

Proboscidea (Mammalia) from the Middle Miocene of Grund and Guntersdorf, Lower Austria

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(with 1 map, 2 tables, 6 text figures and 2 plates)

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Abstract

The proboscidean material from Grund and Guntersdorf is sparse, but contains two genera. *Gomphotherium angustidens* is represented by deciduous dental material and shows new details of the deciduous tooth morphology of the species. A permanent P2, which is unusual for *Gomphotherium*, was present in the Guntersdorf material. The small early to middle Miocene *Prodeinotherium bavaricum* is indicated by a deciduous d4 from Grund. The isolated sesamoid belongs to a small-sized proboscidean.

Key words: *Prodeinotherium*, *Gomphotherium*, Molasse Basin, Grund, Guntersdorf, Middle Miocene

Zusammenfassung

Das Proboscidea-Material aus den Fundstellen Grund und Guntersdorf ist spärlich, aber enthält zwei Gattungen. *Gomphotherium angustidens* ist durch Milchzähne vertreten, die neue Details über die Morphologie der Milchzähne zeigen. Ein P2 ist bei *Gomphotherium* ungewöhnlich. Anhand des Milchzahnes, des d4, konnte die kleine unter-mittelmiozäne Art *Prodeinotherium bavaricum* nachgewiesen werden. Der isolierte Sesamoid-Knochen stammt von einem kleinen Rüsseltier.

Introduction

The localities Grund and Guntersdorf have yielded a few proboscidean specimens. The species *Gomphotherium angustidens*, from the locality Guntersdorf bei Grund, was described for the first time by SCHLESINGER (1917) and illustrated later by OSBORN (1936). *Prodeinotherium bavaricum*, from the locality Grund, was described by HUTTUNEN (2002). The material was also listed in the "Säugetier-Katalog" by PIA & SICKENBERG (1934). Until now, no composite description of this proboscidean material has been available. This paper describes the material from the localities Grund and Guntersdorf bei Grund and compares it with fossils from other European localities. All specimens are stored at the Museum of Natural History in Vienna. The MN Zone estimates for all localities are from the NOW (Neogene of the Old World) online database. The dental terminology for the tooth descriptions is from TASSY (1996). For localisation see map 1.

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Abbreviations:

D – upper deciduous tooth

d – lower deciduous tooth

dext. – dextra (right)

M – upper molar

P – upper premolar

MN – Mammalian Neogene

NHMW – Naturhistorisches Museum in Wien, Austria

sin. – sinistra (left)

– – not present

* – estimated measurement

Descriptions

Family: Gomphotheriidae HAY, 1922

Genus: *Gomphotherium* BURMEISTER, 1837***Gomphotherium angustidens* CUVIER 1817**

Synonymy:

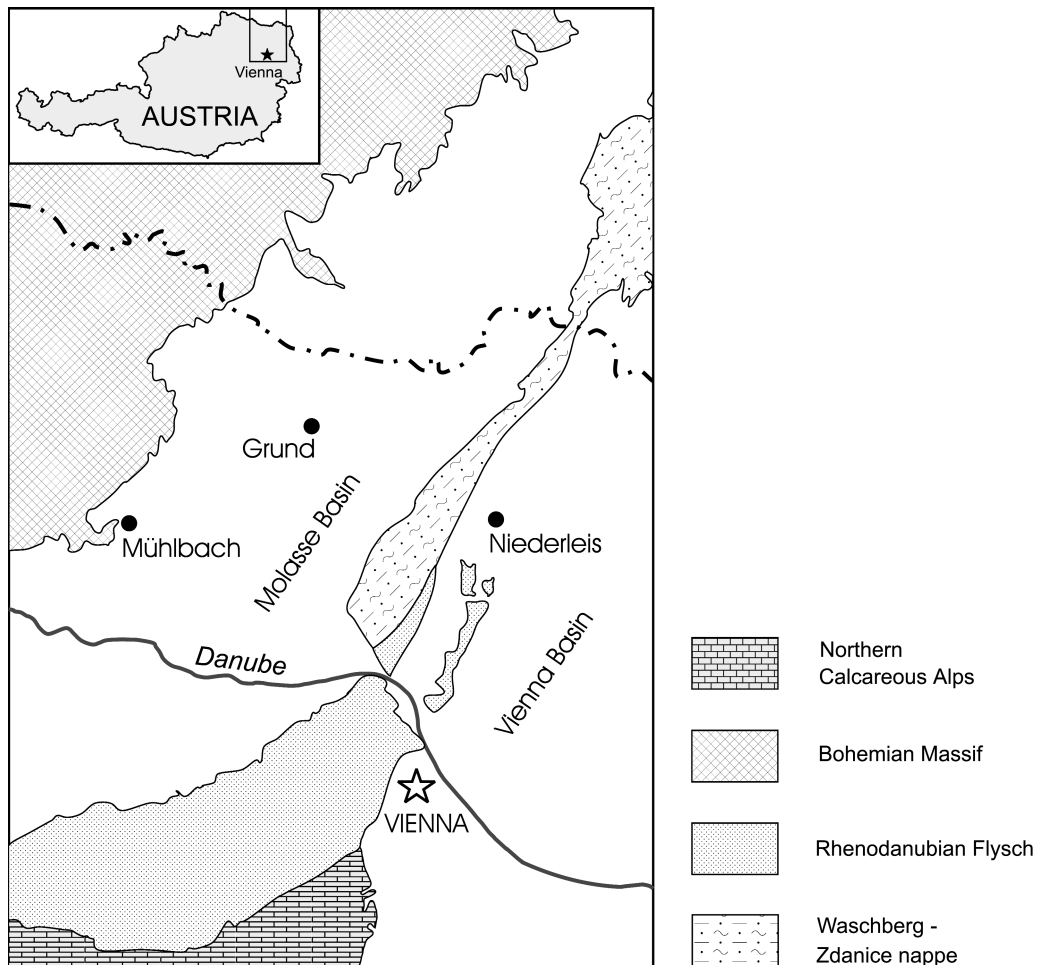
1917 *Mastodon (Bunolophodon) angustidens* – SCHLESINGER: Pl. II, Fig. 2-4.1936 *Mastodon (Bunolophodon) angustidens* – OSBORN: 262, Fig. 203b.1934 *Mastodon (Bunolophodon) angustidens* – PIA & SICKENBERG: 2852, 2853, 2932, 2991.**M a t e r i a l**: Deciduous incisor fragment NHMW Acq. C 6127 ex 1883, maxilla fragment with (D2, D3, D4, P2, P3, M1), NHMW Acq. C. 6125 ex 1883**L o c a l i t y**: Guntersdorf bei Grund**D e s c r i p t i o n**:

Deciduous incisor (Plate 1, Figure 1): The deciduous incisor fragment was probably associated with the maxilla fragment described below. The cross-section of the tooth is oval. The maximum length of the fragment is 62, maximum transverse height 24 and width 19 mm. The fragment has proximally a large, and distally a very small, pulp opening.

Maxilla (Plate 1, Figure 2a+b, Plate 2, Figure 1): The original description of this specimen by SCHLESINGER (1917) was already very detailed and included comparisons with other European specimens (SCHLESINGER 1917: 17-20). The following is a brief description of the morphology of the specimen.

The maxilla fragment includes the deciduous tooththrows (D2, D3, D4) on both sides and the permanent M1 dext., unerupted P2 and P3 dext., an isolated (unerupted) P3 sin., and the alveolus for the unerupted P4. The palate is fragmented. The estimated distance between the D2 dext. et sin. is 72 mm and between the D4 dext. et sin. 82 mm.

D2 dext. et sin.: The tooth outline is elongated to triangular. It is bunodont with four separate cones. A small cingulum is present anteriorly, buccally and posteriorly. The cingulum is also extended anteriorly to form a parastyle, giving the crown a triangular shape. The proto- and paracones are larger than the meta- and hypocones; they are separated by a deep median sulcus and a transverse valley. The buccal para- and metacones are slightly anteriorly positioned in relation to the lingual proto- and hypocones. The paracone is the highest of the cones.



D3 dext. et sin.: The tooth outline is elongated to rectangular. Both the D3 dext. and sin. are heavily worn. The cingulum covers all sides of the tooth. It is somewhat thicker anteriorly and posteriorly than on the lingual and buccal sides and it has also been heavily worn posteriorly. The transverse valley is long, whereas the median sulcus is hardly visible due to wear. The lingual proto- and hypocones are larger than the buccal para- and metacones; they are situated more anteriorly and are more worn than the buccal cones. There is a preparacrista on the buccal side.

D4 dext. et sin. (fragment): The tooth is similarly elongated to rectangular as D3. In contrast to D3, however, it has a slight angle to the previous tooth, giving the toothrow a curved character. The tooth is trilophodont and dentine has been exposed on the protoloph only. An even cingulum surrounds the tooth and it is slightly thinner buccally. The median sulcus is strong and the pretrite cones are slightly anterior in relation to the postrite cones. The tritoloph is complete and unworn. Its pretrite side consists of two smaller conelets, whereas the postrite one has three smaller conelets. Note that the position of D4 sin. in Plate 1, Figure 2 is incorrect (it is upside down). Its position in SCHLESINGER'S Plate II, Figure 2 is correct.

P2 dext (Plate 2, Figure 1): The permanent P2 is unerupted and nearly invisible in the maxilla. (SCHLESINGER's Plate II, Figure 3 was taken before reconstructing the P2 in its original position on top of the deciduous D2, as explained by SCHLESINGER (1917: 14)). The outline of the crown is oval. Anteriorly it bears a pointed, single paracone, and posteriorly there are five small cuspsules covering the posterior edge.

P3 dext. et sin. (Plate 1, Figure 3): The permanent P3 is rounded and unerupted. It has lingually two well-pronounced proto- and hypoconids, separated by a transverse valley and, buccally, four small cuspsules. There are two very small, incipient cuspsules posteriorly. There is a short median sulcus. Posterior to the P3 dext. the P4 alveolus is preserved.

M1 dext.: The tooth is trilophodont and elongated. It is slightly wider anteriorly than posteriorly. Strong anterior and posterior central conules are present in the transverse valleys. The cingulum covers all sides of the tooth. Anteriorly and posteriorly it is pronounced as small cuspsules, and on the postrite side it is reduced. The proto- and metalophs are stronger than the tritoloph. On the pretrite side, they both possess only a single main cone and, on the postrite side, three conelets. The tritoloph has on the postrite side three, and on the pretrite side, two conelets. All lophs have central conules, the proto- and metalophs have one conule anteriorly and posteriorly, and the tritoloph has one conule anteriorly. The postrite side is skewed anteriorly in relation to the pretrite side.

Tab. 1: Measurements (in mm) of the *G. angustidens* cheek teeth from Guntersdorf bei Grund.

| Tooth | Length | Width protoloph | Width metaloph | Width tritoloph |
|--------------|---------------|------------------------|-----------------------------|------------------------|
| D2 dext. | 30 | 21 | 23 | - |
| D2 sin. | 27 | 20 | 22 | - |
| D3 dext. | 39 | 28 | 28 | - |
| D3 sin. | 39 | 29 | 30 | - |
| D4 dext. | 58 | 37 | 41 | 35 |
| D4 sin. | - | - | *36 | 36 |
| M1 dext. | 78 | 47 | 47 | 43 |
| Tooth | Length | Maximum width | Maximum crown height | |
| P2 dext. | 22 | 16 | 10 | |
| P3 dext. | 39 | 29 | 21 | |
| P3 sin. | 34 | 28 | 22 | |

C o m p a r i s o n s : According to the NOW database, the stratigraphic range of *G. angustidens* in Europe spans from MN4 to MN11-12. In absolute age the range is from 18 to 7.1 Ma. According to GÖHLICH (1998: 166), however, the range is from MN4 to MN9.

The comparisons here are restricted to selected *G. angustidens* specimens from the localities Simorre, France (MN6, TASSY 1977), En Péjouan, France (MN7/8, TASSY 1985: 352-359), and Sansan, France (MN6, OSBORN 1936: 255). The deciduous and permanent teeth of *Tetralophodon longirostris* from Geiereck (Laaberger, Wien 10, late Miocene, MN9), Austria, are also included for comparisons (original descriptions in SCHLESINGER 1917: 83-85, Pl. 12, Fig. 1 and Pl. 14, Fig. 3).

D2: The Guntersdorf specimens are both wider and longer than the En Péjouan specimens (Figure 1). The morphologies of the specimens also differ slightly. TASSY (1985: 354) described that the metacone in D2 may be either round or transversally elongated. In addition, a distocrista running from the hypocone may form a simple crest with the incipient cusps of the posterior cingulum. The D2 from Sansan (OSBORN 1936) is similar to the Guntersdorf specimen. Compared with *T. longirostris*, the *G. angustidens* D2 is generally shorter, but wider. *T. longirostris* differs in the morphology of the four main cones: its buccal cones are much stronger than the lingual ones, and the posterior cingulum is very strong.

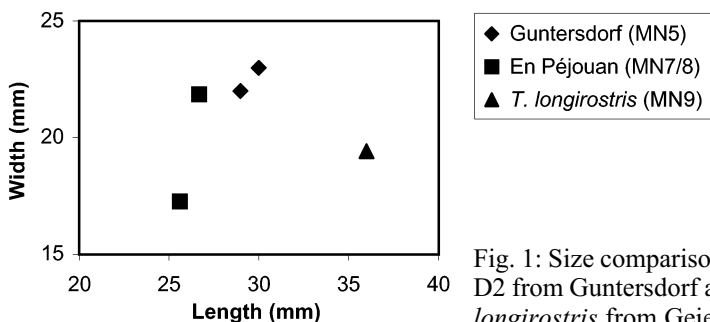


Fig. 1: Size comparisons between the *G. angustidens* D2 from Guntersdorf and En Péjouan, France, and *T. longirostris* from Geiereck (Laaerberg), Austria.

D3: The specimens from Guntersdorf are medium-sized when compared with En Péjouan specimens. En Péjouan specimens also show a great variation in intraspecific size. However, the *G. angustidens* specimens are clearly smaller than *T. longirostris* (Figure 2). TASSY (1985: 354-355) described a morphology very similar to that of the Grund specimens. The main cones form transverse lophs, and on the anterior cingulum there are para- and entostyles. TASSY (1985) also described central conules that cannot be observed in the Guntersdorf specimen because of strong wear. The specimens from both localities bear lingual styles in the valley. The D3 from Sansan (OSBORN 1936) has a longer transverse valley than the Guntersdorf specimen. *T. longirostris*, in contrast, has a trilophodont D3 that is narrower anteriorly than posteriorly.

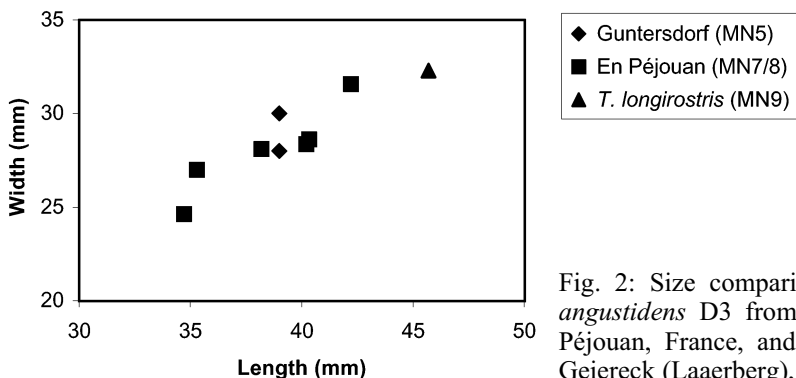


Fig. 2: Size comparisons between the *G. angustidens* D3 from Guntersdorf and En Péjouan, France, and *T. longirostris* from Geiereck (Laaerberg), Austria.

D4: The tooth from Guntersdorf is wider and shorter than the specimen from En Péjouan. In addition, the *T. longirostris* specimen is much larger than *G. angustidens* (Figure 3). TASSY (1985: 355-356) reported a D4 morphology that is more complex than in the permanent M1-2, which does not apply for the Guntersdorf specimens. The specimens from both localities have open valleys. The En Péjouan specimen has main cones divided into three to four conelets, whereas the Guntersdorf specimen has two to three conelets. The En Péjouan specimen has anterior pretrite central conules that are stronger than the posterior central conules. The anterior cingulum has a parasyle. In both specimens the cingulum is strong in the valleys. The D4 from Sansan (OSBORN 1936) seems to have a longer first transverse valley than the Guntersdorf specimen. The *T. longirostris* D4 is tetralophodont, the fourth loph being less strong than the three anterior lophs.

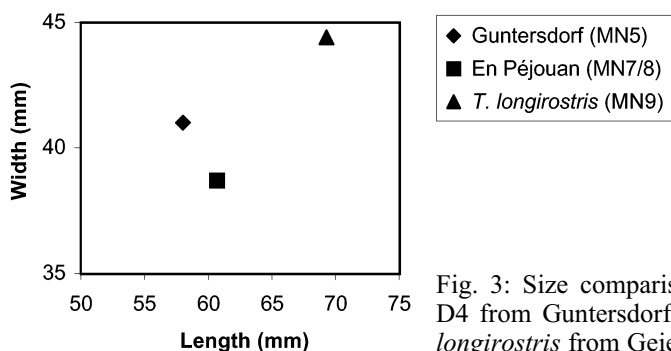


Fig. 3: Size comparisons between the *G. angustidens* D4 from Guntersdorf and En Péjouan, France, and *T. longirostris* from Geiereck (Laaerberg), Austria.

P2: In *Gomphotherium*, as a rule, D3 is replaced by the permanent P3 and D4 is replaced by P4. In the Guntersdorf specimen, D2 is replaced additionally by a small permanent P2. Being oval with an anterior protocone, this tooth is certainly a permanent P2. The presence of this tooth is unusual in *Gomphotherium*. However, a P2 has been previously recorded also in the Miocene genus *Deinotherium* (GRÄF 1957), which suggests that atavistic features were present in several Miocene proboscideans.

P3: The Guntersdorf specimen is both longer and wider than the specimens from En Péjouan (Figure 4). The morphologies from the two localities differ slightly: the En Péjouan specimen has a distocrista running from the hypocone to the posterior cingulum. A protocrista connects the protocone with the cingulum. Unlike the Guntersdorf specimen, the cingulum in the En Péjouan specimens is lingually strong.

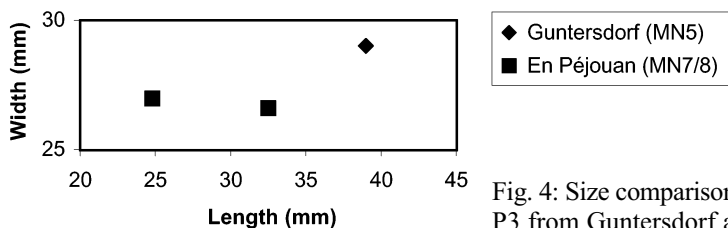


Fig. 4: Size comparisons between the *G. angustidens* P3 from Guntersdorf and En Péjouan, France.

M1: The Guntersdorf specimen is generally within the intraspecific size variation of the *G. angustidens* specimens from Simorre, although it is more slender in relation to its length than the other specimens, with well-developed central conules. The *G. angustidens* M1 is much smaller than in *T. longirostris*. The general morphology of the permanent M1 in *G. angustidens* is characterized by the trilophodont morphology. In *T. longirostris*, M1 is tetralophodont.

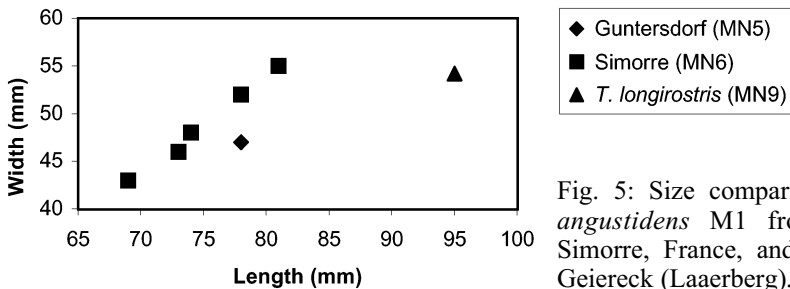


Fig. 5: Size comparisons between the *G. angustidens* M1 from Guntersdorf and Simorre, France, and *T. longirostris* from Geiereck (Laaerberg), Austria.

Family: Deinotheriidae BONAPARTE, 1845

Genus: *Prodeinotherium* ÉHIK, 1931

***Prodeinotherium bavaricum* VON MEYER 1841**

Synonymy:

1934 *Deinotherium bavaricum* – PIA & SICKENBERG: number 2707.

2002 *Prodeinotherium bavaricum* – HUTTUNEN: 260, Pl. 1, Fig. 3.

Material: d4 sin. NHMW2000z0004/0000.

Locality: Grund.

Description (Plate 2, Figure 2): The d4 sin. is trilophodont and elongated. The first valley is longer than the second valley, but the lophids are of nearly equal width. Strong anteromedial cristids extend from the labial meta- and entoconids. They end medial to the lophid. The lingual proproto- and prohypoconids are straight, ending anterior to the conids. The anterior cristids of the tritolophid are both somewhat anteromedially extended. Anterior and posterior cingula are present. Some cingulum is also present in the first median valley lingually and labially as an incipient styloid. There are two roots. Maximum length of the specimen is 58 mm. Width at the first, second and third lophids: 32, 33 and 34 mm.

Comparisons: The d4 specimens come from localities with a known MN Zone: Pontlevoy, France (MN5), Dinotheriensande, Germany (DS) (MN9), Montredon, France (MN10), Polgardi and Baltavar, Hungary (MN13). The size comparisons show that the Grund specimen is between the other *P. bavaricum* specimens from MN5 and MN9. Surprisingly, the Baltavar specimen is much smaller than the other MN13 specimens from Polgardi. HUTTUNEN (2002) estimated the tooth size limit between the genera

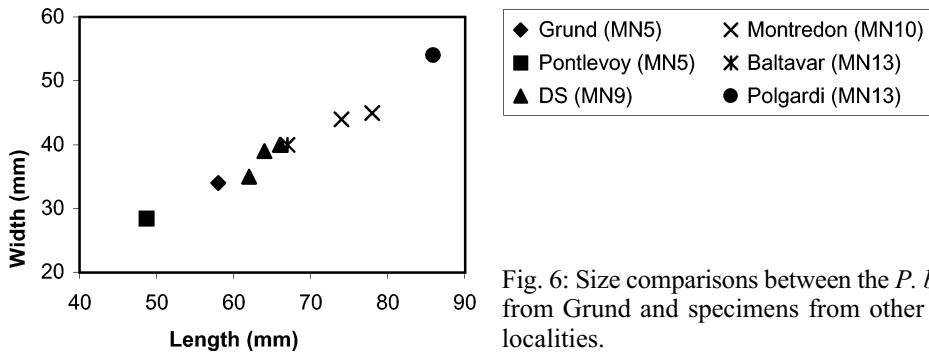


Fig. 6: Size comparisons between the *P. bavaricum* from Grund and specimens from other European localities.

Prodeinotherium and *Deinotherium* to be at 72 mm maximum length, while the tooth morphology for both genera is uniform. Based on this estimate, the Grund specimen is a *P. bavaricum*.

Proboscidea indet.

Material (Plate 2, Figure 3): Sesamoid dext., Inv. Nr. NHMW2002z0136/0001.

Locality: Grund.

Description: The element is a sesamoid bone belonging to the first metacarpal. The form is triangular both in lateral and medial views; in volar view it is oval. The facies articularis dorsalis is oval and flat. Close to the medial margin of the facies there is an elongated depression. The medial side of the bone is flattened, partly due to abrasion, while the lateral side is wide and rounded.

Comparisons: The bone could be identified based on a description of a sesamoid bone of *P. bavaricum* from the locality Unterzolling (MN6), Germany (HUTTUNEN & GÖHLICH in press, Fig.12.9). The general morphology and the size of the articulating facets of the two specimens are very similar, although the maximum dimensions of the Grund specimen are much greater (see Table 2). The associated first metacarpal of *P. bavaricum* from Unterzolling (HUTTUNEN & GÖHLICH in press, Fig. 7.6) is relatively small (maximum length 128 mm, distal width of the trochlea 44 mm and depth 64 mm). Because the articulating facets are so similar, it is possible that the Grund specimen was associated with a first metacarpal of a similar size.

Tab. 2: Measurements (in mm) of the Proboscidea indet. sesamoid bone from Grund and comparisons with *P. bavaricum* from Unterzolling, Germany.

| Measurement sesamoid dext. | Proboscidea indet. Grund (MN5) | <i>P. bavaricum</i> Unterzolling (MN6) |
|--|-----------------------------------|---|
| Maximum height | 61 | 39 |
| Maximum depth | 42 | 35 |
| Maximum width | 38 | 35 |
| Width of the facies articularis dorsalis (to Mc1) | 39 | 32 |
| Height of the facies articularis dorsalis (to Mc1) | 25 | 24 |

Discussion

The diagnostic characters of *G. angustidens* are restricted to the cheek tooth, incisor and mandible morphology, while the deciduous dentition has not been well documented so far. The comparisons made in this study show that the *G. angustidens* deciduous and permanent teeth from the localities Grund and Guntersdorf differ slightly from the material from the French localities En Pélouan and Simorre. This indicates that some intraspecific morphological variation was present, while the main tooth morphology remained the same from MN5 to MN7/8. Also, the size of both the deciduous and permanent teeth was variable. Compared with the *T. longirostris* deciduous dentition, however, the *G. angustidens* teeth are smaller and different in their main morphology. The most important specific characters separating *G. angustidens* from *T. longirostris* deciduous teeth are delicate cones of nearly equal size in D2, two lophes in D3, and trilophodont D4. For the permanent teeth, the presence of P2 in the Guntersdorf specimen is an atavistic feature and M1 is always trilophodont. P3 was not compared with *T. longirostris*.

Due to a small number of d4 specimens in Europe, the size difference between *Prodeinotherium* and *Deinotherium* has not been well established. Based on the estimate by HUTTUNEN (2002), however, the Grund specimen is a *P. bavaricum*.

The sesamoid bone from Grund belonged most likely to a small-sized proboscidean. Further study is required to determine whether the maximum size of this element or the size of the articulating facet could have diagnostic importance. Potentially, the maximum size of the first sesamoid bone depends on the degree of aseriality of the wrist and on the weight distributed on the first metacarpal, which is already known to vary between the different proboscidean genera (TOBIEN 1962).

The species *G. angustidens* and *P. bavaricum* are often found in association in the European Miocene faunas. Based on their different tooth morphologies, the mastodons are characterized as browsers-grazers and the deinotheres as browsers. The mastodons have low-crowned bunolophodont teeth that are adapted for crushing and grinding, whereas the lophodont deinotheres teeth are adapted for cutting. It has been suggested that different factors influenced the evolution of the mastodons and the deinotheres (HARRIS 1975, HUTTUNEN 2000). Indeed, CERLING et al. (1999: 369) were able to record a shift in terms of the C3 and C4 ratios of the stable carbon isotope in the diet of the late Miocene gomphotheres. Gomphotheres changed their diet into a more grazing nutrition at ca. 7.5 Ma, while the deinotheres remained browsers. This ecological difference in the late Miocene, however, does not explain the continuous coexistence of the gomphotheres and deinotheres in the middle Miocene. A dental microwear study or any other paleoecological study would therefore be welcome to demonstrate the paleoecological differences of proboscideans in the localities Grund and Guntersdorf.

Conclusions

- The *G. angustidens* deciduous teeth from the locality Guntersdorf near Grund show new details of the deciduous and permanent tooth morphology. A permanent P2 is present.
- The small size of the Grund d4 specimen shows that it belongs to *P. bavaricum*. It is not morphologically different from other European deinotheres.

- The sesamoid bone from Grund belonged to a small-sized proboscidean that probably used its first metacarpal heavily.

Acknowledgements

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Plate 1

***Gomphotherium angustidens*, Guntersdorf bei Grund**

Fig. 1: deciduous incisor, a. proximal/distal, b. lateral, NHMW Acq. C 6127 ex 1883. – x 0.75

Fig. 2: maxilla, a. dext., occlusal, b. sin., occlusal, NHMW Acq. C 6125 ex 1883. – x 0.75

Fig. 3: P3 sin., occlusal, Acq. C 6125 ex 1883. – x 0.75

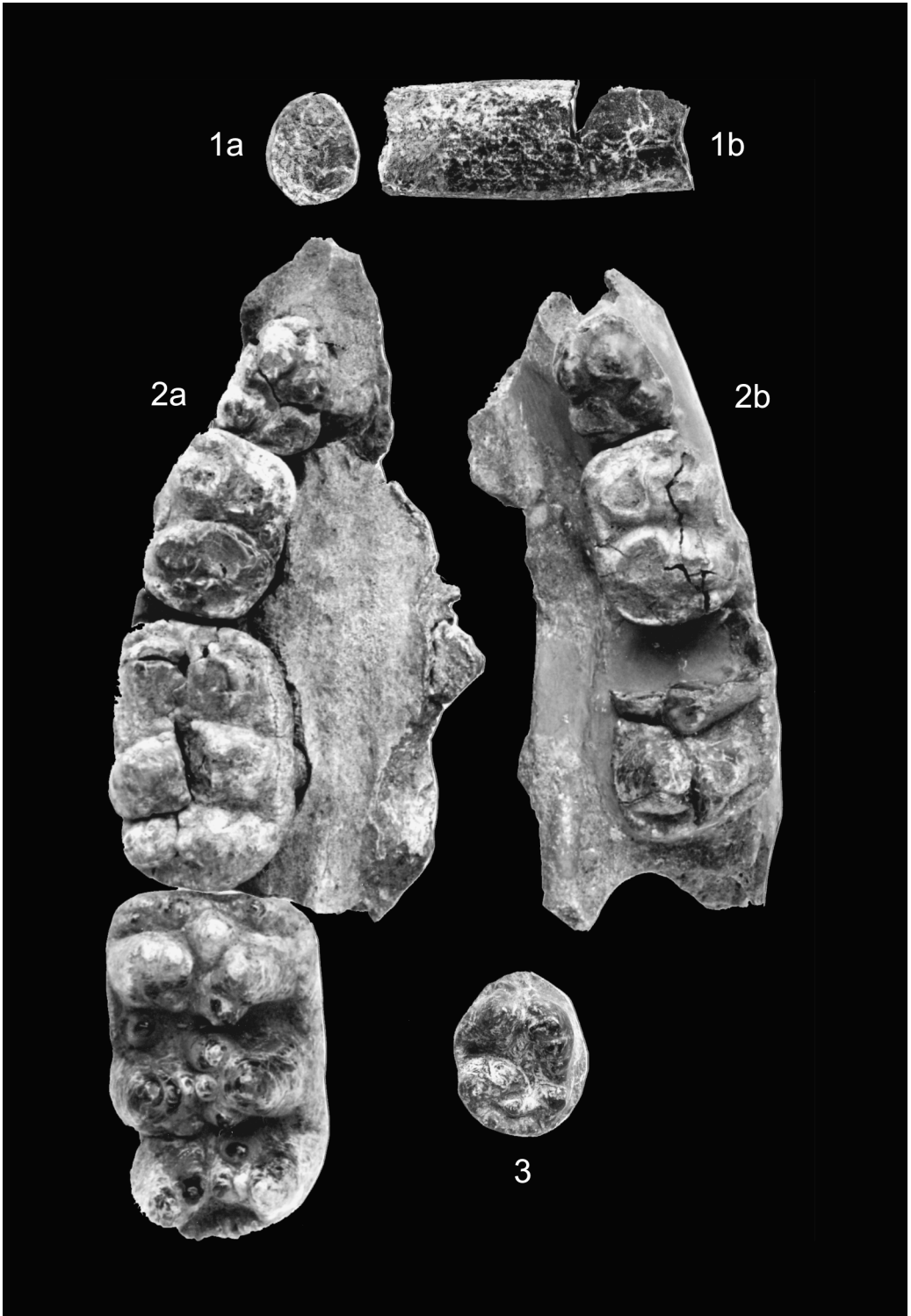


Plate 2

Gomphotherium angustidens, Guntersdorf bei Grund

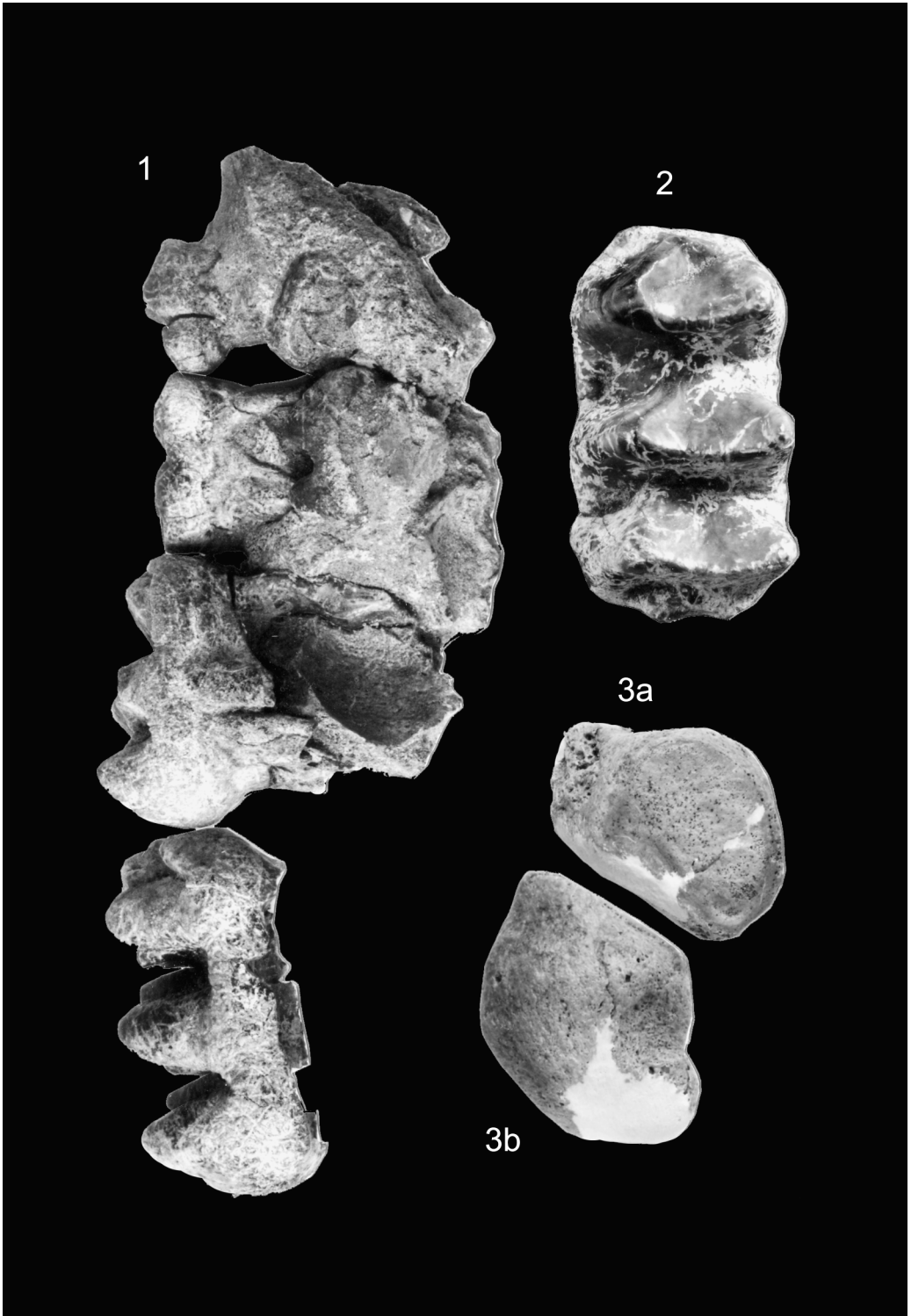
Fig. 1: maxilla dext., medial, NHMW Acq. C 6125 ex 1883. – x 0.75

Prodeinotherium bavaricum, Grund

Fig. 2: d4 sin., occlusal, NHMW 2000z004/0000. – x 1.0

Proboscidea indet., Grund

Fig. 3: sesamoid dext., a. facies articularis dorsalis, b. lateral, Inv. Nr. NHMW2002z0136/0001.
– x 0.75.



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