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The early Vallesian vertebrates of Atzelsdorf (Late Miocene, Austria)

11. Rhinocerotidae and Chalicotheriidae (Perissodactyla)

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(With 2 plates and 5 tables)

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Abstract

Rhinocerotidae and Chalicotheriidae are rare elements among the large mammal remains of Atzelsdorf. Both rhino species *Aceratherium incisivum* KAUP, 1832, and *Brachypotherium goldfussi* (KAUP, 1834) are members of old lineages persisting from the Middle Miocene. There are only a few specimens of each species, but determinable with certainty. The equally rare *Chalicotherium goldfussi* KAUP, 1833 is probably a typical element of the Upper Miocene fauna. Nevertheless this association argues for the continuity of a Middle Miocene type of environment.

Keywords: *Aceratherium incisivum*, *Brachypotherium goldfussi*, *Chalicotherium goldfussi*, Lake Pannon, Vienna Basin, Hollabrunn-Mistelbach Formation

Zusammenfassung

Unter den Großsäuger-Resten von Atzelsdorf sind Rhinocerotiden und Chalicotheriiden spärlich vertreten. Beide Rhinocerotiden-Arten, *Aceratherium incisivum* KAUP, 1832 und *Brachypotherium goldfussi* (KAUP, 1834) gehören Entwicklungslinien an, die aus dem Mittelmiozän persistieren. Sie sind jeweils nur durch wenige Stücke vertreten, die jedoch eine eindeutige Bestimmung ermöglichen. Das ebenso seltene *Chalicotherium goldfussi* KAUP, 1833 ist dagegen wohl als typisch obermiozänes Element zu betrachten. Trotzdem kann diese Assoziation als Beleg für eine Kontinuität mittelmiozäner Lebensverhältnisse gesehen werden.

Schlüsselwörter: *Aceratherium incisivum*, *Brachypotherium goldfussi*, *Chalicotherium goldfussi*, Pannon See, Wiener Becken, Hollabrunn-Mistelbach-Formation

Introduction

Rhinoceroses and Chalicotheres are minor components among the large mammal fauna of Atzelsdorf. So they do not add much additional information about morphology and phylogeny of the represented species but are of interest mainly for the diversity and association of the whole fauna. This is possible because at least one specimen of the present three species can be determined with certainty, even if most specimens are only fragments. Less characteristic fragments may be added to these species in most cases.

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The Atzelsdorf site is located about 35 km NE of Vienna in Lower Austria and is geologically situated at the western margin of the Vienna Basin. The deposits of the Atzelsdorf site belong to the Hollabrunn-Mistelbach Formation; these are delta deposits which have been discharged by the palaeo-Danube into the Lake Pannon during the Late Miocene. Biostratigraphic investigations (HARZHAUSER 2009, this volume) and well-logging correlations led to a correspondence of the Atzelsdorf fauna with the Vienna Basin Pannonian Zone C, basal MN9, and an absolute age of about 11.2-11.1 ma (for more details see HARZHAUSER 2009, this volume).

Methods

The classification of rhinoceroses follows HEISSIG (1973), that of chalicotheres ANQUETIN et al. (2007). Measurements of compared specimens, if not transferred from other authors, are taken with a digital caliper by the author, according to the instructions in HEISSIG (1969, 1972). In these publications also the terminology of rhinoceros cheek-tooth elements is given. The elements of chalicotheres teeth are named according to ZAPFE (1979).

The fossils of Atzelsdorf are housed at the Natural History Museum of Vienna (NHMW). They have been excavated by the NHMW (2003) and by the local collectors G. PENZ (Vienna) and P. SCHEBECZEK (Pellendorf). Presented materials of the latter two private collections are also available at the NHMW in the form of casts.

Abbreviations

ant.	anterior	max.	maximal
BSPG:	Bavarian State Collection of Palaeontology and Geology, Munich	med.	medial
colln	collection	mid.	middle
dext.	dexter	min.	minimal
diam.	diameter	post.	posterior
dist.	distal	proc. olecr.	processus olecrani (ulnae)
fac.	articular facet	semilunate inci.	incisura semilunaris (ulnae)
H	height	sin.	sinister
L	length	troch.	trochlea
lat.	lateral	W	width.

Systematic Palaeontology

Family Rhinocerotidae OWEN, 1845

Subfamily Aceratheriinae DOLLO, 1885

Tribe Aceratheriini DOLLO, 1885

Genus *Aceratherium* KAUP, 1832

Type species: *Aceratherium incisivum* KAUP, 1832

Other species: *A. (Alicornops) pauliacense* (RICHARD, 1937), Early Miocene, *A. (Alicornops) simorreense* (LARTET in LAURILLARD, 1848), Early to Middle Miocene

Remarks: Recent observations at KAUP's type specimens from the Vallesian of Epfelsheim revealed a greater dental similarity between *A. (Alicornops) simorreense* and *Aceratherium incisivum* than expected. The only difference remaining is the size of the big incisors. Furthermore the cranial remains show traces of a faint swelling at the nasal tips in *Aceratherium incisivum*, probably the base of a rudimentary horn that was much smaller than in *A. (Alicornops) simorreense*. Both characters may not exceed subgeneric or even specific rank. So here, as in HEISSIG & FEJFAR (2007), I come back to the original description of *A. (Alicornops)* as a subgenus by GINSBURG & GUÉRIN (1979). I include in this subgenus also the species *A. (Alicornops) pauliacense* (RICHARD, 1937), because this species can not be included in the more primitive genus *Mesaceratherium* as pointed out in HEISSIG & FEJFAR (2007: 50).

Aceratherium incisivum KAUP, 1832

(pl. 1, fig. 1; pl. 2, figs 2, 3)

Material: Tibia sin. proximal fragment (NHMW 2008z0060/0001, ex colln SCHEBECZEK S152), Tibia sin. distal fragment (NHMW 2008z0060/0002, ex colln SCHEBECZEK S151), Astragalus sin. (NHMW 2008z0060/0003, ex colln SCHEBECZEK S151)

Description: Astragalus sin. (pl. 1, fig. 1): The astragalus is rather short but slender. Its asymmetrical trochlea has a rather narrow medial lip. The lateral one is nearly conical and is gently bent to the common edge with the fibula facet. The trochlea is less intensely bent in cranio-caudal sense and has more angular lips than in any genus of the Teleoceratini. So this bone can not be ascribed to a member of this tribe. The fibula facet is convex in transversal direction. On the plantar side the lateroproximal main facet for the calcaneus is deeply concave and has a broad distally bent appendix. A small medial projection of this facet blocks the deep groove which normally runs between this facet and the sustentacular one. Both facets do not join one another because the sustentacular one lies in a different plane, projecting much more backwards. It has an oval outline with nearly horizontal long axis and is widely separated from the laterodistal facet. This excludes also the Rhinocerotinae which have generally a connection of these facets. Both distal facets are short and extend mainly in transversal direction. They form together a blunt edge which is bent only a little distally towards the plantar side. The neck

is closed in front below both lips of the trochlea. In between it is wide and deep, the lower margin of the trochlea forming a large vault above it. This wide and deep groove of the neck is typical for modernized *Aceratheriini* with somewhat shortened limbs. The medial tuberosity is flat and projects only a little medially over the navicular facet.

The size, the deeply excavated neck, and the arrangement of the calcaneus facets correspond well with the astragali of *Aceratherium incisivum* from the Höwenegg (SW-Germany) and from Rudabanya (Hungary). Even if other characters are not so similar this bone can be determined with certainty and proves the presence of this species.

The comparison of other specimens of the same species shows that the astragali offer a large range of variation in several characters. The very short distal facets and the medial projection of the lateroproximal calcaneus facet are special characters of this individual, not observed in any specimen from the Höwenegg or from Rudabanya. Also the closing of the neck below the trochlea lips is unique. Compared to other modernized *Aceratheriini* we find in *Chilotherium* a higher neck, more rounded lips and a generally stronger bent trochlea. The lateroproximal calcaneus facet is less concave in this genus and in *Acerorhinus*, a genus with an otherwise more plesiomorphic astragalus.

Tibia sin., distal fragment (pl. 2, fig. 3): The fragmentary distal part of a tibia was found together with the astragalus. The malleolus tibiae and the cranial tip of the central ridge of the trochlea are missing. The lateral rugosities for the attachment of the fibula are well preserved. They form a high triangular plane which is slightly concave. Its proximal tip continues into a sharp crista interossea. There is no cartilaginous articular surface for the fibula. The determination is certain due to the adherent astragalus.

The only preserved measurements are: maximal diameter = 63 mm, width of the lateral cochlear groove = 36 mm, width of the fibular rugosities = 50 mm, height of the same = 73 mm.

Tibia sin., proximal fragment (pl. 2, fig. 2): Compared with the distal fragment the fragmentary proximal head of a tibia has a different colour and a smoother surface. So it probably represents another individual. The lateral condyle and most of the tuberositas tibiae are broken. Three characters allow a determination. The shaft is slender in contrast to *Brachypotherium*. The concave caudal plane below the condyles is medially bounded by a sharp ridge, which is merging into the rounded edge of the shaft about 60 mm below the condyle. This ridge is common in all *Aceratheriini* but lacking in *Lartetotherium*. The frontal groove of the tuberositas tibiae for the patellar ligament is narrow and forms a straight line with the frontal slope of the medial tuberculum intermedium. In *Lartetotherium*, on the other hand, it is wide and short and separated by a small platform from the tubercula. The crista tibiae is broad and swollen below the

Tab. 1. Measurements (in mm) of astragali of *Aceratherium incisivum*, * from HÜNERMANN (1989: 51), # from HEISSIG (2004: 245)

Locality	age	width			height			diameter		lateroproximal calcan. f. W/H
		max.	troch.	dist.	med.	mid.	lat.	max.	dist.	
Höwenegg*	MN 9	78-83	63-64	69-73	59-63		62-65	48-54	37-39	31-33/39-43
Rudabanya#	MN 9	76-84	68-71	68-71	59-64	53-58	63-68		33-37	31-35/39-43
Atzelsdorf	MN 9	82	71	73	60	53	65	46	34	(34) (40)

tuberosity. All these characters correspond to the tibia of *Aceratherium incisivum* from the Höwenegg, figured in HÜNERMANN (1989: fig. 51). There are no measurements to be taken. The maximal diameter of the head may be estimated at about 100 mm.

Tribe Teleoceratini HAY, 1902

Genus *Brachypotherium* ROGER, 1904

Type species: *Rhinoceros brachypus* LARTET, 1837

Other species: *B. goldfussi* (KAUP, 1834), *B. perimense* (FALCONER & CAUTLEY, 1847), *B. heinzelini* HOOIJER, 1963, *B. lewisi* HOOIJER & PATTERSON, 1972, ? *B. snowi* FOURTEAU, 1918

***Brachypotherium goldfussi* (KAUP, 1834)**

(pl. 1, figs 2-3; pl. 2, fig. 1)

Material: p₂ sin. fragment (NHMW 2008z0061/0001, ex colln SCHEBECZEK S28), dp₄ sin. fragment (NHMW 2008z0061/0002, ex colln SCHEBECZEK S99), carpale 2 sin. (NHMW 2008z0061/0003, ex colln PENZ P31)

Description: p₂ sin. fragment (pl. 1, fig. 2): The fragment of a large, nearly fresh lower premolar comprises only the trigonid. The most characteristic traits are the large size, the extremely shallow labial groove, the lack of any cingula, and the connection of the hypolophid to the metaconid. The size and the flat labial side exclude a determination as *Lartetotherium* or *Aceratherium*, which are both smaller and have a labial groove. The anterior premolars of *Brachypotherium*, however, are very variable. So this genus can be considered as possible determination. The large size and the shallow external groove seem to favour this determination but the symmetrically rounded outer wall of the trigonid is a strange character within the genus. All three cusps of the trigonid are marked by faint swellings on the lingual side.

There are two rather different morphotypes among the front premolars of *Brachypotherium*. One of them is broad and short, with a paraconid reduced to a steeply falling front edge. The other one is long and narrow and has a high elongated paraconid, a little constricted by depressions both on lingual and labial side. Among the specimens from the Lower and the base of the Middle Miocene the short morphotype is more frequent whereas from the higher Middle Miocene onwards there are only long and narrow p₂. They exhibit generally a shallow anterior outer groove which is lacking in the present fragment even if it corresponds to the narrow morphotype in the high paraconid. There is only one known specimen with a rounded outer trigonid wall from the higher Middle Miocene from Çatakbagyaka IV in Anatolia (HEISSIG 1976: 84, pl. 5, figs 8, 9). The total lack of a front cingulum and the connection of the hypolophid to the metaconid have been hitherto unknown in *Brachypotherium*.

Because of the very different proportions of the two morphotypes only specimens of the narrow and long morphotype are included in the comparative measurements.

dp₄ sin. fragment (pl. 2, fig. 1): posterior width: 27.5 mm

The fragment of a lower cheek tooth comprises the posterior wall of the metalophid and the whole talonid. The very shallow labial groove without a clear midline is confined to *Brachypotherium* among the Late Miocene rhinoceroses of Europe. So the tooth is determined with certainty, even if the lack of labial and lingual cingula is rather rare within this species. The central depression of the talonid groove is not well marked. It is transversally orientated and falls considerably to the lingual side where it ends low above the enamel base. This situation is confined among the molars to the last ones, which are excluded by the small size and a strong lateral abrasion mark on the distal side of the present tooth. In milk molars however this deep situation of the talonid groove is normal. In the third milk molar the talonid groove is diagonally orientated. So the present tooth with its transverse groove is to be determined as dp₄. This is in good concordance with the lack of lingual and labial cingula. The distal cingulum forms an arc as in all intermediate molars and milk molars. It is partly removed by lateral abrasion. It continues labially into a swelling of the crown base which does not form a cingulum. This character was also observed in dp₃. No other dp₄ is available for comparison.

Carpale 2 (trapezoid) sin. (pl. 1, fig. 3): The trapezoid has the typical low outline of the Teleoceratini and is not very much expanded caudally. The dorsal surface is broad with convex proximal and distal margins and bears a rather flat, distally situated lateral tuberosity. The palmar side is a diagonally orientated rectangle with a faint median projection. The articular facets form a continuous band around the whole bone. The rectangular proximal facet is saddle shaped and expanded caudally. The transversal convexity is stronger than the anteroposterior concavity which changes dorsally to a short convex rim. The lateral and medial side facets are situated far caudally from the dorsal side. The medial one for the trapezium is flat and nearly vertical. It is distally narrow and forms only a short common edge with the distal facet. The lateral facet is expanded caudally and there broader than in its dorsal part. It faces slightly distally in front and shows a nearly regular torsion so that it faces more and more distally to the rear. Its long edge with the distal facet is therefore blunt, the shorter one with the proximal facet sharp. The distal facet is triangular, mostly flat and only slightly convex in front. The rather flat form of this bone and the strong distal inclination of the lateral facet are very typical for *Brachypotherium*. So this bone is the second undoubted proof for the presence of this genus.

The only trapezoid of *Brachypotherium* from the Middle Miocene of Sansan is considerably broader and higher. In contrast to the present specimen the distal facet is transversally convex. So the medial side facet is lower. The lateral tuberosity of the dorsal

Tab. 2. Measurements (in mm) of p₂ of *Brachypotherium goldfussi* and *B. brachypus*,*see HEISSIG (1976: 84)

Locality	No	species	age	L	anterior W	posterior	H
Redertshausen	BSPG 1957 VII 41	<i>B. brachypus</i>	MN 6	30.0	15.5	17.0	25.0
Massenhausen	BSPG 1951 I 14	<i>B. brachypus</i>	MN 8	30.0	16.5	19.5	31.5
Çatakbagyaka IV*	BSPG 1968 VI 138	<i>B. brachypus</i>	MN 7+8	-	19.5	-	35.0
Gauweinheim	BSPG 1956 I 513	<i>B. goldfussi</i>	MN 9	31.0	18.5	20.0	-
Atzelsdorf	NHMW 2008z0061/0001	<i>B. goldfussi</i>	MN 9	-	17.5	-	21.0

surface is even flatter but more expanded in proximo-distal direction. In this specimen there is a second even smaller projection in a more medial and distal position which is lacking the Atzelsdorf specimen. These small differences do not exceed the normal variability.

Family Chalicotheriidae GILL, 1872

Subfamily Chalicotheriinae GILL, 1872

Genus *Chalicotherium* KAUP, 1833

Type species: *Chalicotherium goldfussi* KAUP, 1833

Remarks: According to ANQUETIN et al. (2007) the species *Anisodon grande* (BLAINVILLE, 1849) should be kept separate from *Chalicotherium* because of its different skull morphology.

***Chalicotherium goldfussi* KAUP, 1833**

(pl. 2, figs. 4, 5)

Material: p₄ dex. (NHMW 2008z0058/0001 ex colln SCHEBECZEK S137), Ulna dex., proximal fragment (NHMW 2008z0058/0002)

Description: p₄ dex. (pl. 2, fig. 4): The only complete specimen of a chalicothere which allows a certain determination is a lower premolar. According to its size and the well developed labial groove between the two lobes it must be determined as p₄. The low, almost unworn crown clearly exhibits all elements. Compared to the talonid the trigonid is very short, consisting only of a diagonally orientated cross loph connecting the metaconid with the protoconid. The protoconid front edge falls steeply without any trace of a paraconid. It continues lingually into the front cingulum. The trigonid basin is only a steeply mesially inclined slope. On its upper margin the short groove between meta- and protoconid terminates in a small pit. The metaconid has a well developed metacristid which falls straight to the base of the talonid groove.

The Crista obliqua begins at the tip of the metaconid and runs diagonally to the sharply angled hypoconid. The hypolophid continues to the entoconid, which is individualized but not isolated by a faint groove. The entoconid has a lingual anterior edge which is stronger in front where it is opposed to the metacristid. The talonid basin is shallow and wide. Its central pit is situated just behind the metacristid. Two faint grooves form the bottom of the basin. One is directed anterolabially, the other one points to the groove of the hypolophid but does not reach it. The labial groove of the tooth rises from the

Tab. 3. Measurements (in mm) of the trapezoid of *Bachypotherium*:

Locality	species	age	W/H anterior	W/H middle	Diameter
Sansan	<i>B. brachypus</i>	MN 6	33 / 30	29 / 23	45
Atzelsdorf	<i>B. goldfussi</i>	MN 9	32 / 28	29 / 25	48

cingulum above the anterior third of the posterior root. It is inclined to the front and ends behind the metaconid. There it is obliterated by wear.

The labial cingulum runs from the backside to the protoconid base. The labial side of the trigonid is without cingulum. The lingual cingulum forms a continuation of the anterior edge of the protoconid to the lingual side. It runs slightly above the base until the entoconid front side with some short interruptions. It is deeply notched lingually between the roots. Below the talonid entrance it includes a small pit.

The abrasion of the tooth forms a steep facet on the backside of the protoconid which extends half down the crown height. On the labial side of the crista obliqua another facet is opposed to this facet and meets it in a distolabially falling nearly rectangular abrasion channel reaching down nearly to the level of the cingulum at the hypoconid base. A smaller, also steeply labially inclined facet is situated at the outer wall of the protoconid front edge. This is also slightly abraded on the top. In the same way the ridge of the crista obliqua is cut by a nearly horizontal abrasion plane until the tip of the hypoconid. The roots are diverging. The complete posterior one is very long compared to the low crown height. The thick enamel cover and the length of the roots exclude the determination as a milk tooth.

Compared with other premolars of this species the tooth is rather short. This is mainly due to the strong reduction of the anterior branch of the trigonid and the total loss of the paraconid. This reduction is stronger than in most teeth from the Dinotheriensande of the Mainz Basin (Germany) and even in the smaller tooth from the Höwenegg. Its bigger size and this special character are clear differences to *Anisodon grande*. Furthermore this species has a less developed metacristid in the p₄.

Ulna dex., proximal fragment (pl. 2, fig. 5): The big subadult ulna lacks the capitulum and the most distal part of the shaft as well as the epiphysis of the olecranon. In spite of the bad condition of the surface the proximal articular facets are preserved. The semilunate incision is very asymmetrical with a wide and caudally expanded medial coronoid process, whereas the lateral one is short and narrow. The broad processus anconaeus turns to the medial side so that the semilunate incision is medially more concave than cranially. Its transversal convex curvature below the processus anconaeus is weak but more expressed in the middle of its height. The incisura radialis extends as a narrow concave band between the coronoid processes and faces craniodistally. Its long common edge with the semilunate incision forms a sharp angle, which is less than 90° near the middle but is blunter towards both ends.

Tab. 4. Measurements (in mm) of the p₄ of different Chalicotheriinae, * from ZAPFE (1979: 38), “ from WEHRLI 1939, + from ZAPFE (1989: 118)

Locality	species	N ^o	age	L	anterior W	posterior
Thannhausen	<i>A. grande</i>	BSPG 1974 I 25	MN 6	19.5-19.6	11.5-13.3	13.9
Neudorf*	<i>A. grande</i>		MN 6	21.0-24.8	14.5-16.1	15.4-18.1
Dinotheriensande“	<i>C. goldfussi</i>		MN 9	29.5-31.5	16.5-19.5	17.5-19.5
Westhofen	<i>C. goldfussi</i>	BSPG 1959 XIII 14	MN 9	26.6	19.1	19.5
Höwenegg+	<i>C. goldfussi</i>		MN 9	25.0	17.8	17.2
Atzelsdorf	<i>C. goldfussi</i>	2008z0058/0001	MN 9	26.1	17.9	19.7

The shaft is triangular in section. The cranial and the mediocaudal sides are broad and slightly concave whereas the narrow lateral side is slightly convex proximally and flat more distally. Proximally the cranial side is flanked by sharp ridges descending from the coronoid processes. The medial one continues distally into the crista interossea. The lateral one changes into some rugosities and continues as the rectangular medial edge. The thick rounded caudal edge of the olecranon distally becomes gradually sharper. The minimal width of the shaft is situated in its proximal fourth. From there the shaft broadens distally and becomes more and more flat.

The shaft and the whole proximal articulation correspond well with the ulna fragments of *Anisodon grande* figured by ZAPFE (1979: fig. 73, 75). In the present specimen the processus anconaeus is somewhat higher and narrower and separated from the olecranon by a deeper saddle. The differences to *Metaschizotherium bavaricum* from Sandelzhausen (Germany) are much more important. In this species the broad and symmetrical processus anconaeus is more plesiomorphic reminding the morphology of rhinoceroses. Above the lateral coronoid process the articular surface of the semilunate incision is replaced by a deep synovial pit. The incisura radialis is more specialised. Its main part is facing distally but the lateral part turns sharply to a broad, vertical appendix. So the pronation position is also fixed in the proximal region while ZAPFE (1979: 123) sees this fixation in *Anisodon grande* only in the distal fusion of radius and ulna. The greater correspondence of *Chalicotherium goldfussi* with *Anisodon grande* compared to *Metaschizotherium bavaricum* in these skeletal characters allows probably the transfer of the results of ZAPFE (1979: 271 ff.) concerning the locomotion mechanisms of *Anisodon grande* also to *Chalicotherium goldfussi*.

Rhinocerotidae vel Chalicotheriidae

Femur dex. medial condyle (NHMW 2008z0058/0000): An isolated medial condyle of a big femur can not be determined exactly as rhinoceros or chalicothere, because the sizes of the species *Chalicotherium goldfussi* and *Brachypotherium goldfussi* which are present in the fauna of Atzelsdorf are not very different. Only the smaller *Aceratherium incisivum* can be excluded by size comparison. The condyle is high oval in outline and has a regular convex curvature in proximo-distal direction. Its transverse curvature is weaker and also regular. It is somewhat more expressed than in the compared chalicothere species. The bone fragment has two punctual lesions at the lateral margin of the condyle in a distance of 25 mm. They look like bite marks of a crocodile. No measurements can be taken.

Tab. 5. Measurements of the ulna of different chalicotheres, *from ZAPFE (1979: 129).

Locality	species	age	width of semilunate incis.	height	width of. proc. olecr.	shaft width min.	diam.
Sandelzhausen	<i>M. bavaricum</i>	MN 5	75	47	23	35	28
Neudorf*	<i>A. grande</i>	MN 6	111-132	48-61			
Atzelsdorf	<i>C. goldfussi</i>	MN 9	105	60	41	45	26

Results

Rhinoceroses and chalicotheres are rare elements in the fauna of Atzelsdorf. Both rhinoceros species, *Aceratherium incisivum* KAUP, 1832 and *Brachypotherium goldfussi* (KAUP, 1834) are non selective browsers, which is indicated by the strong lingual cingula of the upper premolars in both species. They belong to old phylogenetic lineages persisting from the Middle Miocene. Both are represented only by a few remains, which allow nevertheless a certain determination. After ANQUETIN et al. (2007) *Anisodon grande* is not the ancestor of *Chalicotherium goldfussi*. So this species is a typical element of the Upper Miocene fauna, but its environmental requirements may have been not too different from the Middle Miocene species. The association of the three described species is common in the basal Late Miocene of Central Europe. The lack of *Lartetotherium* and *Dihoplus*, both selective browsers as indicated by the lack of lingual cingula in the upper cheek teeth, may indicate that the availability of soft parts of plants was restricted to the months of higher precipitation. Due to the general scarcity of the material there are no rare species. There are also no elements of the savannah or steppe association which is known from Asia to South-East Europe. Also *Hoploaceratherium* is missing, which is frequent in the same time in Rudabanya (Hungary) (HEISSIG 2004) and may have been an element of swampy woodlands.

The present association is composed only of woodland dwellers. Nothing points to bigger areas of swampy or open landscape. Generally we may assume a continuity of Middle Miocene environmental conditions, probably with a more pronounced seasonality.

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Plate 1

Fig. 1: *Aceratherium incisivum* KAUP, 1832, left stragalus (NHMW 2008z0060/0003, ex colln SCHEBECZEK S151), a. cranial, b. caudal, c. distal view.

Fig. 2: *Brachypotherium goldfussi* (KAUP, 1834), left p₂-fragment (NHMW 2008z0061/0001, ex colln SCHEBECZEK S28), a. labial, b. lingual view.

Fig. 3: *Brachypotherium goldfussi* (KAUP, 1834), left carpale 2 (trapezoid) (NHMW 2008z0061/0003, ex colln PENZ P31), a proximal, b. cranial view

All figures in natural size.

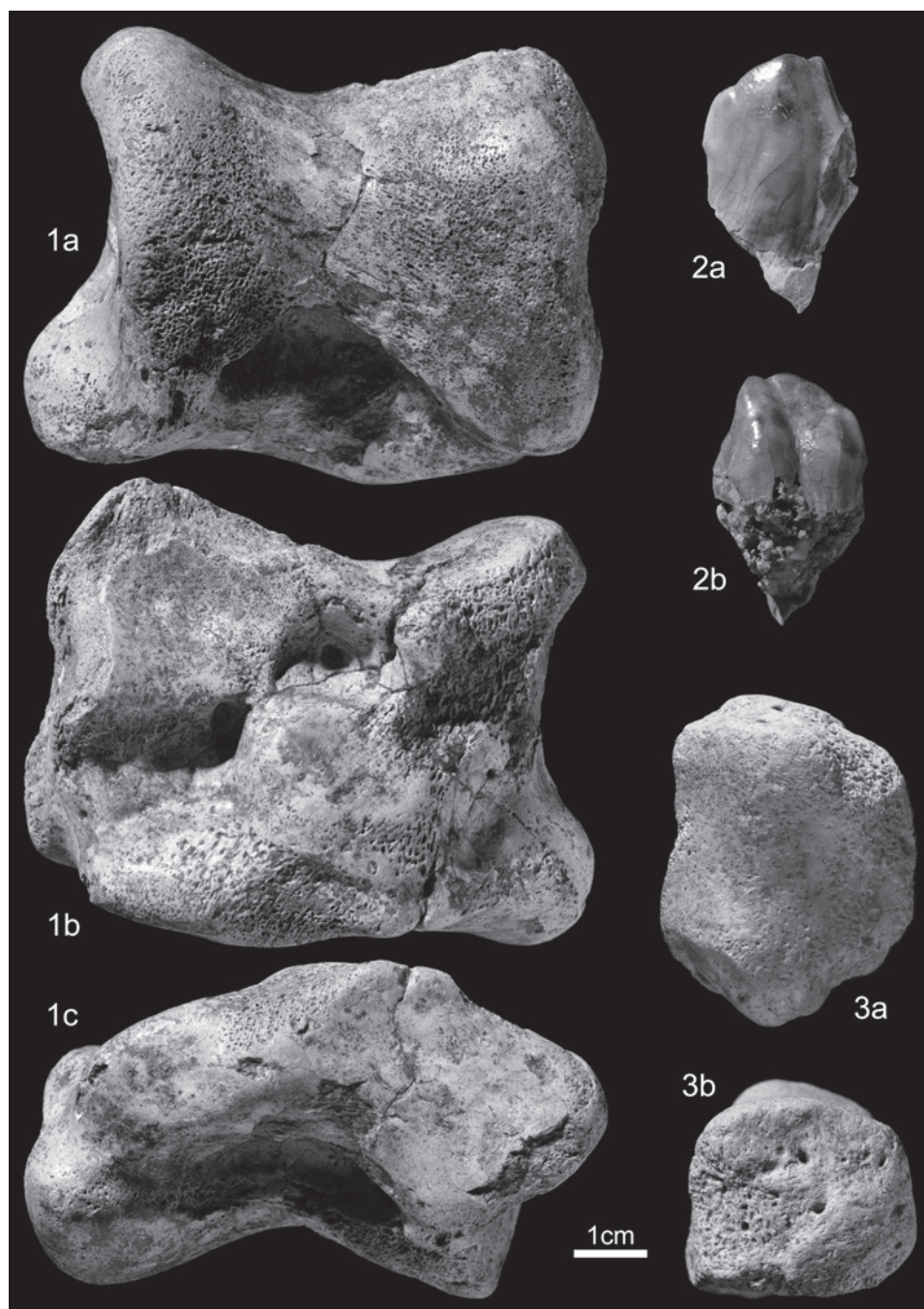


Plate 2

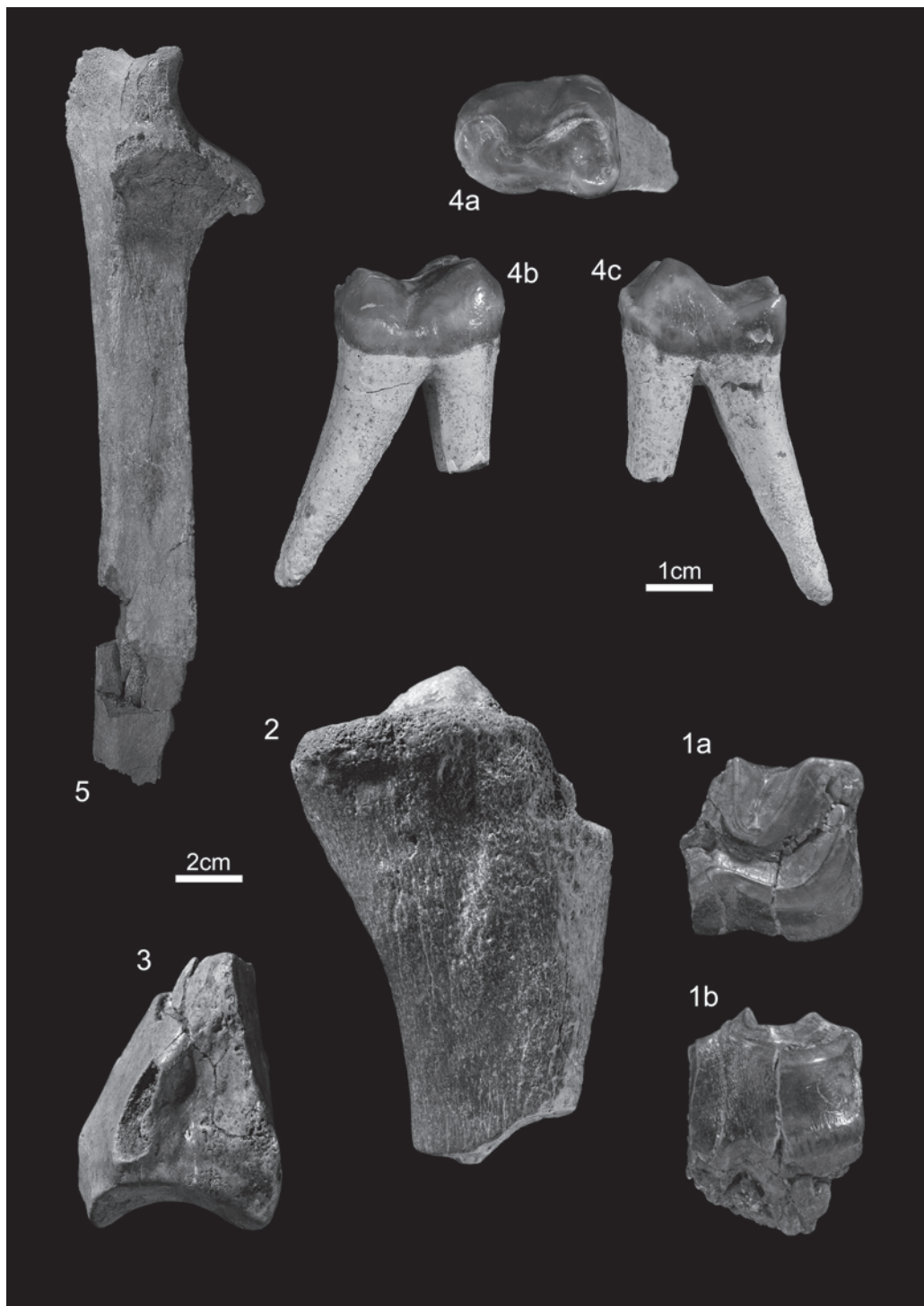
Fig. 1: *Brachypotherium goldfussi* (KAUP, 1834), left dp₄-fragment (NHMW 2008z0061/0002, ex colln SCHEBECZEK S99), a. occlusal, b. labial view, natural size.

Fig. 2: *Aceratherium incisivum* KAUP, 1832, left tibia, proximal fragment (NHMW 2008z0060/0001, ex colln SCHEBECZEK S152), lateral view, ½ natural size.

Fig. 3: *Aceratherium incisivum* KAUP, 1832, left tibia, distal fragment (NHMW 2008z0060/0002, ex colln SCHEBECZEK S151), lateral view, ½ natural size.

Fig. 4: *Chalicotherium goldfussi* KAUP, 1833, right P4 (NHMW 2008z0058/0001, ex colln Schebeczek S137), a. occlusal, b. labial, c. lingual view, natural size.

Fig. 5: *Chalicotherium goldfussi* KAUP, 1833, right ulna proximal fragment (NHMW 2008z0058/0002), cranial view, ½ natural size.



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