# On a Prodeinotherium bavaricum (Proboscidea, Mammalia) skeleton from Franzensbad, Czech Republic 

by Kati Huttunen ${ }^{1}$<br>(with 4 text figures and 4 plates)<br>Manuscript received on June 12 ${ }^{\text {th }}$ 2001, the revised manuscript on January $31^{\text {st }} 2002$


#### Abstract

A partial skeleton of Prodeinotherium bavaricum on exhibit at the Museum of Natural History in Vienna is described. The skeleton originates from the Middle Miocene (MN5) locality Franzensbad, Czech Republic and is one of the best-preserved Prodeinotherium skeletons available. The identification and taxonomic determination was carried out based on a comparative study with other European Deinotheres. The present report is the first comprehensive investigation on the variability of the postcranial morphology of Prodeinotherium in Europe. The results support the contemporary Deinotheriidae taxonomy, which recognizes only one Early to Middle Miocene Prodeinotherium species in Europe. An expanded diagnosis of the genus is provided.


Key words: Deinotheriidae, Franzensbad, Prodeinotherium, Middle Miocene

## Zusammenfassung

Teile des Skeletts von Prodeinotherium bavaricum des Naturhistorischen Museums in Wien werden beschrieben. Das Skelett stammt aus der mittelmiozänen (MN5) Fundstelle Franzensbad, Tschechische Republik und gehört zu den besterhaltenen Prodeinotherium Skeletten der Welt. Die Identifizierung und taxonomische Bestimmung wurde nach einer Vergleichsstudie durchgeführt. Diese Studie ist die erste umfangreiche Studie über die Variabilität der postcranialen Morphologie des Prodeinotherium in Europa. Die Ergebnisse unterstützen der Ansicht der modernen Deinotheriidae-Taxonomie, die nur eine Früh- bis Mittelmiozäne Prodeinotherium Art in Europa kennt. Als Ergebnis wird eine erweiterte Gattungsdiagnose erstellt.

## Introduction

The Franzensbad skeleton (inventory number NHMW2000z0047/0001) is a mounted specimen on exhibit at the Museum of Natural History in Vienna. The earliest record of the skeleton is by Bibier (1884), who described the find from the quarry of the Mattoni Establishment in Franzensbad (Frantiskovy Lazne, Czech Republic, Cheb Basin, 50ㅇ́ $\mathrm{N}, 13^{\circ} 6^{\prime} \mathrm{E}$ ). The quarry was located in a valley between Oberdorf and Aag, where Cypris Shale had been exposed. Bibier mentions that the find was at a depth of 4.5 m in a 15 cm thick horizont of yellow-grey Cypris Shale (Cypris Shale is an Early-Middle

[^0]Miocene Formation that was deposited between ca. 21 and 16.8 Ma after a basinwide flooding event [ŠPICÁKovÁ et al. 2000]). The excavation work was not documented in detail. Some parts of the skull were found (Bibier 1884: 303), but the reconstruction of the skull apparently obscured the original bone. The skeleton was given to the Museum by Mr. Mattoni. In the first presentation of the skeleton Kittl (1908) mentions that the preparation work was done based on a skeleton of an extant elephant and some fossil proboscidean bones. The mounted skeleton was illustrated also by Osborn (1936 Vol. I: 100, see Fig. 1 next page), who listed some proportional mistakes made in its mounting. The following list indicates the current stage of preservation at the NHMW exhibition. The elements have been prepared so that the contact between the original bone and prepared bone is not always visible.

| AXIAL SKELETON | LEFT SIDE | RIGHT SIDE |
| :--- | :--- | :--- |
| Mandible (without incisors) | Rib no. 2 (no head) | Rib no. 2 (no head) |
| Atlas | Rib no. 3 (proximal 2/3 preserved) | Rib no. 3 (head and neck original) |
| Axis | Rib no. 6 (proximal half preserved) | Rib no. 4 (distal end prepared) |
| Vertebrae cervicales no. 4, 6 | Rib no. 7 (complete, caput prepared) | Rib no. 5 (distal 1/3 prepared) |
| Vertebrae thoracicae no. 5,9 <br> (only corpus) | Rib no. 8 (distal end prepared) | Rib no. 7 (head and neck original) |
| Vertebra thoracica no. 10 <br> (only corpus) | Scapula (spina scapulae and fossa <br> supraspinata prepared) | Scapula (spina scapulae and <br> fossa supraspinata prepared) |
| Vertebra thoracica no. 17 <br> (only corpus) | Humerus (ca. proximal 1/2 prepared) | Ulna (surface fractures, mainly <br> on medial side prepared) |
| Vertebra thoracica no. 18, 22 <br> (only corpus) | Radius (proximal 1/2 and distal epiphysis <br> original) | Cuneiform |
| Os sacrum | Ulna (cranial fractures prepared) | Scaphoid |
| Ossa pelvis (fragment) | Unciform | Unciform |
| Vertebrae caudalis no. 1-5 <br> (fragments) | Os metacarpale secundarium, <br> os metacarpale tertium | Magnum |
|  | Femur (collum and trochanter major prepared) | ?Trapezoid (partly broken) |
|  | Patella | Os metacarpale tertium, <br> Os metacarpale quartum |
|  | Astragalus | Femur (collum and trochanter <br> major prepared) |
|  | Calcaneum | Patella |
|  | Navicular | Fibula (proximal 1/3 plaster, <br> distal fractures prepared) |
|  | Astragalus |  |

This work describes some elements of the Franzensbad skeleton. Since the skeleton is already mounted, only certain elements could be removed for study and only partial measurements could be taken (see Fig. 2). For some elements, most of the measurements were estimates and therefore only one side was measured (e.g. ulna). Photographs of the elements could be taken only from certain views. The photographs concentrate on the original bone material.


Fig. 1: An original illustration indicating the preserved elements of the Franzensbad skeleton (after Osborn 1936 Vol. I: text. fig. 100).


Fig. 2: An illustration indicating the bones described in this study.


Fig. 3: Directions used in the descriptions (after GöHLICH 1998).

In the description, the measurements used are partly from the work of HARrIS (1973) and Göhlich (1998). These measurements reflect not only the general dimensions of the Deinotheriidae skeletal elements, but also their generic characters. The anatomical nomenclature used is from Schaller (1992). The terminology for anatomical directions is of Göhlich (1998: 108) (see also Fig. 3).

The following abbreviations were used in this study:

| * | not measurable because of <br> breakage or preparation | dext. | dextra (right) | p3 lower tooth |  |
| :--- | :--- | :--- | :--- | :--- | :--- |
| *n | estimated measurement because <br> of breakage or preparation | P3 metacarpal | upper tooth | sin. | sinistra (left) |

Collections (incl. comparative material):
BSP Bayerische Staatssammlung für Paläontologie und Historische Geologie, München, Germany
HLMD Hessisches Landesmuseum, Darmstadt, Germany
LMJ Landesmuseum Joanneum, Graz, Austria
ML Muséum d'Histoire Naturelle de Lyon, France
MNHN Muséum National d'Histoire Naturelle, Paris, France

NHMW Naturhistorisches Museum in Wien, Austria
HNHM Natural History Museum, Budapest, Hungary
PM Institut für Paläontologie, Mainz, Germany
PMSU Paleontological Museum of the Sofia University, Bulgaria

## Taxonomy

## Prodeinotherium bavaricum von Meyer 1831

In the latest revision of the family Deinotheriidae (HARrIS 1973), three species of the genus Prodeinotherium are recognized based on geographic distribution in Africa ( $P$. hobleyi), south Asia ( $P$. pentapotamiae) and Europe ( $P$. bavaricum). The morphological differences between the species in the original descriptions are minute dental characters. It has already been documented that the postcranial material of Prodeinotherium from the Early to Middle Miocene of Africa is similar to the European Prodeinotherium (Harris 1973, 1978). Therefore some authors have doubted the justification of geographically dividing Prodeinotherium into species (Harris 1976, Shoshani et al. 1996). As detailed comparisons between the African, Asian and European material are not available, this study conservatively recognizes the Franzenbad specimen as the European species $P$. bavaricum.

## Description

Mandible (Pl. 1, Fig. 1): The Franzensbad mandible is complete; only the tusks (i2) are missing. The toothrows are complete (with $\mathrm{p} 3, \mathrm{p} 4, \mathrm{~m} 1, \mathrm{~m} 2, \mathrm{~m} 3$ ). The premolars and m 1 are worn, whereas the posterior molars are in an early stage of wear. The p3 has anteriorly parallel proto- and metaconids and there is a very strong anterior cingulum. The tooth outline is more rectangular than triangular. The other tooth positions have the characteristic deinothere morphologies: $\mathrm{p} 4, \mathrm{~m} 2$ and m 3 are bilophodont, m 1 is trilophodont.

The entire surface of the mandibular symphysis is porous, indicating that the symphysis and the incisors were still increasing in size. In lateral view, the corpus mandibulae and specimen overall are low. The symphysis projects far anteriorly. The surface of the ramus mandibulae is slightly concave. This is for the musculus masseter insertion (after the muscle reconstruction of HARRIS 1975). Two mental foramina are present, one anterior to p 4 and one anterior to p 3 . The corpus mandibulae is straight-to-rounded until p 4 , where the symphyseal flexure begins. The processus coronoideus is slightly shorter than the caput mandibulae. The posterior edge from the angulus mandibulae to the caput is slightly convace. In medial view, the muscle insertions are not clearly visible. There is a depression between the processus coronoideus and the caput, indicating an insertion for musculus pterygoideus lateralis. There is another concavity on the angulus for insertion of the musculus pterygoideus medialis. There is a depression, probably for the musculus digastricus, on the posterior side of the symphysis. In anterior view, the symphysis is protruding and long and the toothrows are medially inclined.

| Mandible measurements (mm) |  |
| :--- | :---: |
| Distance from angulus mandibulae to the incisor alveolus | 518 |
| Distance from angulus mandibulae to caput | 310 |
| Depth between caput and processus coronoideus | 230 |
| Length symphysis from p3 alveolus to incisor alveolus | 280 |
| Toothrow length | 310 |
| Height of the corpus mandibulae at $\mathrm{m} 2, \mathrm{~m} 3$ | 110,120 |
| Width of the corpus mandibulae at p4, $\mathrm{m} 1, \mathrm{~m} 2, \mathrm{~m} 3$ | $95,105,110,120$ |
| Anteroposterior length of the symphysis | 185 |
| Width of the symphysis at incisor alveoli | 165 |
| Width of the symphysis at p3 alveoli | 123 |

Atlas: The atlas is not entirely visible in the mounted skeleton and therefore no good measurements or photographs could be taken. Only the general features can be described. The atlas gives an impression of being high because the arcus dorsalis bears a large tuberculum dorsale that extends over the entire width of the arcus. In cranial view, the occipital facets (fovea articularis cranialis) are comma-shaped, slightly concave, and large. They extend from the edge of the arcus dorsalis down to the arcus ventralis. The tuberculum dorsale is rough on this side. In caudal view, the triangular axis facet surfaces are only very slightly concave. Their medial edges follow the neural canal; the proximal edges do not extend far because they are separated by a depression from the arcus dorsalis. The distal edges follow horizontally the arcus ventralis. The arcus ventralis has a rugose surface and slopes strongly caudally and distally at a large, triangular fovea dentis. The processus transversi are at the level of the axis facets and the foramen transversaria. In dorsal view, the processus transversi are wide in craniocaudal direction and the foramen vertebrale laterale are visible below the tuberculum dorsale. The tips of the processus transversi have a rugose surface. In ventral view, the strong slope of the arcus ventralis is projected in caudal direction by a minute tuberculum ventrale.
Scapula (Pl. 1, Fig. 2): The scapula sin. and dext. are preserved only partially. The original illustration by Kittl (1908) shows that circa the proximal half of the scapula dext. is missing. Fig. 1 reveals also that the scapula sin. was fragmentary: both the spina and margo cranialis and dorsalis were broken off. Preparation work has covered the original edges so that the true form is no longer visible. However, as the preparation attempted to follow the natural contours of the specimens, some general features for both can be recorded. On the lateral facies, the original bone is visible in the areas of cavitas glenoidalis, the collum, margo cranialis and caudalis, and circa half of the spina scapulae. The fossa supraspinata and the margo dorsalis are not preserved. The cavitas glenoidalis is rectangular and strongly concave. On the craniolateral side it bears a large and round tuberculum that extends distal to the level of the opening of the cavitas glenoidalis. Proximal to the collum, margo cranialis and caudalis widen to form cranial and caudal angles, whose extent cannot be exactly determined. The angles were prepared to be round. The large fossa infraspinata is concave close to the spina, but in the direction of the margo caudalis it becomes convex. The highest elevation of the spina is at its distal half. The highest elevation bears a tuberosity, but it is uncertain how much of it is original. There is a well-pronounced acromion, constituting a wide distal portion
of the spina. On the medial facies, the proximal portion is not preserved. Opposite to the spina on the lateral facies, there is an elevation, and the cranial and caudal halves are concave.

| Scapula measurements (mm) | dext. | Scapula measurements (mm) | dext. |
| :--- | :---: | :--- | :---: |
| Maximum height along spina scapulae | 688 | Length cavitas glenoidalis | 165 |
| Maximum width | $*$ | Width cavitas glenoidalis | 105 |

Humerus (Pl. 2, Fig. 2-3): The original bone of the humerus sin. is not visible in its proximal portion above the tuberositas deltoidea; only the caput humeri epiphysis has not been reconstructed. Also, in the illustration by Kittl (1908), the proximal part of the bone was already completely prepared. The maximum length of the prepared humerus is probably close to the original length of the bone. The general form of the bone is short and wide. The cranial sulcus intertubercularis extends to about one third of the length of the facies cranialis. The distal end is complete. The tuberositas deltoidea extends laterally nearly to the level of the epicondylus lateralis. It diminishes in distal direction, continuing as a crista humeri, and ends just proximal to the level of the epicondylus lateralis. The epicondylus lateralis is high, placed higher above the trochlea than the epicondylus medialis. It continues as a crista supracondylaris lateralis proximocaudally, forming a deep sulcus musculi brachialis with the crista humeri. The shaft reaches its minimum width at the level of the sulcus. The epicondylus medialis continues proximally as a crista supracondylus medialis. The epicondylus medialis is also thin at the level of the shaft's minimum width and then widens proximally. The fossa olecrani on the caudal side is relatively deep, providing a stable articulation with the ulna.

| Humerus measurements (mm) | sin. |
| :--- | :---: |
| Maximum length (estimated) | ${ }^{*} 790$ |
| Width at proximal edge of epicondylus latearlis | 220 |
| Length from epidcondylus lateralis to distal end of condyle | 200 |
| Width at epicondylus medialis | ${ }^{*} 240$ |
| Length from epicondylus medialis to distal end of condylus medialis | 180 |
| Width of articular surfaces on trochlea | 175 |
| Minimum width shaft above epicondylus lateralis | 104 |
| Minimum depth shaft above epicondylus lateralis | 103 |
| Depth of articular surface of condylus medialis | 100 |
| Depth of articular surface of condylus lateralis | 85 |

Ulna (Pl. 2, Fig. 1-3): Both ulna sin. and dext. are in good condition; only surface fractures have been prepared. In the mounted position, the ulnar articulations with the radius and humerus are well visible. The incisura trochlearis is situated in a relatively deep humerus fossa olecrani. The tuber olecrani is in lateral view at the level of the processus anconaeus. The tuber olecrani is wide and medially extended. From the tuber olecrani, a straight margo caudalis runs in distal direction. It divides the facies medialis and lateralis. On the lateral facies, two proximodistally running surfaces are visible. The lat-
erovolar surface is strongly concave and clearly separated by an edge from the processus coronoideus lateralis, which widens above the concave facet. The laterodorsal surface is flat and somewhat triangular. It begins from the dorsal tip of the processus coronoideus lateralis and widens distally. Proximally on the medial facies, there are large and deep concavities that flatten out distally in the middle of the shaft. Approximately at this level, the flat radius facet extends medially. In dorsal view, the bone gives a straight, columnar impression. The incisura radialis divides the processus cornoideus medialis and lateralis. The incisura radialis is not well visible in the mounted specimen, but it can be discerned that the lateral half is larger than the medial half. The proximal portion of the incisura trochlearis is deeply placed within the fossa olecrani. The general impression of the incisura trochlearis is closed and deep. The distal epiphysis has a volarly-projected extension. The distal facies carpea for articulation with the lunar is concave dorsally and the volar part is convex (see also Pl. 3, Fig. 2-3).

| Ulna measurements (mm) | sin. | Ulna measurements $(\mathrm{mm})$ | sin. |
| :--- | :---: | :--- | :---: |
| Maximum height | $* 800$ | Proximal width at processus coronoideus | 165 |
| Width olecranon | 130 | Width midpoint shaft | 110 |
| Depth olecranon below incisura trochlearis | 150 | Depth midpoint shaft | 89 |
| Width incisura trochlearis | $*$ |  |  |

Radius (Pl. 2, Fig. 2): The radius sin. preserves its proximal half and distal epiphysis. Its form is slender proximally and wide distally. The radius lies in the incisura radialis of the ulna, continues from there distomedially and turns at the half length of the corpus radii medially. The proximal surface of the radius, fovea capitis radii, is triangular and bears two triangular and concave proximal surfaces: a smaller medial and a larger lateral one that are separated by a craniovolar elevation. The articulation with the ulna on the volar side of the caput radii is not visible. However, there is a large tuberositas radii on the volar side of the bone, distal to the articulation with the ulna. The cross-sectional form of the radial shaft varies along the diaphysis. Immediately distal to the caput it is round-to-triangular, and on the dorsal side a deep concavity is present. In the direction of the shaft half in which the crista interossea and the shaft are skewed medially in relation to the ulna, the form changes to mediolaterally flattened one. The distal half of the shaft is not visible due to preparation, but an overall form that is mediolaterally flattened (as typical of the pronation position of the radius in Proboscidea) is probably correct. The distal epiphysis bears a trochlea radii (see also Pl. 3, Fig. 2-3). It has a facies articularis carpea both to the lunar and scaphoid. The distal facet has a dorsal flat-convex half and a strongly convex volar half.

| Radius measurements $(\mathrm{mm})$ | sin. | Radius measurements $(\mathrm{mm})$ | sin. |
| :--- | :---: | :--- | :---: |
| Maximum length | 695 | Distal width | 230 |
| Proximal width at caput radii | 89 | Distal depth | * |
| Proximal depth at caput radii | 70 |  |  |

Scaphoid (os carpi radiale) (Pl. 3, Fig. 1): The scaphoid dext. is incorrectly mounted. The correct position of the specimen should be distal to the radius, medial to the lunar
and proximal to the trapezium. It has a porous and uneven medial surface. In medial view its dorsal edge is strongly curved to a W -shaped edge. The volar edge is strongly convex pointing volarly. The proximal facet slopes strongly dorsally and the distal facet is convex. The orientation of the facets is lateral. Proximally, the slightly concave facet articulates with the radius. From this facet a round-to-triangular, flat lateral facet to the lunar continues laterally. Distally, there is a convex facet to the trapezoid that continues in proximal direction slightly to the lateral side, where it should end proximal to the magnum. Also from this facet there is a lateral continuation: a small round-to-triangular, flat distal facet to the lunar. Approximately in the middle of the lateral side, a distinct depression is present.

| Scaphoid measurements $(\mathrm{mm})$ | sin. | Scaphoid measurements $(\mathrm{mm})$ | sin. |
| :--- | :---: | :--- | :---: |
| Maximum height | 115 | Depth facies articularis proximalis (for radius) | 48 |
| Depth | 50 | Depth proximal facies articularis lateralis (for lunar) | 15 |

Cuneiform (os carpi ulnare) (Pl. 3, Fig. 2-4): The cuneiform dext. is preserved. The form of the specimen is very elephantoid-like in its articular surfaces and general form. In dorsal view the bone is round-to-triangular with a prominent laterovolar extension. In anterior view the proximal facet that articulates with ulna is laterally sloping. In addition, in proximal view the proximal facet is dorsovolarly on the medial side concave and then slopes strongly laterally. The distal surface has a facet for the unciform. The facet is flat medially and concave and round laterally. The laterovolar extension has on its distal surface an elongated, additional facet for articulation with McV . The volar surface bears a flat facet to the pisiform. The form of the facet is rectangular with a laterodistal extension. The cranial surface of the bone bears a lateral depression. The medial surface bears long proximal and distal facets to the the lunar. The distal facet is wider than the proximal.

| Cuneiform measurements (mm) | dext. | Cuneiform measurements (mm) | dext. |
| :--- | :---: | :--- | :---: |
| Maximum length | 90 | Depth facies articularis distalis (for unciform) | 96 |
| Maximum width | 155 | Width facies articularis distalis (for unciform) | 95 |
| Height dorsal surface | 53 | Length laterovolar process | 102 |
| Height volar surface | 62 | Width laterovolar process | 40 |
| Depth facies articularis proximalis (for ulna) | 86 | Depth laterovolar process | 35 |
| Width facies articularis proximalis (for ulna) | 103 |  |  |

Magnum (os carpale tertium) (Pl. 3, Fig. 3): The magnum dext. is mounted and its position in the middle of the carpal bones prohibits many of the measurements. Nonetheless, it can be confirmed that the magnum of Prodeinotherium is very elephantoid-like. In dorsal view it is mediolaterally compressed, but it widens out posteriorly in the medial direction. The proximal surface that is occupied by the lunar (cast) is flat dorsally and elevated volarly. The mediovolar corner has an extension giving the proximal facet an L-shape in medial direction. The L-formed extension is the place where the scaphoid is in contact with the magnum. The distal surface is slightly concave and has a wide dor-
sal and a narrow volar surface, between which lies the greatest concavity. The magnum has two contacts for the metacarpals. On the distomedial side of the distal surface articulates with McII, whereas most of the distal, concave surface articulates with McIII. On the medial side there are large and flat proximaodorsal and volar facets to the trapezoid. The lateral surface bears a long proximal facet for the unciform. There is no mediodistal articulation with the unciform. On the volar surface, a large tuberosity is present.

| Magnum measurements (mm) | dext. | Magnum measurements (mm) | dext. |
| :--- | :---: | :--- | :---: |
| Maximum depth | ${ }^{*}$ | Depth dorsal edge | 70 |
| Width dorsal edge | 75 | Depth volar edge | 90 |
| Width volar edge | 75 | Length proximal facet | 90 |

Unciform (os carpale quartum) (Pl. 3, Fig. 2-4): The unciform dext. and sin. are complete. In all views except medial and lateral, the form of the element is nearly triangular. The proximal surface is convex in a craniovolar direction, but it also slopes strongly laterally. The lateral edge of the proximal surface follows the cuneiform extension. The distal facets to the metacarpals are formed differently. The McIII facet on the medial edge is almost vertical in dorsal view. The McIV facet is the largest of the three facets and is elevated in volar direction, forming a slight concavity. The McV facet slopes strongly proximally in lateral direction. The volar surface bears a large tuberosity; some of the McV facet is also visible in this view. On the medial side there is a proximal articulation with the magnum. This is a tall and continuous facet. There is no distal articulation with the magnum on the medial surface.

| Unciform measurements (mm) | dext. |
| :--- | :---: |
| Maximum length | 111 |
| Maximum width | 98 |
| Maximum height | 80 |
| Length facies articularis proximalis | 89 |
| Width facies articularis proximalis | 121 |
| Length facies articularis distalis (for McV) | 74 |
| Width lateral facies articularis distalis (for McV) | 58 |
| Length lateral facies articularis distalis (for McIV) | ${ }^{*}$ |
| Width facies articularis distalis (for McIV) | 66 |
| Length medial facies articularis distalis (for McIII) | ${ }^{*}$ |
| Width medial facies articularis distalis (for MclII) | ${ }^{*}$ |

Os metacarpale secundum (McII) (Pl. 3, Fig. 4): The McII sin. is complete. The proximal end bears two elongate facets that are of approximately equal size. The lateral facies articularis proximalis to the magnum slopes slightly laterally, the medial facies articularis proximalis to the trapezoid is slightly concave. The McIII facet on the lateral side of the proximal end is continuous but not high, and the trapezium facet medially on the proximal end is rounded and small. The continuous margo medialis and margo lateralis separate the facies dorsalis and volaris. The corpus is columnar in shape. At the distal end, the trochlea slopes in medial direction. On the volar side of the trochlea, the
sesamoid contacts are well developed and deep. The surface of the corpus has many tendon attachments. The distal attachments, present as small tuberosities, are proximal to the medial and lateral sides of the trochlea. There are depressions distal to the medial and lateral metacarpal facets.

| Mcll measurements (mm) | sin. | Mcll measurements (mm) | sin. |
| :--- | :---: | :--- | :---: |
| Maximum height | ${ }^{*} 145$ | Width trochlea | 78 |
| Length trochlea | 68 |  |  |

Os metacarpale tertium (McIII) (Pl. 3, Fig. 3-4): The McIII dext. is complete. The facies articularis proximal bears one triangular facet for articulation with the magnum. In dorsal view, its edge is concave, but in lateral view it is dorsally flat and then slopes volarly. Laterally, an almost vertical facet to the unciform is present and, distal to that, at an angle of ca. 45 degrees, there is a McIV facet. Medially, there is a continuous and thin facet for McII. The corpus is columnar, divided by margo medialis and lateralis into dorsal and volar facies. The trochlea is symmetrical. Many tendon insertion points are present along the corpus. The most prominent attachments are distal to the medial and lateral articulating facets, and on the dorsal surface they are distal to the proximal facet.

| McIII measurements (mm) | dext. |
| :--- | :---: |
| Height | ${ }^{*} 160$ |
| Depth trochlea | ${ }^{*} 65$ |
| Width trochlea | ${ }^{*} 65$ |
| Length medial facies articularis proximalis (for magnum) | ${ }^{*} 85$ |
| Width medial facies articularis proximalis (for magnum) | ${ }^{*} 65$ |
| Length lateral facies articularis distalis (for unciform) | ${ }^{*} 85$ |
| Width lateral facies articularis distalis (for unciform) | ${ }^{*}$ |

Os metacarpale quartum (McIV): McIV dext. is complete. The proximal facies articularis is somewhat triangular. In medial view, the proximal head is strongly elevated volarly and the dorsal side is slightly convex, the volar side concave. The trochlea declines laterally. The corpus is columnar and has the characters of the metacarpals described above.

| McIV measurements (mm) | dext. | McIV measurements (mm) | dext. |
| :--- | :---: | :--- | :---: |
| Height | ${ }^{*} 130$ | Depth trochlea | ${ }^{*} 70$ |
| Length facies articularis proximalis | ${ }^{*} 69$ | Width trochlea | ${ }^{*} 75$ |
| Width facies articularis proximalis | ${ }^{*} 69$ | Width facies articularis medialis (for MclII) | ${ }^{*} 25$ |

Ossa pelvis (Pl. 1, Fig. 3): The pelvis is badly damaged and many of the original fractures and edges have been reconstructed. Only the overall pelvic dimensions can be estimated because the symphysis is missing and only the cranial part of the os pubis is preserved. In cranial view, the medial edges of the ilium are preserved. Most of the ala ilica surface has been reconstructed as almost flat with some concavity in the middle. The
corpus ossis pubis is thin and the eminentia iliopubica is very small. In caudal view, the distal edges of the corpus ossili ilii between tuber coxae and lateral edge of the acerabuli are strongly concave. In this view, most of the facies glutaea has been reconstructed.

| Ossa pelvis measurements (mm) |  |
| :--- | :---: |
| Maximum width | 1200 |
| Maximum height (from ilium to symphysis cranial) | 600 |
| Width from acetabuli sin. to dext. (measured at lateral edges) | 670 |
| Length ilium (margo sacralis - tuber coxae) | 600 |
| Width ilium (tuber coxae sin. - dext.) | 440 |
| Width corpus ossis ilii | 175 |
| Height and width acetabulum | 140,160 |
| Craniocaudal and lateromedial width of corpus ossi pubis | 94,72 |
| Height and width of apertura pelvina | 420,450 |

Femur (Pl. 1, Fig. 4): Both femur dext. and sin. are preserved. On both sides, the collum ossis femoris and trochanter major have been prepared. In the original illustrations of Kittl (1908) and in Fig. 1, the trochanter sin. is missing. Overall, the femur is elongate. The cranial surface is convex and the caudal surface is flat. The minimum width is circa at the middle of the shaft. Proximal to the condyles, the corpus widenes. Proximally, the caput is round and not clearly separated from the trochanter major by a collum. The reconstructed fossa trochanteria is shallow, but this is not necessarily correct. Distal to the caput, on the medial side, a minute trochanter minor is visible. On the unfused distal epiphysis, the articulating condyles for tibia are complete. On the cranial side there is a trochlea ossis femoris that bears well-pronounced, sharp elevations for articulation with the patella. Caudally, the condylus medialis and lateralis are separated by a small and deep fossa intercondylaris. The condylus medialis is slightly wider than the lateral. The facies poplitea proximal to the condyles is shallow and rounded. There is also a well-pronounced medial and a less pronounced lateral, epicondyle.

| Femur measurements (mm) | dext. | Femur measurements (mm) | dext. |
| :--- | :---: | :--- | :---: |
| Maximum length | 1055 | Width at condyles | 200 |
| Width caput | 155 | Width over the condyli | 95 |
| Width at middle of shaft | 112 | Width fossa intercondylaris | 40 |
| Depth at middle of shaft | 100 |  |  |

Patella (Pl. 1, Fig. 4): Both patella dext. and sin. are complete. They have been mounted directly on the femora and their articulating facets are therefore not measurable. The form is rounded with a prominent medial tuberosity on the facies cranialis. There are two articulating surfaces to the femur that are concave in proximodistal direction, but separated by a median elevation. The lateral facies articularis is wider than the medial.

| Patella measurements $(\mathrm{mm})$ | sin. | Patella measurements $(\mathrm{mm})$ | sin. |
| :--- | :---: | :--- | :---: |
| Maximum length | 119 | Maximum width | 105 |

Fibula (Pl. 2, Fig. 4): The fibula dext. lacks its caput, the shaft proximal to the unfused distal epiphysis and some of the plantar shaft. In mounted position the fibula runs proximodistally from the plantar tibia to the lateral side of the tibia, and has distal articulations with the tibia, lateral astragalus and calcaneum. The overall form of the fibula has not suffered much from its missing pieces. In cross-section, the proximal form is triangular, pointing in a dorsal direction. Distally, the shaft initially becomes rounded and in the distal half it becomes mediolaterally flattened. In lateral view, the shaft widens out in the distal half. The distal facets for astragalus and calcaneus articulation - facies articularis malleoli - are concave and skewed in a medial direction. There is a small, rounded medial facet for articulation with the lateral tibia.

| Fibula measurements (mm) | dext. | Fibula measurements (mm) | dext. |
| :--- | :---: | :--- | :---: |
| Length | 620 | Width in the middle of shaft | 31 |
| Width distal end | 20 | Depth in the middle of shaft | 34 |
| Depth distal end | 70 |  |  |

Calcaneum (os tarsi fibulare) (Pl. 2, Fig. 5): Unfortunately the complete calcaneum sin. is mounted so that its articulating facets cannot be studied. The tuber calcanei is, in plantar view, higher than wide.

| Calcaneum measurements (mm) | sin. | Calcaneum measurements (mm) | sin. |
| :--- | :---: | :--- | :---: |
| Maximum length | ${ }^{*} 210$ | Width lateral facies articularis talaris | ${ }^{*} 65$ |
| Width proximal surface | ${ }^{*} 115$ | Length tuber calcanei | 110 |
| Width medial facies articularis talaris | ${ }^{*} 30$ |  |  |

Astragalus (os tarsi tibiale) (Pl. 2, Fig. 5): Unfortunately the astragalus dext. and sin., both complete, are mounted so that their articulating facets could not be studied. In medial view, a plantomedial tuberculum is visible. The proximal tibial surface is rectangular and convex. The articulation with the navicular is on the plantar side. The facet for the fibula, on the lateral side, is convex on the surface and rectangular in outline.

| Astragalus measurements (mm) | sin. | Astragalus measurements (mm) | sin. |
| :--- | :---: | :--- | :---: |
| Maximum width | ${ }^{*} 120$ | Width proximal tibial facet | ${ }^{* 100}$ |
| Length proximal tibial facet | ${ }^{*} 90$ |  |  |

Navicular (os tarsi centrale) (Pl. 2, Fig. 5): Although well preserved, the navicular sin. is nearly invisible in the mounted position. The specimen is correctly mounted proximally, but not distally. Altogether four distal facets are present, but only three distal facets have been identified. (Only meso- and ectocuneiform casts have been mounted distal to the navicular.) The general form is rounded with a small plantomedial extension. The facies articulars proximalis for astragalus is concave. The distal facets are slightly differently formed. In dorsal view, the lateral facet that articulates with the cuboid is elevated laterally. The second and third facet in medial direction for ecto- and mesocuneiform articulation are nearly flat with slight convexity. The medial facet for
articulation with endocuneiform is small and not clearly separate from the mesocuneiform facet. The thickness along the dorsal edge of the bone is even. The bone on the dorsal edge is porous, indicating a juvenile growth stage.

| Navicular measurements (mm) | $\sin$. |
| :--- | :---: |
| Total length and width | ${ }^{*}$ |
| Length and width astragalus facet | 85 |
| Width lateral facies articularis distalis (for cuboid) | ${ }^{*} 36$ |
| Width medial facies articularis distalis (for endo-, meso- and ectocuneiform) | $* 46,36,27$ |

## Comparisons and discussion

The description of the Franzenbad skeleton is important bcause the diagnostic characters of the Deintoheriidae postcranial skeleton are very poorly recorded. The first descriptions of associated elements were published by Stefanescu (1894) on the Romanian Deinotherium gigantissimum, by Е́нıк (1930) on the Hungarian Prodeinotherium hungaricum and by Stromer (1938) on Deinotherium giganteum finds from the Flinzsande of München, Germany. The first summary of the Deinotheriidae postcranial characters was written by Dietrich (1916). Later, Tobien (1962), and Bergounioux \& Crouzel (1962a, b) followed this work by describing some general characters of the genus Deinotherium in Europe. Мотtl (1969), in her description of the Styrian (SE-Austria) Proboscidea material gave diagnostic characters that separate the species Tetralophodon longirostris and D. giganteum. The first lists on the differences between the Deinotheriidae and the Elephantoidea and between the genera Prodeinotherium and Deinotherium were published by Harris $(1973,1978)$. The revised diagnoses of both Deinotheriidae genera by Harris $(1973,1978)$ already include three distinct postcranial characters. Consequently, the best postcranial diagnoses of Prodeinotherium are only at the generic level. The Franzensbad skeleton provides an excellent starting point for a further study of generic characters because all elements belong to single individual. The following comparisons summarize the known morphological characters and discuss them in the light of the information provided by the Franzensbad skeleton and additional comparative material.
Comparative material:
BSP - mandible and several postcranial elements (Unterzolling skeleton, Bavaria, BSP 1977 I 299, Middle Miocene, MN6)
HLMD - radius (Eppelsheim, Dinotheriensande HLMD Din 1027, Late Miocene, MN9)
LMJ - atlas (Holzmannsdorfsberg LMJ 61634, Late Miocene)
ML - mandible (La Grive M, France, Middle Micocene, MN7/8)
MNHN - unciform, navicular (Chevilly, Pontlevoy, France CHE2, FP2697, FP131, Early and Middle Miocene, MN4)
NHMW - mandibles (Kettlasbrunn, Austria NHMW1973/1620, Brunn-Vösendorf, Austria, NHMW2000z0046, Schwechat, Austria NHMW2000z0045, all Late Miocene)
HNHM - atlas (Györzentmarton, V.6819)
PM - postcranial elements (Höwenegg skeleton, casts, Germany, Late Miocene, MN9)


Fig. 4: Prodeinotherium and Deinotherium toothrow comparisons.

Mandible: The comparative material from the Middle and Late Miocene of Europe indicates strongly that all deinothere mandibles share the same basic morphology with a downturned symphysis, lower incisors, straight corpus mandibulae and a straight angulus. Differences between Prodeinotherium and Deinotherium may be detected in the dimensions of the mandible, teeth and in p3 tooth morphology. The Franzensbad toothrow (see Fig. 4) is of similar size as the Prodeinotherium toothrow from Unterzolling. The Deinotherium toothrows from La Grive, France (Middle Miocene) and the Austrian Late Miocene localities are larger.

The measurements of the comparative material (below) show that the symphyseal flexure is related to the anteroposterior extent of the symphysis - the longer the symphysis, the stronger the flexure. A common character to all Deinotherium specimens is a welldeveloped depression between the processus coronoideus and the caput for insertion of the musculus temporalis lateralis. The same region is nearly flat in Prodeinotherium. The La Grive mandible (original description as D. levius, Depéret, 1887) shares all characters of the Deinotherium mandibulae.

The dimensions of the Prodeinotherium mandible from Unterzolling are larger than those of the Franzensbad specimen, although the occlusal plane (toothrow and corpus mandibulae) are of similar size. This may be due differences in ontogenetic development, as the Unterzolling skeleton is that of an older individual than the Franzensbad skeleton. A similar difference is present also between the Brunn-Vösendorf and Schwechat specimens from Austria (detailed specimen descriptions in Huttunen 2000).

It is interesting how the large incisor size could be compensated by the cranial morphology and musculature to enable a similar orthal movement for mastication in the dif-ferent-sized individuals. The feeding mechanisms for proboscideans have been studied by Chang (1929), Gräf (1956), Maglio (1972), and by Harris (1975). The mandible morphology and muscle insertion reconstructions of HARRIS (1975: figs. 6B, 7A, 7B) show that the forces acting in opposite direction of the mass of the lower incisors are provided by temporal, masseter, and digastric muscles that all originate from the surface
of the ramus. Comparing the cranial morphology of Prodeinotherium and Deinotherium points to a strong modification and increase of the muscle insertion areas in the largesized deinotheres even though the mandible morphology remained the same. The Prodeinotherium cranium is characterized by a low rostrum that is parallel to the mandibular symphysis and by a skull roof that is long and wide (diagnosis by Harris 1973). The area for temporal and masseter muscle insertions are of moderate size. The Deinotherium cranium is different with an anteriorly steeply downturned skull rostrum, narrow external nares and rostral trough, and with steeply inclined occiput (Harris 1973, 1983). The area for temporal and masseter muscle insertions are of moderate size. Further important modifications in Deinotherium are muscle insertions for the temporalis muscle and masseter on the maxilla distal and anterior to the orbit; these insertions are strongly concave and high. Even though mandibular morphology is the same in both genera, it may be assumed that the power of the feeding mechanisms was enhanced or became more efficient in Deinotherium compared to Prodeinotherium. Therefore it may be assumed that the Prodeinotherium mandibles from Franzensbad and Unterzolling were associated with a different kind of cranium than the La Grive and Austrian mandibles.

|  | Prodeinotherium | Deinotherium |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Measurement (mm) | Unterzolling, Germany | La Grive M, France | Brunn-Vösendorf, Austria | Schwechat, Austria | Kettlasbrunn, Austria |
| Mandibular plane | 680 | 710 | *600 | * | - |
| Distance from angulus mandibulae to caput | 330 | 400 | - | *380 | - |
| Depth between caput and the processus coronoideus | 280 | 250 | - | 330 | - |
| Length from the symphysis from p3 alveolus to incisor alveolus | 350 | 400 | - | - | 430 |
| Toothrow length | 310 | 333 | *380 | 380 | 410 |
| Height of the corpus mandibulae at $\mathrm{m} 2, \mathrm{~m} 3$ | $\begin{aligned} & 120 \\ & 115 \end{aligned}$ | $\begin{aligned} & 155 \\ & 145 \end{aligned}$ | $\begin{aligned} & 150 \\ & 147 \end{aligned}$ | $\begin{aligned} & 200 \\ & 180 \end{aligned}$ | $\begin{aligned} & 210 \\ & 170 \end{aligned}$ |
| Width of the corpus mandibulae at p4, m1, m2, m3 | $\begin{aligned} & 109 \\ & 100 \\ & 113 \\ & 119 \end{aligned}$ | * | $\begin{aligned} & 100 \\ & 105 \\ & 125 \\ & 145 \end{aligned}$ | $\begin{aligned} & 135 \\ & 165 \\ & 175 \end{aligned}$ | $\begin{aligned} & 120 \\ & 140 \end{aligned}$ |
| Anteroposterior depth of the symphysis | 185 | * | - | - | 360 |
| Width of the symphysis at incisor alveoli | 209 | 190 | - | - | 310 |
| Width of the symphysis at p3 alveoli | 185 | 120 | - | - | 160 |

Atlas: The general characters of the deinothere atlas are: an open neural canal, orientation and shape of the axis facets, visible foramen in cranial view, and a large odontoid fossa (Mottl 1969). The Prodeinotherium specimen from Chevilly, France, is a small, juvenile specimen. It has a general Prodeinotherium arcus dorsalis because the tubercu-
lus dorsale covers the surface of the arcus. It differs from the adult specimens in the orientation of the axis facets, which clearly point medially. Since it is a juvenile specimen (width at occipital facets 190), this might be an early ontogenetic stage. The Deinotherium specimens from Holzmannsdorfsberg, Austria (width at occipital facets 255 , maximum width 370 , height 210) and Györzentmarton, Hungary (width at occipital facets 330 , maximum width $* 450$, height 320 ) represent two distinct size classes. Whereas the Austrian specimen is Prodeinotherium-like, the Hungarian specimen is different in that the tuberculum dorsale is a high knob instead of an elongated crest and the neural canal is extermely open and large. The same morphology is also present in the mounted skeleton from Eserovo, Bulgaria. This evidence suggets that all deinotheres have a fairly similar atlas morphology, but that the largest specimens of Deinotherium differ in the capacity of the neural canal and the tuberculum dorsale.
Scapula: Harris $(1973,1978)$ has identified a generic difference in the form of the meta- and acromion: they are present in Prodeinotherium and absent in Deinotherium. These characters are confirmed here, even if the comparative material was too fragmentary for detailed measurements. It is apparent that the scapulae of Deinotherium are larger than Prodeinotherium and that morphological variation is present within Prodeinotherium. The Prodeinotherium scapulae from Unterzolling, Germany, have slightly smaller cavitas glenoidalis (length and width sin. 202, 134 and dext. 199, 134) than the Franzensbad specimen. The Unterzolling specimens bear a distal part of the spina scapulae but no remnants of an acromion. In the Deinotherium specimen from Eserovo, both infra- and supraspinous fossa are triangular, the supraspinous fossa being only about one-fourth the width of the infraspinous fossa. Cranial and caudal angles are sharply pointed. The spina lacks an acromion and tuber spina scapulae. It is an elongated structure with maximum elevation at its distal end, which is reduced in proximal direction. It is curved slightly cranially along its proximal third, where it also merges with the margo dorsalis. The spina scapulae is concave caudally and convex cranially. The morphological differences in Deinotherium in relation to Prodeinotherium have been interpreted by Harris (1978) as due to cursorial modifications in the former.
Humerus: Harris $(1973,1978)$ listed the form of the lateral epicondyle as the most important character to distinguish between Deinotheriidae genera. He was of the opinion that in Prodeinotherium it tapers proximally while in Deinotherium it does not. No clear tapering of the lateral epicondyle could be observed in the comparative material. There is a clear morphological difference in the lateral epicondyles between the genera, but this is related to the extent of the crista epicondylus lateralis, and not to the lateral epicondyle. In both genera, the crista epicondylus lateralis continues proximocaudally. In Prodeinotherium the crista continues farther on the lateral side and then turns medially. In Deinotherium the crista turns sharper medially. The crista humeri is not present or reduced in Deinotherium. The resulting morphology is a deep sulcus musculi brachialis in Prodeinotherium that is lacking in Deinotherium. The Franzensbad specimen has somewhat similar proportions as the Unterzolling specimen. Note, however, that epicondylar morphology differs between these specimens. The Franzensbad specimen has a medial extension on the medial epicondyle, which is lacking in the Unterzolling specimen. The outline of the lateral epicondyle is round to uneven in cranial view in the Unterzolling specimen, whereas the Franzensbad specimen is irregular.

Ulna: There has been no previous investigation of the generic differences of the deinothere ulnar morphology. The new comparative material suggests that in Prodeinotherium this bone is uniform in morphology, varying only in size. The incisura radialis and the incisura trochlearis on the Prodeinotherium ulna are deep, while these structures are very shallow in Deinotherium ulnae. Additional characters of the Deinotherium ulna from Eserovo include that the distal third of the bone is mediolaterally flattened in relation to the proximal part, as the median articulation with the radius takes place there. The incisura radialis is hardly visible. The dorsal facet is, in its proximal third, skewed medially to articulate with the lateral side of the radius.
Radius: Harris $(1973,1978)$ has identified as a character differentiating deinothere genera a contrast in the relative size of proximal and distal ends of the bone: in Deinotherium this difference is much larger than in Prodeinotherium. The Franzensbad radius is from a juvenile specimen, perhaps explaining the formation of the large, still growing distal epiphysis. The specimen from Eppelsheim was badly deformed, but the overall size (length 630 mm ) suggests that it is a Prodeinotherium. A Deinotherium radius from Eserovo shows no distinct triangular-to-round neck distal to the caput radii as seen in Prodeinotherium and its entire shaft is mediolaterally flattened. The radius does not extend much medially, but occupies the medial area that is reduced in the ulna.
Scaphoid: One complete Deinotherium specimen was available. The scaphoid dext. of Höwenegg, Germany, is one third larger than the Franzensbad specimen (height 163 mm ). In medial view, the dorsal edge has a slight S-form, but the volar edge is convex. In lateral view, the facets differ slightly. There is no differential distal facet to the lunar. Instead, the distal trapezoid facet continues on the lateral side, forming a large, flat, continuous area of articulation where the proximal part is additionally in contact with magnum. The form of the Deinotherium scaphoid is an indication of a differential arrangement of the carpal bones compared to the wrist in Prodeinotherium. The distal facet is not distally in contact with the lunar, only with the trapezoid and magnum.

Cuneiform: According to Harris (1978: 319), the volar-lateral process of Deinotherium is longer and more ventrally inclined than that of Prodeinotherium. According to Tobien (1962: 232), the process does not articulate with the fifth metacarpal. The Eserovo specimen did articulate with the fifth metacarpal, but it is uncertain whether this was due to the preparation and reconstruction of the specimen. Another character listed by Harris (1978: 319) to distinguish deinothere genera is the formation of the distal unciform surface. In Prodeinotherium it should be concavoconvex, and in Deinotherium biconcave. The distal surface of the Franzensbad specimen is not concavoconvex, but rather flat-toconcave. All study specimens have a lateral depression on the dorsal surface, which seems to be a general character of deinotheres. Accepted generic differences are therefore in the form of the distal facet and in size (Harris 1978). The orientation of the volar-lateral process is generally sharper in distal direction in Deinotherium and it probably did not articulate with the fifth metacarpal (as in Tobien 1962).
Magnum: Only Deinotherium comparative material was available. In general, there are only small differences between the two genera. The Deinotherium magnum sin. of Eserovo differs from Prodeinotherium in the form of distal articulation. It has distal contacts to McII and McIII. McIII is not entirely distal to the magnum, but it is placed distally to the lateral half of the unciform, enhancing the aserial organization of the manus.

Harris (1978) has recorded as a generic difference that Prodeinotherium has a small volar-medial extension, but that this is still larger in Prodeinotherium than in Deinotherium. Tassy (1986) recorded variability in the medial facets to the trapezoid of P. hobleyi. These characters could not be studied in the Franzensbad skeleton because the specimen was mounted.
Unciform: Comparative material of both genera was available. The Prodeinotherium specimens were nearly identical to the Franzensbad specimen, differing mainly in proportions. The Höwenegg and Eserovo Deinotherium specimens have a proximal facet that has a strong, convex part in the dorsomedial corner and the rest sloping in volar and lateral direction. Generic differences are present on the distal surface. Tobien (1962) stated, based on the Höwenegg material, that the area of the distal facet in Deinotherium decreases in the order McIV $>$ McIII $>\mathrm{McV}$. This differs from the Prodeinotherium condition of the Franzensbad specimen, where the order is McIV>McV>McIII and the McIII articulation is on the medial edge, not clearly distal to the unciform. Harris (1973) observed for the African P. hobleyi that the McV facet is the largest distal facet. Also, according to Harris (1978), the proximal cuneiform facet in Deinotherium extends farther volar-laterally and distally and tapers more abruptly volarly.
Pelvis: The Prodeinotherium from Unterzolling is very fragmentary. It is a fragment of the corpus os ilii dext. with the dorsal half of the acetabulum. The distance between the lateral edge of the acetabulum and the tuber coxae is 370 mm . The estimated width of the acetabulum is $* 180 \mathrm{~mm}$, which is larger than in the Franzensbad specimen. Since both the study specimen and the comparison object were fragments, no more detailed morphological data could be obtained.
Fibula: A complete Deinotherium fibula from Eserovo was available for study. The proportional difference is remarkable (length 1170). The form of the shaft changes in crosssection so that below the caput it is round, changing then to dorsoplantarly flattened. In the distalmost part the form becomes round. In the proximal half the dorsal side facing the tibia is slightly concave. The distal end of the bone is much wider than the distal facet, which is not the case in Prodeinotherium. The plantar edge of the epiphysis bears a large tuberosity.
Astragalus: Tobien (1962) recognized an important deinothere feature: the navicular facet is situated on the plantar side so that all three distal facets are visible in distal view (Tobien 1962: 234). Harris (1973) stated that the Prodeinotherium tibial facet is rectangular and convex with a prominent tuberculum. The Prodeinotherium from Unterzolling has an extended plantomedial process that is stronger than in the Franzensbad specimen, which suggests that there is intraspecific variation in this element.
Navicular: The Unterzolling specimen differs from the Franzensbad specimen: its plantomedial extension is large and separated from the navicular by a small neck. The form of the extension is much more reduced in the Franzensbad specimen. There are also accessory facets to calcaneum on the plantomedial side of the bone. The Pontlevoy (France) specimens are also variable. Specimen number FP2697 is small and is from a juvenile individual whereas the specimen number FP131 is distinct with an accessory facet on the proximal surface of the plantomedial extension. The accessory contacts to calcaneum have not been recorded for Prodeinotherium before.

## Conclusions

The comparisons with other European Deinotheriidae mandibular and postcranial material confirm that the Franzensbad skeleton is similar to other Middle Miocene Prodeinotherium finds of Europe. The study also supports the division of the family Deinotheriidae into two distinct genera, Prodeinotherium and Deinotherium. The comparisons provide an extended diagnosis for $P$. bavaricum. The yet undescribed cranial and postcranial remains in Europe (Langenau, Germany and Montreal de Gers, France) will certainly provide additional characters to this list.

A summary of the most important characters of the skeleton in Prodeinotherium and Deinotherium, based on comparisons of European material, is listed in tabular form below:

| ELEMENT | Prodeinotherium | Deinotherium |
| :---: | :---: | :---: |
| Mandible | Narrow corpus mandibulae, incisors may be long but not stout, ramus never posteriorly extended. | In the largest specimens the angle and ramus mandibulae may be posteriorly extended. |
| Atlas | Open canalis vertebralis, foramen vertebrale are visible in the cranial view, open fovea dentale, medial edges of the axis facets may be slightly medially pointed. | Largest specimens have a knob-like tuberculus dorsale. |
| Scapula <br> (HARRIS 1978) | Stout spine, metacromion and acromion, supraspinous fossa well developed. | Reduced spine and no metacromion or acromion, supraspinous fossa reduced. |
| Humerus | Deep sulcus m. brachialis, well-pronounced crista humeri. | Reduced crista humeri and sulcus m. brachialis. |
| Ulna | Lateral edge present yielding a four-sided form in transverse section, deep incisura radii. Deep incisura trochlearis. | Triangular form in transverse section, open and shallow incisura radii, distal end mediolaterally compressed. Reduced incisura trochlearis. |
| Radius | Form of the diaphysis is triangular at proximal end and mediolaterally flattened at distal end. At the neck a strong muscle attachment. | Form of the diaphysis more mediolaterally flattened in the proximal diaphysis. No clear deep muscle attachment at the neck. |
| Lunar <br> (HARRIS 1978) | Radial facet covers most of proximal surface, magnum facet is concave-convex. | Radial facet extends less far posteriorly, magnum facet almost flat. |
| Scaphoid | Dorsal edge W-formed, distal articulation with trapezium and trapezoid. | Dorsal edge S-formed. |
| Cuneiform | Distal facet flat-concave. | Distal facet biconcave. |
| Unciform (HARRIS 1978, Huttunen 2000) | Cuneiform facet roughly triangular, largest distal facet is for McV. <br> Medial articulation with magnum present. | Cuneiform facet extends farther volarly, laterally and distally and tapers more abruptly volarly. Distal facet for Mclll larger, facet for McV is nearly vertical, mediodistal articulation with magnum present. |
| Magnum (Harris 1978) | Proximal surface has large volar-medial projection. | Volar-medial projection is less pronounced. |
| Fibula | Form of shaft round at proximal end, lateromedially flattened in the distal half. | Form of shaft proximally flattened. |
| Astragalus (HARRIS 1978, Huttunen 2000) | Tibial facet rectangular and convex, strong plantomedial tuberculum, may be separated by a neck. | Tibial facet rectangular but nearly flat, reduced plantomedial tuberculum, lateral navicular facet may be extended in plantar direction. |

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## Plate 1

Prodeinotherium bavaricum from Franzensbad (NHMW2000z0047/0001)
mounted at the exhibition of NHMW.


## Plate 2

Prodeinotherium bavaricum from Franzensbad (NHMW2000z0047/0001)
Fig. 1: Mandible, lateral. - x 0.15 .
Fig. 2: Scapula dext., lateral. - x 0.16 .
Fig. 3: Ossa pelvis, ventral. - x 0.08 .
Fig. 4: Femur dext., cranial. - x 0.08 .
Fig. 5: Femur dext., caudal. - x 0.08 .


## Plate 3

Prodeinotherium bavaricum from Franzensbad (NHMW2000z0047/0001)
Fig. 1: Humerus sin., cranial, ulna, radius sin., dorsal. - x 0.14 .
Fig. 2: Ulna, radius sin., dorso-lateral. - x 0.14 .
Fig. 3: Ulna dext., lateral. - x 0.13 .
Fig. 4: Fibula dext., lateral. - x 0.13 .
Fig. 5: Tarsus dext., lateral. -x 0.13 .


## Plate 4

Prodeinotherium bavaricum from Franzensbad (NHMW2000z0047/0001)
Fig. 1: Scaphoid sin., lateral. - x 0.5 .
Fig. 2: Ulna, cuneiform, unciform sin., lateral. - x 0.30.
Fig. 3: Manus sin., dorsal, - x 0.19 .
Fig. 4: Unciform, McII, McIII dext., dorsal - x 0.27 .



[^0]:    ${ }^{1}$ c/o Naturhistorisches Museum Wien, Geologisch-Paläontologische Abteilung, Postfach 417, A-1014 Wien. - Austria. - e-mail: kati_jh@yahoo.de

