **a**, vue latérale/médiale ? **b**, vue dorsale. **9**. Sésamoïde B : **a**, vue latérale/médiale ? **b**, vue dorsale.

Table 24
Measurements (mm) of the navicular dext. of *Prodeinotherium bavaricum* from Unterzolling
Tableau 24
Mensurations (mm) du naviculaire dext. de *Prodeinotherium bavaricum* de Unterzolling

Maximum width	124
Maximum depth	118
Maximum height	52
Physiological height, measured at the centre	32
Width of the facies articularis proximalis	103
Depth of the facies articularis proximalis	83
Depth of the facies articularis distalis	124
Depth of the facies articularis distalis	80
Width of the plantar facies articularis	Damaged
Depth of the plantar facies articularis	Damaged

The navicular dext. is nearly complete. It is broken only on the plantar side. The shape of the bone is oval, with a prominent plantarmedial process, which slopes in a distal direction. The process is very strong and separated from the astragalus facet by a collum. The proximal surface consists of a large, oval, and concave astragalus facet. Laterally on the plantarmedial process, there is a flat facet for the calcaneus (A). There is another, small facet for the calcaneus on the plantolateral edge of the bone (A"). In distal view, there are four facets side by side. The medial facet is the smallest and is situated on the medial edge of the bone and oriented mediodistally. It articulates with the proximal endocuneiform. It has an angle of circa 130° to the next lateral facet. The mesocuneiform facet is triangular (narrows in a plantar direction) and slightly convex. The ectocuneiform facet is triangular and slightly convex. The lateral cuboid facet is triangular but it is broken in the plantar end. The facet is slightly concave and has a 160° angle to the ectocuneiform facet.

Comparison: The Unterzolling specimen differs from the Franzensbad specimen by its plantarmedial process being larger and separated from the navicular by a small neck. The form of the process is much more reduced in the Franzensbad specimen. Additional *Prodeinotherium* specimens from Pontlevoy, France, were variable (specimens at Muséum National d'Histoire Naturelle, Paris). Specimen number FP2697 is smaller, but it is from a juvenile individual. Specimen number FP131 has an accessory facet on the proximal surface of the plantarmedial process. The accessory facet articulates with the calcaneus. This feature is not present in the Unterzolling specimen.

Endocuneiform (*os tarsi primum*) (Fig. 12(3); Table 25)

The endocuneiform sin. is complete. The element is mediolaterally flattened. In lateral view, it is trapezoidal, with an elongated dorsodistal edge. The proximal facet for navicular articulation is round and steeply oriented proximolaterally. Distally, it joins a small lateral facet for mesocuneiform articulation. Its outline is a half circle. The lateral side bears a round tuberosity in the middle. On the dorsodistal margin of the lateral side, there is a half circle-shaped facet for Mt2. The distal end is covered by an oval, flat Mt1 facet.

Table 25
Measurements (mm) of the endocuneiform sin. of *Prodeinotherium bavaricum* from Unterzolling
Tableau 25
Mensurations (mm) de l'endocunéiforme sin. de *Prodeinotherium bavaricum* de Unterzolling

Maximum width	36
Maximum depth	65
Maximum height	96
Width of facies articularis proximalis for navicular	29
Depth of facies articularis proximalis for navicular	31
Depth of proximal facies articularis dorsalis for mesocuneiform	18
Height of proximal facies articularis dorsalis for mesocuneiform	11
Width of distal facies articularis dorsalis for Mt2	22
Height of distal facies articularis dorsalis for Mt2	19
Width of facies articularis distalis for Mt1	35
Depth of facies articularis distalis for Mt1	56

Mesocuneiform (*os tarsi secundum*) (Fig. 12(4); Table 26)

The mesocuneiform dext. is complete. In proximal view, it is nearly triangular, and the lateral edge is longer than the medial edge. The proximal facet for the navicular occupies the entire proximal surface. It is dorsally slightly convex, and it flattens out in a plantar direction. The distal facet for Mt2 is slightly concave. The medial side bears a minute facet in the middle of the proximal edge for the endocuneiform. The lateral side has both proximally and distally elongated facets for ectocuneiform articulation on its dorsal half.

Cuboid (*os tarsi quartum*) (Fig. 12(5); Table 27)

The cuboid sin. is broken only on the lateral side. The shape of the cuboid is triangular. The proximal side bears two flat facets. The larger lateral one is piriform and articulates with the calcaneus. The smaller medial one for navicular articulation is mostly broken off. There are two distal facets that have an angle of about 130° to each other. The medial one is more horizontal, while the lateral one is inclined laterally. The medial (partly broken) facet is rounded and articulates with the Mt4. The lateral one is half circle-shaped and articulates with the Mt5. The bone be-

Table 26
Measurements (mm) of the mesocuneiform dext. of *Prodeinotherium bavaricum* from Unterzolling
Tableau 26
Mensurations (mm) du mésocunéiforme dext. de *Prodeinotherium bavaricum* de Unterzolling

Dorsal width	54
Maximum depth	81
Diagonal depth	86
Maximum height	42
Width of the facies articularis proximalis	49
Depth of the facies articularis proximalis	67
Height of the proximal facies articularis lateralis	13
Depth of the proximal facies articularis lateralis	27
Height of the distal facies articularis lateralis	13
Depth of the distal facies articularis lateralis	34
Height of the facies articularis medialis	9
Depth of the facies articularis medialis	27
Width of the facies articularis distalis	46
Depth of the facies articularis distalis	64

Table 27
Measurements (mm) of the cuboid sin. of *Prodeinotherium bavaricum* from Unterzolling
Tableau 27
Mensurations (mm) du cuboïde sin. de *Prodeinotherium bavaricum* de Unterzolling

Maximum height	52
Maximum depth	100
Width of lateral facies articularis proximalis for calcaneus	67
Depth of lateral facies articularis proximalis for calcaneus	80
Depth of facies articularis distalis for Mt4, Mt5	72

comes a little thinner in a plantar direction. The plantar end has a well-pronounced tuberosity.

Os metatarsale quartum? (*Mt4?*) (Fig. 12(6); Table 28)

The Mt4? is complete; only the proximal edges are damaged. The bone thickens only slightly on the proximal and distal end. The proximal facet is not well preserved. In the middle of the proximal edge of the lateral side is a small oval facet for Mt5? The dorsal margin of the distal trochlea is skewed. This and the general shape of the proximal end suggest that the bone is an Mt4 dext.

Table 28
Measurements (mm) of the Mt4? sin. of *Prodeinotherium bavaricum* from Unterzolling
Tableau 28
Mensurations (mm) de Mt4? sin. de *Prodeinotherium bavaricum* de Unterzolling

Maximum length	136
Proximal width	71
Proximal depth	77
Width of the facies articularis proximalis	*69
Depth of the facies articularis proximalis	*74
Minimum width of the diaphysis	63
Minimum depth of the diaphysis	55
Minimum perimeter of the diaphysis	203
Distal width	75
Distal depth (of the trochlea)	73
Width of the trochlea	69

Table 29
Measurements (mm) of the phalanx proximalis ?2 sin. of *Prodeinotherium bavaricum* from Unterzolling
Tableau 29
Mensurations (mm) de la phalange proximale ?2 sin. de *Prodeinotherium bavaricum* de Unterzolling

Maximum length	75
Proximal width	69
Proximal depth	50
Width of the fovea articularis	61
Depth of the fovea articularis	46
Minimum depth of the diaphysis	39
Distal width	59
Distal depth	37
Width of the facies articularis distalis	49
Depth of the facies articularis distalis	34

Phalanx proximalis (Fig. 12(7); Table 29)

Phalanx proximalis ?2 sin.: The specimen is complete. The specimen shares morphology with the phalanx proximalis ?2 sin., but is smaller, and the volar margin of the fovea articularis proximalis is slightly convex. The asymmetric outline and the size of the element suggest that it might belong to Mt2 sin.

Ossa sesamoidea (Fig. 12(8, 9); Table 30)

Five sesamoids (A–E) are preserved. The plump one (A) (Fig. 12(9)) has an oval and flat dorsal facet. Because of the size and because there is no medial/lateral facet, it could be designated to an Mc1.

The slender one (B) (Fig. 12(8)) is mediolaterally flattened and has a pointed proximal apex and an elongated concave dorsal facet. A very thin lateral facet for the second sesamoid (of the same metapodial) shows that this is the left side of a sesamoid pair. It is not possible to show if it belongs to a metacarpal or -tarsal.

Three sesamoids (C–E) of nearly the same size and morphology belong to sesamoids pairs. The facies articularis dorsalis is triangular in specimen C and rounded in specimens D and E. A thin lateral/medial articulating facet is preserved only in specimen C. It is not possible to show if the specimens belong to metacarpals or –tarsals.

5. Discussion

Deinotheriidae have a special, somewhat primitive, mandibular and dental morphology. However, as the Unterzolling material shows, the morphology of the postcranial skeleton shares remarkable similarities (number of elements, virtually identical morphology in several elements) with Elephantoidea. It is, therefore, still justified to assign the family Deinotheriidae to Proboscidea, even if Gregor et al. (2000) recently suggested that Deinotheriidae are related to Sirenia rather than to Proboscidea, basing their argument on dental and mandibular similarities, but without providing any discussion on possible convergence, i.e. parallel evolution of similar characters in non-related groups.

Table 30
Measurements (mm) of the ossa sesamoidea of *Prodeinotherium bavaricum* from Unterzolling
Tableau 30
Mensurations (mm) des os sésamoïdes de *Prodeinotherium bavaricum* de Unterzolling

	A	B	C	D	E
Maximum height	39	54	42	41	42
Maximum depth	35	27	27	28	27
Maximum width	35	26	29	29	28
Width of the facies articularis dorsalis	32	25	28	25	24
Height of the facies articularis dorsalis	24	36	35	32	35

The documentation of the Unterzolling skeleton gives a new, detailed overview of the postcranial characters of the European *Prodeinotherium*. The *P. bavaricum* skeleton from Unterzolling (MN6) is similar to the Franzensbad skeleton from the Czech Republic (MN5). Both skeletons share the same morphology, although they differ in size. The Unterzolling individual is older, which could be identified by the fused epiphyses of the long bones and by the stronger wear on teeth. Both individuals have similar tooth size, but the Unterzolling mandible is larger than the Franzensbad mandible. This is probably due to sexual dimorphism. The tooth size of the Unterzolling specimen is similar to that of other *Prodeinotherium* teeth from the Middle to Late Miocene of Europe. The European Early to Middle Miocene *Prodeinotherium* teeth share a constant tooth morphology, specifically the same p3 morphology with two parallel anterior conids, proto-, and metaconid, which are not present in *Deinotherium*. The Unterzolling p3 morphology matches also closely the *P. bavaricum* lectotype (Gräf, 1957), but differs in hypolophid morphology from the p3 of *P. hungaricum* (Éhik, 1930). The p4–m3 are very similar in their basic morphology. Differences occur in the cingulum strength and strength of the protocristids.

As already described in Section 4, *P. bavaricum* is not well defined by a species diagnosis. Three *Prodeinotherium* species are recognized in three geographic areas: Europe, Asia, and Africa. They are based on the first descriptions of the small, Early to Middle Miocene species in each region. All three species supposedly share the same postcranial morphology (generic diagnosis by Harris, 1973), while the species diagnoses have remained unclear. In Europe, the original description of *P. bavaricum* stresses the importance of tooth size for species diagnosis. Gräf (1957) added new diagnostic dental characters for this species, but they were not considered diagnostic in the most recent comparisons by Antoine (1994) and Huttunen (in press b). At present, the European species *P. bavaricum* does not have a diagnosis that would differentiate it from the Asian or African *Prodeinotherium* species. Harris (1973, 1978) already demonstrated that the same tooth morphology is known from Europe, Asia, and Africa. Harris (1976) also suggested that the *Prodeinotherium* species could be synonymized. This means that further comparisons between European, Asian, and African cranial and postcranial materials are necessary before a taxonomic revision for the genus *Prodeinotherium* can be given.

6. Conclusions

The following list includes the most important and outstanding morphological features of the Unterzolling *P. bavaricum*.

• *Mandible*. The general size of the mandible is strikingly large in relation to the size of the toothrow. It is either a male specimen or an older individual than the Franzensbad mandible. Since sexual dimorphism in Deinotheriidae has not been studied earlier, the meaning of this feature remains unclear. The toothrow morphology and size are similar to other Middle Miocene *P. bavaricum* teeth in Europe.

• *Trapezium*. The form of the bone is mediolaterally flattened and round triangular in outline. The outline, size, and form of the facets are considerably different from other *P. bavaricum* trapezium elements from Langenau (Germany) and Montreal de Gers (France) (R. Ziegler and P. Tassy, pers. comm.), and also from *Gomphotherium* (Göhlich, 1998).

• *Metacarpals*. Both the carpal and metacarpal bones are aserial (the lunar articulates both with trapezoideum and unciform, and the metacarpals are not directly aligned below the carpal bones). The metacarpals are less aserial than in *Deinotherium* (Tobien, 1962). Mc1 is functional, which means that it is not reduced in size as in *Deinotherium* (Tobien, 1962). In comparison with *Deinotherium*, the Mc3 facet of the unciform is placed more distomedially.

• *Tibia*. Medially on the distal end, the distal margin bears a notch for the plantarmedial process of the astragalus.

• *Astragalus*. The plantarmedial process is strong and extended, and it is separated from the body by a small neck. The proximal facet extends along the process.

• *Navicular*. The navicular has a strong plantarmedial process with a small neck. There are additional facets for the calcaneus laterally on the plantarmedial process and on the plantolateral edge of the bone. Corresponding facets are present in the calcaneus.

• *Endocuneiform*. The distal facet for Mt1 is large. Therefore, the Mt1 (not preserved) is probably not reduced in size as in *Deinotherium*.

Future documentation of other European *P. bavaricum* material (e.g. skeletons from Langenau, Germany, and Montreal de Gers, France) is necessary in order to demonstrate the taxonomic significance of these features. In addition, comparisons between *P. bavaricum* from Europe, *P. pentapotamiae* from Asia, and *P. hobleyi* from Africa will clarify the interrelationships between the three *Prodeinotherium* species.

Acknowledgements

We thank cand. biol. Laura Schulz (Munich) and Dr. Martin Pickford (Paris) for improving the English and dipl. geol. Jerôme Priéto (Munich) for improving the French. For discussions and helpful comments, we are grateful to Professor Kurt Heissig (Munich), Professor Pascal Tassy (Paris) and Dr. Reinhard Ziegler (Stuttgart). The pictures were taken by Mr. Gustav Bergmeier (Munich). We also thank Dr. Martin Pickford and Professor Pascal Tassy for critically reviewing the manuscript. This research project was supported by a DAAD (Deutscher Akademischer Austauschdienst) research scholarship to Kati Huttunen.

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