Anchitherium aurelianense (Equidae, Mammalia) from the Middle Miocene of the Bohlinger Schlucht, South-West Germany

SAMUEL GIERSCH & RAYMOND L. BERNOR

Abstract
The Middle Miocene (Upper Badenian, MN6) locality Bohlinger Schlucht (Hegau District, South-West Germany) has yielded a diverse assemblage of land mammals and lower vertebrates. After discovery in 2003, the ongoing excavations increased the number of taxa and here we report on the first equid remains of Anchitherium aurelianense from the locality. The best taxonomic referral of this specimen is to the subspecies A. aurelianense hippoides. A comparison of the Bohlinger Schlucht locality to contemporaneous Western Europe localities is further discussed herein.

Kurzfassung
Anchitherium aurelianense (Equidae, Mammalia) aus dem Mittelmiozän der Bohlinger Schlucht, Südwest-Deutschland

Authors
SAMUEL GIERSCH, Staatliches Museum für Naturkunde, Referat für Paläontologie und Evolutionsforschung, Erbprinzenstraße 13, D-76133 Karlsruhe; E-Mail: samuel.giersch@smnk.de
RAYMOND L. BERNOR, College of Medicine, Department of Anatomy, Laboratory of Evolutionary Biology, Howard University, 520 W. St. N.W., Washington D.C. 20059 E-mail: rbernor@comcast.net and rbernor@nsf.gov

1 Introduction
The narrow and steep canyon of “Bohlinger Schlucht” is located on the Höri-peninsula near the western margin of Lake Constance in South West Germany (topographic map 8219, Singen (Hohentwiel), R 692156, H 85186; fig. 1). There we find exposed sediments of the Middle Miocene Upper Freshwater Molasse. The
locality was first discovered in the middle of the 19th century and has been recognized as being an important Miocene fossil plant site (Heer 1859, Hantke 1954, Rutte 1956). The “Schrotzburg”-marls in the upper part of the Bohlinger Schlucht have yielded a diverse macro- and micro-flora, which was recently used for analysis of palaeoclimate of the Middle Miocene (Uppermost Badenian-Lowermost Sarmatian) central Molasse basin (Uhl et al. 2003, 2006). Additionally, in 2003 vertebrate fossil bearing layers were discovered by one of the authors (SG) in the Bohlinger Schlucht. The fossil bearing horizons are within muscovite-rich, finegrained, loosely consolidated sands of the “Steinbalmensande”. Inside the Steinbalmensande occur the “Krokodil-Schichten” in several horizons. These layers are channel-fillings consisting of reworked, coarse-grained clays and marls which contain bone fragments and teeth of mammals and reptiles as well as molluscs and plant remains. More than 300 specimens of 22 different mammal taxa and five reptile taxa including the crocodylian Diplocynodon were discovered during first excavations in 2003. The mammal assemblage includes both micro- and macro-mammal remains and is correlative with the upper part of mammal-Zone MN6, Upper Badenian (Giersch 2004 a, b). The occurrence of a well dated fauna next to palaeoclimatologically significant plant-remains makes the Bohlinger Schlucht an extraordinarily important site for palaeoecological studies of the Middle Miocene in South West Germany. Ongoing excavations unearthed further mammal taxa and the faunal list of 2006 contains the first equid remains of Anchitherium aurelianense, which we describe herein.

2 Material and Methods

The investigated material includes a fragment of the left mandible with m2 and m3. The specimen was prepared from its sandy matrix using hand tools and fixed with cyan acrylate glue. The specimen is housed in the palaeontological collection of the Staatliches Museum für Naturkunde in Karlsruhe with the collection number SMNK-PAL. 6600.

For classification and terminology of dental structures we follow Aibusch-Siewert (1983) and Daxner-Höck & Bernor (2009). Digital photos were taken by the Authors.

Comparative material

Original material from Sansan (MN6): NMB SS 4877, 4878, 4879, housed in the Naturhistorisches Museum in Basel (Switzerland).

Original material and casts from Steinheim (MN7): SMNS 43843 a, b, c, housed in the Museum für Naturkunde in Stuttgart.

Abbreviations

L Maximum length of the tooth crown
m1/2 lower first or second molar
m2 second lower molar
m3 third lower molar
SMNK Staatliches Museum für Naturkunde in Karlsruhe
SMNS Staatliches Museum für Naturkunde in Stuttgart
NMB Naturhistorisches Museum Basel
Wa Maximum width of anterior crescent of tooth crown
Wp Maximum width of posterior crescent of tooth crown

3 Systematic Palaeontology

Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Genus Anchitherium Cuvier, 1812
Anchitherium aurelianense (Cuvier, 1812) (Fig. 2, Tab. 1)

Type locality: Montabussyard (France), Early Miozene (MN4).

Locality: Bohlinger Schlucht near Bohlingen (Baden-Württemberg), Upper Freshwater Molasse, Steinbalmensande; Middle Miocene (Early Astaracian, MN6); 14,0-13,5 Ma.

Material: Specimen SMNK-PAL. 6600, Fragment of the left mandible with m2 and m3 in situ.

Table 1. SMNK-PAL. 6600 Anchitherium aurelianense (Cuvier, 1812) from the Bohlinger Schlucht, Upper Freshwater Molasse (MN6), measurements in mm:

<table>
<thead>
<tr>
<th>Position</th>
<th>L</th>
<th>Wa</th>
<th>Wp</th>
</tr>
</thead>
<tbody>
<tr>
<td>m2 inf. sin.</td>
<td>20.1</td>
<td>13.9</td>
<td>12.6</td>
</tr>
<tr>
<td>m3 inf. sin.</td>
<td>21.3</td>
<td>12.3</td>
<td>10.9</td>
</tr>
</tbody>
</table>
Anchitherium aurelianense from Bohlinger Schlucht SMNK-PAL 6600, left dentary with m2-m3 in A): lingual; B): occlusal and C): labial views. Scale: 10 mm. – Foto: S.Giersch.
4 Description

The fragment of the left mandible is broken mesial to m2. The root of the ramus mandibulae is preserved distal to m3. The insertion scar for temporomandibularis muscle is lost. The dentition is brachydont with a crown height of approximately 50% of anterioposterior tooth length.

m2: The second molar is rectangular to trapezoidal shaped in occlusal outline. A deep, labiolingually running ectoflexid divides the tooth crown into two crescent-shaped portions which are open lingually. The anterior crescent is formed by the paralophid and protolophid. Metalophid and hypolophid form the posterior crescent. Metaconid, metastylid and entoconid are prominent cusps that protrude 2 mm above the occlusal plane. A small groove separates the metalophid from the metastylid. Ento- and metaflexid are posterolabially curved. The metaflexid is lingually closed by a slight lingual cingulid, which courses from the paraconid distally and comprises a small enamel cuspid anterolingual to the metaconid. A labial cingulid nearly extends from the paraconid to the entoconid, being interrupted only at the base of the hypoconid. There is a prominent, albeit low crowned ectostylid at the base of the crown. The ectoflexid is closed labially by accessory enamel wrinkes. The crown exhibits a heavily worn distal aspect. The width of the posterior crescent is smaller than the anterior crescent.

m3: The third molar resembles the general shape and proportions of m2; however, a prominent hypoconulid effects a lengthing of the crown distally. A deep hypoflexid separates the hypoconulid from the hypoconid. An additional cuspid is located between the entoconid and hypoconulid on the posterolingual edge of the crown. The labial cingulum is complete except for a brief abbreviation on the hypoconid; the ectostylid is less pronounced than in m2. The labial enamel walls of both teeth exhibit a fine, horizontally orientated striation.

5 Discussion

The medium sized brachydont equid Anchitherium first occured in Europe during the early Miocene in the mammal-Zone MN3 (Abusch-Siewert 1983). In the middle Miocene Anchitherium is abundant and the dominant equid within the mammal assemblages throughout Europe. Between 11.2 Ma and 10.6 Ma Anchitherium cooc-

![Figure 3. Length to anterior width of m1/2 in different subspecies of A. aurelianense. Database after our own measurements and Abusch-Siewert (1983). The ellipses mark the 95% confidence interval.](image-url)
curs in Europe with the larger *Hippotherium* and *Cormohipparion* and becomes abruptly extinct shortly after basal Late Miocene (BERNOR & ARMOUR-CHELU 1999, DAXNER-HÖCK & BERNOR 2009, KAISER 2009).

ABUSCH-SIEWERT (1983) recognized three subspecies-lineages in European *Anchitherium aurelianense*. Based on morphological differences in dentitions, *A. aurelianense aurelianense* (CUVIER, 1812), *A. aurelianense steinheimense* ABUSCH-SIEWERT, 1983 and *A. aurelianense hippoides* (LARTET, 1851) were identified. *Anchitherium a. aurelianense* ranged from Wintershof-West (MN3) to Sandelzhausen and Georgensgmünd (MN5). *Anchitherium a. steinheimense* is reported from Steinheim (MN7) and *A. a. hippoides* is recorded from Sansan (MN6) and La Grive (MN7) (DAXNER-HÖCK & BERNOR 2009). The evolutionary lineage of Central European *Anchitherium aurelianense* exhibits a general trend towards size-increase and simplification of dental pattern, however large sample-sizes are essential to identify subspecies, because the dentitions show a wide variability in morphology and overlap in size-ranges (fig. 3 and 4 here and ABUSCH-SIEWERT 1983).

Therefore, the single specimen from Bohlinger Schlucht is really insufficient to certainly refer this sample to the subspecies level. Nevertheless, a general trend can be recognized in SMNK-PAL. 6600: The measurements of m2 and m3 in *Anchitherium* from the Bohlinger Schlucht (fig. 3 and 4) compare well with the middle of size-classes of Sansan *A. a. hippoides* (see also ABUSCH-SIEWERT 1983, p. 280, fig. 92; p. 281, fig. 93 and 94). Additional morphological characters visible in SMNK-PAL. 6600 and typical for *A. a. hippoides* include the pronounced hypoconulid and complete labial cingulid. A direct comparison with similar teeth from Sansan housed in the NMB supports the attribution of the Bohlinger Schlucht anchither to *Anchitherium a. hippoides*.

The comparison of measurements of SMNK-PAL. 6600 with the older *A. a. aurelianense* from Sandelzhausen shows that the majority of the comparable teeth of *A. a. aurelianense* are distinctly smaller (see fig. 3 and 4 and ABUSCH-SIEWERT 1983, p. 76, fig. 15; p. 83, fig. 16). Therefore, a referral of the Bohlinger Schlucht specimen with *A. a. aurelianense* seems to be more unlikely.

Size differences between the younger *A. a. steinheimense* and SMNK-PAL. 6600 are less

Figure 4. Length to anterior width of m3 in different subspecies of *A. aurelianense*. Database after our own measurements and ABUSCH-SIEWERT (1983). The ellipses mark the 95% confidence interval.
pronounced, however, the m3 from Bohlinger Schlucht is clearly wider than all known m3 from Steinheim (fig. 4 and ABUSCH-SIEWERT 1983, p. 218, fig. 93 and 94). The overall morphology and size of SMNK-PAL. 6600 compares best A. a. hippocides, which is known from contemporaneous localities.

Although a certain identification to the subspecies rank is not possible for the Bohlinger Schlucht Anchitherium-material, the occurrence of a possible Anchitherium aurelianense hippocides again underscores the MN6 correlation of this locality (GIERSCH 2004 b). Discovery of additional material should increase the usefulness of subspecies for biostratigraphic and biochronologic studies. Using the mesowear method, a tool for reconstructing palaeoedietary regimes, KAISER (2009) showed that the Sandelzhausen (MN5) Anchitherium aurelianense were able to cope with a rather abrasive diet. Such diet (e.g. C, grasses or sclerophyll vegetation) probably slightly increased their rate in the molasse basin vegetation during Badenian, when the Middle Miocene climatic optimum ends. Increasing seasonality and dryer periods (BOHME 2003) probably led to more open woodlands. The occurrence of drier habitats in the vicinity of the Bohlinger Schlucht is indicated by both micro- and macro-mammals as well as molluscs (GIERSCH 2004 b). Therefore, Anchitherium probably found adequate habitats in the molasse basin and competed directly with the hypsodont equids Cormohipparion and Hippotherium after their arrival in early Vallee-
sian (MN9). Anchitherium likely became extinct within MN9 due to a combination of competition with hipparionine horses (KAISER 2009) and the change of habitats from more closed subtropical forest to open country temperate woodlands.

Acknowledgements

We thank L. COSTEUR for the possibility to work in the collection of the Naturhistorisches Museum in Basel (Switzerland). BERNOR wishes to acknowledge funding from the National Science Foundation including EAR0125009 and BCS-0321893 (Revealing Hominid Origins Initiative to F. CLARK HOWELL and TIM WHITE) for his work on this project. We gratefully acknowledge careful and constructive reviews of this manuscript by G. ROSSNER (Munich), R. ZIEGLER (Stuttgart) and H.-W. MITTMANN (Karlsruhe).

References

ABUSCH-SIEWERT, S. (1983): Gebissmorphologische Untersuchungen an eurasischen Anchitherien (Equidae, Mammalia) unter besonderer Berücksich-
tigung der Fundstelle Sandelzhausen. – Courier For-

chen (Verlag Friedrich Pfeil).

BOHME, M. (2003): The miocene climatic optimum: evidence from ectothermic vertebrates of Central Europe. – Paleogeography Paleoclimatology, Paleo-

seums Wien, 111 A: 557-584.

GIERSCH, S. (2004 a): Eine neue mittelmiozäne Wirbel-

GIERSCH, S. (2004 b): Die Fauna aus den mittelmiozä-
en Krokokarstlischen der Bohlinger Schlucht, ein Beitrag zur Paläökologie und Biostratigraphie der Oberen Süsswassermolasse am Schiener Berg (Baden-

HÄNKE, R. (1954): Die fossile Flora der obermiozä-
en Oehninger-Fundstelle Schrotzburg. – Denkschrift der Schweizer naturforschenden Gesellschaft, Ab-
handlungen, 2: 27-118.


KAISER, T. M. (2009): Anchitherium aurelianense (Equi-

